

How newly recruited cohorts are formed in the trochid gastropod population
(*Umbonium moniliferum*) on an intertidal sandflat in western Kyushu, Japan

Sumit Mandal^a, Akio Tamaki^{b,*}, Satoshi Ohashi^c, Seiji Takeuchi^a, Yoshihiro Agata^a,
Yusuke Takahara^b, Kazuyuki Harada^a, Fumihiko Yamada^d

^aGraduate School of Science and Technology, Nagasaki University, Nagasaki 852-8521,
Japan

^bFaculty of Fisheries, Nagasaki University, Nagasaki 852-8521, Japan

^cNagasaki Prefectural Institute of Fisheries, Nagasaki 851-2213, Japan

^dGraduate School of Science and Technology, Kumamoto University, Kumamoto
860-8555, Japan

*Corresponding author. E-mail address: tamaki@nagasaki-u.ac.jp (A. Tamaki),
telephone number: +81-95-819-2856, fax number: +81-95-819-2799, complete postal
address: Faculty of Fisheries, Nagasaki University, Bunkyo-machi 1-14, Nagasaki
852-8521, Japan

ABSTRACT

In macrobenthos with meroplanktonic larvae, larval settlement and recruitment are two crucial processes for population cohort formation, yet only a few studies have given explicit definitions for newly settled and recruited juveniles (settlers and recruits) and descriptions of those processes with relevant time scales. Using a comprehensive approach, our study demonstrated a clear pattern in cohort formation of the trochid gastropod population (*Umbonium moniliferum*) on an intertidal sandflat, southwestern Japan, in the breeding seasons of 2002 and 2007-2009. The study included (1) daily monitoring for spawned eggs and competent larvae in the field and laboratory, (2) daily and fortnightly monitoring for juveniles, and (3) collection of larvae in the water column and in situ simulation of larval retention, releasing drift cards within an embayment embracing the sandflat. The population with shell widths of 5-14 mm occupied the lower shore in densities of about 1,000 inds. m⁻², spawning gametes for lecithotrophic larval development with the shortest duration of 3 d during late September through October. The settlers occurring per day and the newly recruited cohort in the size-frequency distribution were defined as juveniles belonging to the smallest size class (0.20 and 0.21 mm) and to the most left-hand normal distribution group, respectively. The growth rate was estimated at 0.02 mm d⁻¹. A synchronous mass egg spawning took place 2-4 d after neap tide, followed by the sequential occurrence of veligers and settlers in high densities, which was completed by the next neap tide, leading to the formation of one newly recruited cohort. Three distinct cohorts were produced consecutively, most probably due to this semilunar cycle. The iteroparous spawning was supposedly performed by the same females. By the

following spring, the three cohorts had fused into a single young-of-the year cohort. Veligers were present across all depth layers in the water column down to 20 m, with a quarter being present within the surface 1 m. Drift cards were driven ashore, with cumulative retrieval rates of 50 and 70 % 3 and 9 d after release, respectively, suggesting that hydrodynamics allowed good retention of larvae in the water surface. Using an exponentially decreasing function describing competent larval numbers in a 2 to 9-d period after fertilization in the laboratory, the degree of self-recruitment in the population was assessed under the assumption of complete retention and no mortality of larvae due to predation. The results suggested the presence of some allochthonous subsidy.

Keywords: trochid gastropod, lechithotrophic larva, intertidal sandflat, settlement, recruitment, cohort

1. Introduction

In the study of metapopulation dynamics of coastal benthic macro-invertebrates with a meroplanktonic larval phase, increased attention has been paid to the dispersal and survival processes in the pelagic stage (Cowen and Sponaugle, 2009; Metaxas and Saunders, 2009). Confining our attention to the dynamics of a local population of such a metapopulation, the assessment of the relative importance of pre- and post-settlement processes has been a central topic (Ólafsson et al., 1994; Caley et al., 1996; Hunt and Scheibling, 1997). Crucial to this assessment is an appropriate description of how the abundance of competent larvae is connected to that of early-stage juveniles (Keough

and Downes, 1982; Connell, 1985; McGuinness and Davis, 1989; Eckman, 1996; Bownes and McQuaid, 2009). The description is inevitably associated with the need for establishing explicit definitions of two key terms, settlement and recruitment (Caley et al., 1996; Jenkins et al., 2009). However, the definitions have often been accompanied by semantic ambiguity and are obliged to be operational in practice, depending on the sampling frequency and target body size set by researchers (Booth, 1991; Michener and Kenny, 1991; Gosselin and Qian, 1997; Pineda, 2000). Settlement is the successful passage from the competent (or post-) larval stage to the benthic stage, concurrent with metamorphosis. The density of newly settled juveniles (= settlers) can be adequately estimated only after having determined their “minimum body size” and an “initial growth rate” to preclude overlapped counts of juveniles on sequential sampling occasions. Newly recruited juveniles (= recruits) are considered to be those settlers that have survived to a “specified size” for a “certain period of time” following settlement. The uncertainty in discriminating settlers and recruits can be exemplified by a demographic analysis of benthic populations, in which the separation of multiple cohorts for a composite body-size (or age)-frequency distribution is one basic procedure (Ebert, 1999; van der Meer, 2005). Most routinely, normal distribution curves are fitted to a size-frequency distribution to delineate discrete cohorts, of which the most left-hand group is usually assigned to the newly recruited cohort. It is generally assumed that recruitment peak is completed in a “short period of time” (van der Meer, 2005). However, the shape of the most left-hand group is not always of a complete normal distribution at the time of sampling (e.g. Tamaki, 1985; Shepherd et al., 1992). The presence of such truncated size-frequency group indicates that the process from settlement to recruitment is still underway. At least, a fraction of juveniles belonging

to the smallest size class must be settlers. So far few studies trying to describe the transition from competent larvae, via larval settlement, to juvenile recruitment, especially those dealing with soft-sediment macrobenthos, have explicitly given quantities to the terms with double quotation marks listed above.

With varying degrees of clearness in the definition of settlement and recruitment, a number of studies have recorded the relationship between the availability of competent larvae and the abundance of settlers and/or recruits for members of a limited taxonomic groups of coastal macrobenthos (octocorals – Harii and Kayanne, 2003; bivalves – Michener and Kenny, 1991, Feller et al., 1992, Chícharo and Chícharo, 2001, Ishii et al., 2001, LeBlanc and Miron, 2006, Porri et al., 2006, Rilov et al., 2008; gastropods – Berry, 1987, McShane et al., 1988, Sasaki and Shepherd, 1995; polychaetes – Feller et al., 1992, Verdier-Bonnet et al., 1997, Dubois et al., 2007; cirripeds – Minchinton and Scheibling, 1991, Gaines and Bertness, 1992; decapod crustaceans – Eggleston and Armstrong, 1995, Incze et al., 2000, Moksness and Wennhage, 2001, Queiroga et al., 2006; bryozoans – Yoshioka, 1982; ophiuroids – Turon et al., 2000; echinoids – López et al., 1998). The results of these studies indicate that the abundances of competent larvae and settlers/recruits are either correlated or decoupled. In order to achieve a more comprehensive understanding of the degree of pelagic-benthic coupling in the population dynamics of coastal macrobenthos, three processes other than the one around settlement are also to be examined (Eckman, 1996; Pineda, 2000; Cowen and Sponaugle, 2009; Metaxas and Saunders, 2009): (1) spawning and releasing of propagules (i.e. gametes/larvae) by adults, (2) larval dispersal, and (3) larval survival. This comprehensive research framework more or less entails a metapopulation perspective. However, attempts at sequential monitoring are lacking for the

abundances of released propagules, competent larvae, and settlers, considering the relative contributions of autochthonous and allochthonous propagules. This monitoring approach would boost our grasp of the processes conducive to the formation of a newly recruited cohort in the benthic body-size (or age)-frequency distribution (e.g. Yoshioka 1982, 1986).

Concerning the open versus closed nature of local macrobenthic populations, recent emphasis has been placed on the prevalence of local retention of larvae (Kinlan et al., 2005; Cowen and Sponaugle, 2009). Among other things, larvae with shorter planktonic larval durations (PLDs) are more likely to be retained near their natal habitats and hence self-recruited (Todd, 1998; Harii and Kayanne, 2003; Shanks, 2009). In this respect, the possibility of detecting local coupling of adult reproductive output and larval settlement/recruitment known as stock-recruitment relationship would be generally higher in species with lecithotrophic (i.e. non-feeding) larval development than in those with planktotrophic development (but see Hughes et al. (2000) for a regional-scale dispersal of lecithotrophic coral larvae). The PLDs in these two species groups last for minutes to days and weeks to months, respectively (Thorson, 1950; Young and Chia, 1987). The other tractability of lecithotrophic groups is that survival rates of larvae reared in large numbers in the laboratory could be used to predict a temporal declining pattern in larval concentration in the field if the water temperatures determining larval developmental rates in the laboratory and field are comparable (cf. Reitzel et al., 2004; Strathmann, 2007). It is more difficult to estimate ontogenetic mortality rates for planktotrophic larvae at sea, as they are affected by starvation and longer dispersal periods in addition to predation and physiological stress (Olson and Olson, 1989; Rumrill, 1990; Ellien et al., 2004; Pedersen et al., 2008).

Dispersal of lecithotrophic larvae with up to several-hour PLDs restricted to the extreme vicinity of the adults was demonstrated for colonial forms such as octocorals and ascidians, in which visual tracking of large larvae or quantitative assessment of larval and settler abundances was feasible (Olson, 1985; Grosberg, 1987; Harii and Kayanne, 2003). A wider but still limited dispersal of those larvae with up to several-day PLDs and a corresponding change in settler/recruit abundances were recorded for members of a hard-substratum epifaunal assemblage, including sponges, bryozoans, and ascidians (Todd, 1998) and for a number of fisheries' target species of abalones inhabiting shallow subtidal boulder substrata (McShane, 1995; Sasaki and Shepherd, 1995; Onitsuka et al., 2007). Compared with these studies in hard substrata, the examples of monitoring of abundances throughout larval and juvenile stages for lecithotrophic macrobenthic species in soft sediments are much rarer (e.g. serial studies on a trochid gastropod: Berry and Zambri, 1983; Berry, 1986, 1987).

The trochid gastropod, *Umbonium moniliferum* (Lamarck, 1822), is a soft-sediment epibenthic snail, residing in the upper 1 cm of the sediment column. It is one of the most dominant members of the macrobenthic community on intertidal sandflats in Japanese waters, accompanied by an assemblage of predators, ectoparasites, and inhabitants of its empty shells (Shimoyama, 1985; Tamaki, 1994; Asakura, 1995; Ogaya, 2004). *U. moniliferum* has a lecithotrophic pelagic larva, with its shortest PLD being estimated at 3 d (S. Mandal et al., unpublished data). In waters further south, extending from Southeast Asian to Persian Gulf coasts, a congeneric species, *U. vestiarium*, attains remarkably high densities on sandy shores, filling an ecological niche similar to that of *U. moniliferum* (Fretter, 1975; Berry and Zambri, 1983; Morton and Morton, 1983; Reise, 1991; Abdul-Salam and Sreelatha, 1998). The synchronized

mass-spawning periodicities in terms of diel, tidal, and semilunar components within a relatively limited annual breeding season and the short PLD (2 d) in *U. vestiarius* (see Berry and Zambri, 1983; Berry, 1986, 1987) and expected similar traits in *U. moniliferum* would make these species ideal for assessing the degree of local coupling of adult reproductive output and larval settlement/recruitment abundance.

The objective of the present study is to demonstrate how newly recruited cohorts are formed within a single breeding season for the local population of *Umbonium moniliferum* inhabiting an intertidal sandflat in southwestern Japan (Tamaki and Kikuchi, 1983; Tamaki, 1994). An intensive sampling effort including monthly and daily components was carried out to monitor the abundances of spawned eggs and competent larvae in the water column, and of juveniles on the sandflat. Of the juveniles, settlers were discriminated from recruits using an initial growth-rate estimate from cohort analysis. Sampling for the larval vertical migration pattern in the water column, and release and retrieval of drift cards were performed in an embayment facing the sandflat to assess the degree of local retention of larvae. Using a large container in the laboratory, the shortest PLD was determined, and an observation on the temporal change in the abundances of massively spawned eggs and larvae was made to detect iteroparous spawning bouts by adults within a breeding season and to predict competent larval availability for settlement over an extended period beyond the shortest PLD. Based on these results under the assumption of self-recruitment, the correspondence between the numbers of spawned eggs from and settlers onto a unit area of the sandflat was examined to assess the degree of local coupling between pre- and post-settlement stages, eventually conducive to the formation of a newly recruited cohort. Finally, multiple distinct recruitment cohorts observed during the breeding season were shown

to merge, forming a single young-of-the-year cohort in the adult population.

2. Materials and methods

2.1. Study site, and *U. moniliferum* life history, biology and population ecology

The site for intertidal study (Tomioka sandflat) is located within a shallow embayment (Tomioka Bay; water depths ≤ 20 -25 m; 8.5 km alongshore \times 2 km cross-shore) at the northwestern corner of Amakusa-Shimoshima Island in western Kyushu, Japan (130°02'E, 32°31'N; Fig. 1; Tamaki et al., 2010). The waters around Tomioka Bay are under a mesotidal, semidiurnal tidal regime, with the average tidal range at spring tides being about 3 m. The M_2 tidal currents are dominant in the current field, with much prevalence of the east over north components, and the maximum current speeds are 150 cm s⁻¹ around the strait between Tachibana Bay and Ariake Sound (Fujiie et al., 2006). At a 20-m deep station around the outer margin of Tomioka Bay, the maximum current speeds are 50 cm s⁻¹ and 10 cm s⁻¹ at spring and neap tides, respectively (A. Tamaki et al., unpublished data). Inside the bay, the current speeds become slower (Suzuki et al., 1982). During spring tides, the Tomioka sandflat extends for 150-700 m seaward and 4 km alongshore. It faces northeastwards, receiving northerly-wind-induced waves from October to May (Tamaki, 1987). Since 1979, the monitoring of the sandflat benthic community has been continued in a rectangular area extending for 310 m seaward to the mean low water spring tide level (MLWS) and for 300 m alongshore (Fig. 1, inset panel). The intertidal range of the sandflat was shortened by 20 m in 1993 due to reclamation of the uppermost shore. The sampling of macrobenthos was conducted along four shore-normal transects

running from the upper flat to the low water line (Tamaki and Kikuchi, 1983; Tamaki, 1985, 1987, 1994). One of the four transects was used for the present study.

Hereafter Stn X denotes the transect station that is X m seaward from the upper shoreline. The elevation is almost flat from the upper shoreline to Stn 130 located at around the mean low water neap tide level (MLWN), from which it lowered to the MLWS, with a constant inclination of 1/230 (Wardiatno et al., 2003). The maximum duration of exposure per tide at spring tides ranges from 3.4 to 6.0 h over the year. The sediments are moderately well-sorted fine sands, with 0.3-1.7 % silt-clay contents.

The annual reproductive season for *Umbonium moniliferum* on the Tomioka sandflat ranges from early September to early December, with its main part being from late September to early November (Tamaki, 1994). Synchronized mass spawning of eggs and sperm (i.e. dioecious broadcast spawner) was observed in the laboratory (Harada et al., 2005). A newly spawned egg is 0.17 mm in diameter, enveloped by a 0.10-mm thick, vitelline membrane and gelatinous coating. Embryos are negatively buoyant and metamorphose into trochophores approximately 6 h after fertilization, at which time larvae hatch out of the disintegrating gelatinous coating. Veligers appear 2 h later, and those with 0.20-mm shell width begin to crawl on the substratum 48 h after fertilization. With the shedding of the velum, veligers complete metamorphosis into settlers. Juveniles grow rapidly in their first year to form a single cohort in the adult population, reaching 5 to 9-mm shell widths in August (Tamaki, 1994; A. Tamaki, unpublished data). They mature by the end of September and live for another three years. In 1979, adults occupied the lower half shore, lying between MLWN and MLWS, with densities (overall mean, 2,000 inds. m⁻²) varying in a zonal pattern parallel to the shoreline (Tamaki and Kikuchi, 1983; Tamaki, 1994; Fig. 1). The adult's intertidal position

would be related to its suspension-feeding habit for phytoplankton (cf. Fretter, 1975). By contrast, juveniles were distributed landward, with their highest-density zone situated a little seaward of the MLWN (Tamaki, 1994). Since 1979, a drastic change in the population has taken place (Tamaki, 1994; Flach and Tamaki, 2001). The population declined steadily to extinction in 1986. This was attributed to a remarkable distribution expansion of the callianassid (ghost) shrimp, *Nihonotrypaea harmandi* (Bouvier, 1901), over the entire sandflat, which caused increased bioturbation of sediments. Since 1995, however, the ghost shrimp population declined back to its former densities, which was followed by signs of recovery of the *U. moniliferum* population in 1998 (Flach and Tamaki, 2001). This population replenishment appears to have required larval supply from other local populations.

2.2. Monitoring for egg and larval abundances of *U. moniliferum* in the field

The monitoring for concentrations of spawned eggs and larvae in the field was conducted during the period from 29 September (1 d before spring tide) to 22 October (1 d after neap tide) in 2008. Note that the dates of spring and neap tides are designated according to the maximum and minimum differences in consecutive high and low tidal heights, respectively. The actual water depth on the sandflat was automatically recorded at Stn 230 every 10 min during the period from 27 September to 28 October, using a pressure gauge (sensor positioned 1.4 cm above the sandflat surface; Wave Hunter 99, IO Technic, Co.). Around every predicted local high tide, 540 l of surface seawater was bucketed at the uppermost point of the transect, which was completed within 20 to 40 min (mean, 29 min). The sampling time spanned across daytime and nighttime (sunrise and sunset times shifted from 6:15 to 6:30 and

from 18:04 to 17:40 over the monitoring period). The collected water sample was passed through a plankton net with 0.063-mm mesh openings. The content in the cod end of the net was concentrated and placed at -25°C in a freezer approximately 20 min after the termination of water sample collection. It was taken into consideration that the development of embryos progressed rapidly during this 20-min duration. In the laboratory, the thawed sample was examined to determine the rate of egg fertilization and the stage of all embryos and larvae according to the developmental time course given in Harada et al. (2005). In the veliger-stage larva, the operculum is formed 25 h after egg fertilization. With opercula, the soft tissue was withdrawn into the shell when placed in the freezer. Identification of sub-stages for those veliger-stage larvae was not made. For each sampling occasion, the duration that elapsed from the time of egg spawning to that of becoming frozen was estimated based on the most prevalent embryonic or larval stage in the sample. As egg spawning and fertilization occurred coincidentally (Harada et al., 2005), the estimated time of fertilization was regarded as equal to that of egg spawning. Furthermore, as (1) the egg fertilization rate was high ($\approx 95\%$ in the field; see Section 3.7), (2) the duration of the embryonic stage is short (6 h), and (3) the survival rate of the early-stage larvae in the laboratory was high (94 % 1 d after egg fertilization; see Section 3.6), the embryonic concentration on each sampling occasion was regarded as a surrogate for the spawned-egg concentration and plotted at the supposed egg-spawning time. This time was back calculated from the mid-point of each sampling period using the estimated duration that had elapsed from the time of egg spawning plus the above-mentioned 20 min. The larval concentration value was plotted at the mid-point of each sampling period.

Salinity (Practical Salinity Scale) and temperature of the seawater were

automatically recorded at Stn 230 every 10 min during the period from 13 September to 29 October, using a conductivity and temperature logger (sensors positioned 30 cm above the sandflat surface; Compact-CT, JFE Alec, Co.). The data recorded only during the period of water submergence were extracted. The period with salinities ≤ 10 associated with rise and fall of the water surface was regarded as that under exposure. To smooth variations in temperature over time, a nonparametric, nearest neighbor local-linear regression (Loess) was performed using Systat Software (2006), to which polynomial of degree 1 as smoother and sampling proportion of 0.1 were applied. The seasonal northerly winds induce onshore surface currents, which might promote larval retention around the sandflat. Wind velocity data recorded every 10 min at a meteorological observation station situated near the sandflat (triangle mark in inset panel of Fig. 1) were downloaded from an open-access web site run by the local government (Kumamoto Prefecture; <http://cyber.pref.kumamoto.jp/bousai/>).

*2.3. Monitoring for settler abundance of *U. moniliferum* in the field*

The monitoring for density of juveniles was conducted on the sandflat under exposed conditions during daytime low tide daily from 10 October (2 d after neap tide) to 22 October (1 d after neap tide), and separately on 13 September (4 d before spring tide), 29 September (1 d before spring tide), and 29 October (spring tide) in 2008. A maximum of ten sampling stations were established along the transect, every 20 m from Stn 10 to Stn 190. The last station was the most seaward exposed one over the consecutive sampling period in the middle of October. To examine spatial variation in juvenile density, samples were collected from all stations on 14 October (2 d before spring tide). To monitor daily changing patterns in juvenile density and shell-width

composition, samples were collected at Stn 90. This station was the most seaward station that was exposed nearly every day (no samples were collected on 17 October due to the unavailability of exposure time). At each station two sediment samples were collected using a 100-cm² square quadrat frame to a depth of 1 cm, which were fixed whole (i.e. unsieved) with 10-% neutralized seawater formalin containing rose bengal. In the laboratory juveniles were sorted out and their shell widths measured to the nearest 0.01 mm under a dissecting microscope (at 50× magnification) equipped with a CCD camera. The shell-width-frequency distribution was made, with a size-class interval of 0.02 mm, and hence two values were included in each size class (e.g. 0.20 and 0.21 mm). Following Aizawa and Takiguchi (1999), normal-distribution curves corresponding to supposed cohorts were fitted to the composite size-frequency distributions. The newly recruited cohort was defined as the most left-hand complete normal-distribution group. The group with the smallest-sized juveniles situated further left to that cohort, constituting a truncated size-frequency distribution, was left intact. Based on an estimated individual growth rate from the cohort analysis, the settlers available per day were defined by their shell-width values. The sequence of daily variation in settler density leading to a newly recruited cohort was examined in conjunction with daily variation in egg and larval concentrations in the water column (Section 2.2).

2.4. Monitoring for U. moniliferum juvenile cohorts throughout the breeding season

To identify all newly recruited cohorts occurring throughout one breeding season, the sampling was conducted on the sandflat during daytime or nighttime low tide every spring tide from 7 October 2002 to 2 February 2003 (nine times). Sixteen sampling

stations were established between Stn 0 and Stn 290 along the transect, with the distance between two adjacent stations being 20 m, except for 10 m between Stns 0 and 10. At each station eight sediment samples were collected using a 50-cm² square quadrat frame to a depth of 1 cm, except for six 60-cm² core samples on 7 October 2002. No samples could be collected at Stns 270 and 290 on 22 October 2002 and at Stn 290 on 20 February 2003 due to submergence. The collected samples were processed as given in Section 2.3, except for the use of 0.04 mm for a unit shell-width-class interval. To confirm the formation of a single, fused overwintering young-of-the-year cohort in the adult population, four sediment samples were collected to a depth of 3 cm at each of the 16 stations on 3 April 2003, using a 625-cm² square quadrat frame, which were sieved through a 0.5-mm mesh sieve and fixed. The shell widths of the specimens were measured with a digital caliper to the nearest 0.1 mm to construct a shell-width-frequency distribution with a size-class interval of 0.4 mm.

2.5. Determination of sex ratio and size-specific fecundity of U. moniliferum

Adults used for determining sex ratio and size-specific fecundity were collected on the sandflat every spring tide during the breeding season of 2002 and measured for their shell widths. In the laboratory, eggs or sperm in the gonads were examined under a stereomicroscope. The number of ripe eggs (mature oocytes surrounded by a thick gelatinous coating) in female specimens collected on 6 and 22 October were counted. The parameters in non-linear regression equations for number of eggs (y) versus shell width (x) were established using “R” (R Development Core Team, 2008), where four functions, (1) exponential, $y = a b^x$, (2) power, $y = ax^b$, (3) Gompertz, $y = a b \exp(-cx)$, and (4) logistic, $y = a [1 + b \exp(-cx)]^{-1}$, were examined. The best-fitted function of

the above four was selected based on the smallest value in Akaike's Information Criterion (Akaike, 1973).

2.6. Estimation for density of eggs potentially spawned by *U. moniliferum* adults

To estimate the maximally available number of eggs spawned by the adults from a unit area of the sandflat, samples were collected on 3 August 2008. At each of the 16 stations described in Section 2.4 and one additional station (Stn 260), one sediment sample to a depth of 10 cm was collected using a 625-cm² quadrat frame and sieved through a 0.5-mm mesh sieve. The shell widths of the specimens were measured to construct a shell-width-frequency distribution. The total number of eggs carried by the females was obtained based on the sex ratio (1:1; Section 2.5 and see Section 3.1) and size-specific fecundity equation (Section 2.5). Only the sampling stations containing adults were considered for their mean egg density (see Section 3.4). The number of eggs for each size class was calculated by multiplying the number of eggs corresponding to the median shell width and half the number of adults belonging to that size class. There was a possibility that the population fecundity estimate in the main breeding month (October) was a little different from that for August due to growth and mortality occurring between the two months. To correct for this, samples were collected with a 100-cm² corer at two stations on 18 August and 29 October 2008 and sieved through a 0.5-mm mesh sieve ($n = 16$ and 17 at Stn 140 in August and October, respectively; $n = 17$ and 25 at Stn 240, respectively). Each of the shell-width-frequency distributions of *Umbonium moniliferum* corresponding to the four sampling sets was standardized to 100 cm² (unit core area), and one combined distribution was generated for each sampling date. The normal-distribution curves

representing cohorts that were recruited in different years were fitted to these shell-width-frequency distributions. For each cohort, the daily individual growth rate and daily mortality rate were calculated from the increments in shell-width modes and from the changes in adult densities between the two dates, respectively. Using these two parameters, the normal-distribution groups fitted to the shell-width-frequency distribution on 3 August mentioned above were transformed into those on the starting date of the monitoring for egg and larval concentrations in this year (29 September; Section 2.2) and the mean number of eggs per 625 cm² (unit quadrat area) estimated.

2.7. Detection of vertical migration of U. moniliferum larvae in the water column

To detect vertical migration of larvae in phase with diel and/or tidal cycles, a depth-stratified sampling from the water column was conducted on board the RV “Kakuyo-Maru” (155 tonne) of Nagasaki University, which was anchored at a station 1.5 km off the lowest edge of the Tomioka sandflat (star mark in inset panel of Fig. 1; depth at highest tide, 24.7 m). Eight sets of seawater samples were collected between 13:45 on 22 October and 12:08 on 23 October 2007. The difference in tidal levels between two consecutive high and low tides varied from 1.5 to 1.9 m (between neap and spring tides). The weather was fine and the sea was generally calm with occasional turbulence caused by northerly winds. The mid-point of the period for each sampling set was originally planned to coincide with high-, low-, or mid-tides, but the actual time-lag varied from 5 to 64 min. During each sampling set, 450 l of seawater was lifted at an average rate of 0.6 l s⁻¹ from each of the five sequential depth layers of 20, 15, 10, 5, and 1 m below the sea surface, using an underwater diaphragm pump (Model NDP-20BAH, Yamada, Co.) and a graduated hose with a mouth-opening diameter of

2.5 cm. The actual sampling depths were recorded with a depth logger with an accuracy of 0.3 % to the full depth range (Compact-TD, JFE Alec, Co.). The treatment for the collected water sample was the same as given in Section 2.2. Based on the concentration values of larvae at respective depth layers, the weighted mean depth (WMD) of larval position was calculated as $\Sigma(C_i d_i) / \Sigma C_i$, where C_i stands for larval concentration at depth d_i (i , depth layer number; Pearre, 2003).

2.8. Release and retrieval of drift cards in the field

To assess the degree of retention of *Umbonium moniliferum* larvae within Tomioka Bay, 800 drift cards were dropped from a small vessel at a 6-m deep station 260 m off the lowest edge of the Tomioka sandflat at 15:51 on 27 October 2009, which was just before the predicted local high-tide time (16:04) at neap tide (cross mark in inset panel of Fig. 1). The weather was fine and the sea was calm. The tidal phase for the release was determined with respect to both semilunar and daily cycles so that the expected egg-spawning timing by adults of *U. moniliferum* would be simulated (see Section 3.7). The card was intended to mimic larvae present in the surface layer of the water column (i.e. within 1 m; see Section 3.8). The card was made of a 0.25-mm thick, yellow-colored biodegradable paper with a water-repellent coating, 10.0×14.8 cm in size and 3.5 g in weight with a 0.9-g weight attached to one corner (Heiwado Printing, Co., Tokyo). In seawater, the card stood upright, with the corner opposite to the weight protruding 1 cm above the surface. The collection of cards that had been driven ashore started from the low tide in the morning of 28 October. A search was conducted along the upper shoreline of the sandflat and its northward extension including the cove and sand-spit parts (thick line in inset panel of Fig. 1). Subsequent

collection was made daily from the low tide around noon of 30 October to 5 November at a 24-h interval (no sampling on 4 November) and separately on 13 November.

2.9. Laboratory monitoring for egg spawning and larval survivorship of U. moniliferum

To confirm iteroparous egg-spawning bouts by adults and to obtain a measure of the availability of competent larvae for settlement beyond their shortest PLD, mature adults, spawned eggs, and embryos and larvae were maintained in aquaria inside a laboratory by the sea (Nagasaki Prefectural Institute of Fisheries at 129°46.26'E and 32°48.51'N) during the breeding season of 2008. The collection of spawned eggs and the subsequent rearing of embryos and larvae were conducted using a set of three black 76-cm tall 500-l polycarbonate tanks that were bathed in running ambient seawater within a 300 cm × 300 cm × 50-cm tall tub (Fig. 2). The running seawater introduced into the tub was filtered through a cartridge filter with 10-μm mesh openings (TOCEL, Advantec, Co.). The water was circulated through the tanks and tub with polyvinyl chloride pipes. The first tank accommodated adults ("adult" tank), from which spawned eggs were siphoned off into a nylon-net bag hung in the second tank ("egg" tank; net diameter, 90 cm; height, 53 cm; mesh opening, 70 μm). The third tank was used for the rearing of embryos and larvae ("larval" tank). Adults were collected from the Tomioka sandflat on 29 September ($N = 2,040$) and 14 October ($N = 2,755$) and placed in the adult tank within each respective day. The first and second adult groups were maintained in separate tubs until 26 and 31 October, respectively (referred to as Rearing Sets 1 and 2). Seawater temperature and salinity was monitored with a Compact-CT in the adult tank.

The water in the tub was pumped up into the adult tank at the rate of 10 l min⁻¹

during the “daytime” (from 7:00 to 17:00), with cessation during the “nighttime”. Immediately after stopping the water flow at 17:00, cultured microalgae were fed to adults (approximate daily ration of 2.5×10^{10} cells of *Chaetoceros gracilis* and 3.0×10^{10} cells of *Pavlova lutheri*). The dead adults were removed and enumerated daily. The spawned eggs collected in the bag of the egg tank were concentrated and retrieved at around 9:00 daily. To estimate the total number of spawned eggs, they were diluted to 20 l with filtered seawater and well mixed, from which 1-ml samples ($n = 8$ to 47) were pipetted for the immediate enumeration of eggs under a light microscope (100 or 200 \times). The determination of embryonic and larval stages was made to estimate the time of spawning and fertilization according to Harada et al. (2005). The egg (embryo, larva) number count and stage determination were conducted between 10:00 and 11:00; egg spawning never occurred between 11:00 and 17:00 (S. Mandal et al., unpublished data). After completing spawned-egg collection, both the bag in the egg tank and the adult tank were thoroughly washed off and re-installed. When each Rearing Set was terminated, all adults were fixed with 10-% neutralized seawater formalin. The shell widths for 500 (Set 1) and 650 (Set 2) specimens were measured. The shell-width-frequency distributions were used to obtain an estimate of the number of spawned eggs as given in Section 2.6.

On two dates when mass egg-spawning events happened (4 and 18 October; see Section 3.6), each larval rearing set started (Larval Rearing Sets 1 and 2 on Day 0). On these dates, the above-mentioned 20-l sample was divided into the 1-l and 19-l subsamples. The former was used for estimating the fertilization rate of the spawned eggs, of which 500 were examined alive. The latter was for embryonic and larval rearing; the larval tank had almost the same bag setup as in the egg tank (Fig. 2). The

water introduced into the bag emerged through a number of small holes along a horizontal pipe that lay close to the bottom net, generating a gentle rotation of seawater inside the bag. The subsequent change in larval concentration was examined by pipetting water samples. The volume and number of samples varied depending on larval concentration [1 ml ($n = 10$ to 48) to 2 l ($n = 3$ to 9)]. For calculating the rate of reduction in the larvae contained in the tank between any two successive occasions, their removal by the sampling was taken into account. In Larval Rearing Set 1, sampling was conducted on Day 0, 1, and 2, after which the rearing and sampling system resulted in failure. In Larval Rearing Set 2, an extended rearing was successful, with sampling conducted on Day 0, 1, 4, and thereafter every 2 or 3 d until Day 17. Larvae began to crawl on the bottom net on Day 2. Most of these larvae would eventually die due to the unnatural substratum conditions, becoming “waste” accumulated on the bottom. However, such waste might still contain a substantial number of live larvae that had not undergone metamorphosis, capable of swimming. The larvae contained in the waste were collected and returned to the bag. On Day 17, the larvae remaining in the tank were transferred to a 1-l container and their subsequent survivorship and metamorphosis monitored until Day 32, with daily exchange of gently aerated seawater.

The daily change in the embryonic and larval mean number in the larval tank was expressed as the relative percentage of the initial value, where the combined results from the two Larval Rearing Sets were used. For each set, the initial number of fertilized eggs was estimated by multiplying the estimated number of spawned eggs by their fertilization rate. The curve predicting daily availability of competent larvae for settlement from Day 2 to Day 9 was expressed as an exponential function, $y = a b^x$,

where x and y stand for day number and relative larval abundance (only very few larvae remained after Day 9; see Section 3.6). The two parameters (a , b) were determined by a nonlinear least square regression, using “R” (R Development Core Team, 2008).

2.10. Determination of the shortest PLD of *U. moniliferum* in the laboratory

The shortest PLD was determined, using a setup similar to that described in Section 2.9. In this case the larval tank was isolated from a tub containing the other two tanks, with filtered seawater flowing through. Adults for gamete spawning and sediments for larval settlement were collected from an intertidal sandflat about 30 km north of Nagasaki Prefectural Institute of Fisheries (Yanagi-Hama sandflat) during low tide on 5 October 2009. The surface 1-cm sediment sample was frozen and kept at -80°C until use, in which almost no juveniles of *Umbonium moniliferum* were present. A mass gamete spawning happened at around the estimated time of 7:15 on 7 October. At 15:30, approximately 1,267,000 larvae were put into a net bag in the larval tank (net diameter, 120 cm; height, 70 cm). Six $18\text{ cm} \times 20\text{ cm} \times 9\text{-cm}$ tall polyethylene trays had been placed on the bottom net, each containing a small amount of thawed sediment spread uniformly with an estimated thickness of 0.6 to 0.9 mm. The seawater salinity and temperature was recorded using a Compact-CT. The retrieval of trays started at 3:00 on 9 October (i.e. 1.8 d after egg fertilization) and continued at a regular interval of 12 h one at a time. Aliquots of sediment with some quantity of water were collected with a pipette ($n = 5$ to 13 for each tray; mean volume of sediment, 0.05 ml). The presence of live settlers was examined under a stereomicroscope and their numbers were counted. Settlers were discriminated from late-stage veligers based on the loss of velum. Finally, the volume of each sediment sample was measured to estimate the

number of settlers per unit volume. The shell width was measured for 6 to 21 settlers from each tray.

3. Results

3.1. Sex ratio and size-specific fecundity of *U. moniliferum*

The 895 specimens collected in 2002 were comprised of 423 males and 472 females, giving a sex ratio not significantly deviating from 1:1 ($\chi^2 = 2.68$; $d.f. = 1$; $p = 0.10$).

The same year, with fortnightly monitoring (Section 2.4), both developed testes and ovaries with ripe eggs in the population were first found on 8 September and became invisible on 20 December. The smallest mature male (5.3-mm shell width) and female (5.0 mm) belonged to the young-of-the-year group (0+ year cohort). On 8 September, the shell widths were greater than 5.2 mm in 97.1 % of the 0+ year cohort. The best-fitted regression equation for egg number versus shell width in the 5.0 to 12.2-mm females was given as a logistic function, in which two females with extremely high and low egg numbers (4,786 and 17 eggs) were excluded from analysis as the outliers (Fig. 3). A female with mean shell width of 8.6 mm is expected to have 1,757 ripe eggs.

3.2. Size-frequency distribution of adults of *U. moniliferum* and population fecundity

Two distinct normal-distribution groups were recognized for each of the shell-width-frequency distributions of the specimens collected with a 100-cm² corer on 18 August and 29 October 2008 (Fig. 4a). These two groups corresponded to the 0+ year cohort, and 1+ and older year cohort, respectively (Tamaki, 1994). The individual growth rates between the two dates were estimated at 0.019 mm d⁻¹ and 0.0105 mm d⁻¹

and the mortality rate at 0.0039 d^{-1} and zero, respectively. The zero mortality value was actually a 50 % increase, which was probably the result of natural population variability and sampling artifacts. The two distinct normal-distribution groups were also detected in the shell-width-frequency distribution of the specimens collected with a 625-cm^2 quadrat frame on 3 August 2008, where the adults' distribution along the transect was limited to ten contiguous sampling stations on the lower shore (Fig. 4b; see Section 3.4). Using the size-specific fecundity equation and the 1:1 sex ratio (Section 3.1) and assuming that all adult *Umbonium moniliferum* participated in the spawning event (see Section 3.6, second paragraph), these August females ($\geq 5\text{-mm}$ shell width) were expected to have a mean of $56,547\text{ eggs }625\text{ cm}^{-2}$. The supposed female population on 29 September 2008 (Fig. 4b), which was extrapolated from the 3 August data using the individual growth rate and mortality rate, was expected to have a mean of $59,735\text{ eggs }625\text{ cm}^{-2}$. As there was only a 5.6-% difference between the two egg-number estimates, the latter value was used for analysis of the ratio of the number of potentially available competent larvae to that of actual settlers (Section 4, ninth paragraph).

3.3. Size-frequency distribution of juveniles of *U. moniliferum* and definition of settlers

Of the shell-width-frequency distributions of juveniles for the samplings conducted on the sandflat in 2008, normal-distribution groups could be fitted to the smallest- or second smallest-size groups on 20-22 and 29 October (Fig. 5). The breeding season started in early September, but the substantial newly recruited cohort of the year was recognized first on 10 October, though only a small number of individuals were present, not forming a normal distribution. A distinct, second newly recruited cohort was

established during the middle of October. The abruptly increased larval settlement and the heaviest one occurred on 11 and 14 October, respectively. By 22 October, the first newly recruited cohort had been virtually absorbed by this second one. On 29 October, another distinct settler group appeared to the left of the second newly recruited cohort, with a comparatively large number of individuals. This settler group would become the third newly recruited cohort of the year. The initial juvenile growth rate was estimated at 0.017 mm d^{-1} (one shell-width-class shift per day), which was a mean of the six daily increment values (Table 1). The settlers occurring per day therefore can be defined as juveniles with shell widths of 0.20 and 0.21 mm, which conforms to the members belonging to the smallest shell-width class. The juvenile mortality rate can be estimated from the change in the total numbers of juveniles of the second newly recruited cohort between 22 and 29 October. However, the juvenile number on 22 October was apparently much smaller than those on the preceding five dates, which would have been due to a sampling error. Adopting the juvenile number on 21 October, the daily mortality rate was estimated at 0.043 d^{-1} .

3.4. Distribution of juveniles and adults of U. moniliferum along the transect

The center of the juvenile distribution along the transect on the sandflat on 14 October 2008 was situated at Stns 150 and 170, which were 20 to 40 m seaward of the MLWN (Fig. 6a). The juvenile densities at these stations were about 1,830 and 1,280 inds. 100 cm^{-2} . The densities at Stn 190 and landward stations were much lower. This distribution pattern was basically the same as that recorded in October 1980, where the densities were tapering to zero towards Stns 250 and 0, respectively (Tamaki, 1994). When the juvenile densities at Stns 210 and 230 in the present study are linearly

interpolated between the value at Stn 190 and zero at Stn 250, the juveniles at Stn 90 used for daily monitoring for settler density during the period from 10 to 22 October 2008 (Section 3.3) would account for 5.8 % of all juveniles that existed along the transect (see Section 4, ninth paragraph).

The distribution of adults was limited to the lower half of the transect on 3 August 2008, which was situated seawards of the center of the juvenile distribution (Fig. 6b). The densities of the 0+ year cohort (shell widths ≤ 9.9 mm; Fig. 4b) were the highest on the middle shore (about 110 inds. 625 cm^{-2}), generally decreasing seawards, while the center of the distribution of the 1+ and older year cohort (shell widths ≥ 10.0 mm) was on the lower shore, with densities of about 30 inds. 625 cm^{-2} . The mean \pm SD density from the two cohorts inclusive was 70.4 ± 38.8 inds. 625 cm^{-2} ($n = 10$) or 84.9 ± 27.2 inds. 625 cm^{-2} ($n = 8$, excluding Stns 130 and 290, which were the terminal stations inhabited by adults). These mean values were about half the mean density value recorded in 1980 (Tamaki, 1994).

3.5. Shortest PLD of *U. moniliferum*

The seawater salinity and temperature in the laboratory tank in October 2009 varied from 33.0 to 33.2 and from 23.5 to 24.9°C, respectively, which was largely the same as the values recorded in the field during the middle of October 2008 (see Section 3.7).

On Day 1.8, approximately 50 to 60 % of the veligers crawled on the sediment, with the remainder swimming in the water column. The proportion reached about 90 % on Day 2.3. The settlers first appeared on Day 3.3, with the mean \pm SD density in the sediment being 26.3 ± 36.9 settlers ml^{-1} . The densities on the subsequent two dates were 300.5 ± 268.4 and 292.9 ± 182.6 settlers ml^{-1} . The shell widths for the subsample

from these settlers were either 0.20 or 0.21 mm ($N = 6$ to 21), which agreed with the definition of settler size as determined by the field sample (Section 3.3).

3.6. Egg spawning and competent larval availability of U. moniliferum in the laboratory

The seawater temperature in the adult tank ranged from 25.3 to 21.7°C (Fig. 7a). In the overall trend depicted with a smoothed line, (1) there was an initial rapid decrease from 25.0 (28 September) to 23.9°C (3 October), followed by a gradual one to 23.3°C (15 October), and (2) the value increased again to 23.8°C (19-23 October), followed by a continuous drop to 22.2°C (1-4 November). The seawater salinity was fairly constant at 33.4 over the entire period, with a minimum value of 32.5 (Fig. 7b).

The mass egg spawning happened twice in the adult group used for Rearing Set 1 in 2008. The first one took place between 3 and 6 October, which was 5 to 2 d before neap tide (Fig. 8a,c). The total number of spawned eggs estimated from the direct sampling (by pipetting) was 2,149,887 (mean number per sample from each date was used; number of adults of both sexes inclusive on 4 October = 2,029), with 95.8 % of the total egg number recorded on 4 October and 3.9 % the next day. Embryos and larvae for Larval Rearing Set 1 were derived from the eggs spawned on 4 October, in which the egg fertilization rate was 92.0 % and the embryos were at the blastula or gastrula stages at 10:30. The time of egg spawning was estimated at 6:30-7:30. The mean number of spawned eggs per female was 2,118 (estimated number of females = 1,015 based on the 1:1 sex ratio; Section 3.1). The total number of eggs held by all females expected from the shell-width-frequency distribution of the subsample (mean \pm SD shell width = 10.3 ± 1.3 mm, $N = 650$ for both sexes) was 2,180,136. The

expected total egg number was close to the above-mentioned direct-sampling-based estimate, with a difference of 1.4 %. The second mass egg spawning took place on 15 October at around the estimated time of 8:10 (Fig. 8c). The directly estimated total number of spawned eggs held by 885 females was 1,372,500. Thus the mean number of spawned eggs per female was 1,551, which was 73 % of that in the first mass egg-spawning event. Finally, one minor egg spawning took place during the period from 22 to 26 October, with the total number of spawned eggs being 10,842 (data not shown in Fig. 8c).

In the adult group used for Rearing Set 2, one bout of mass egg spawning happened continuously during the period from 18 to 23 October, followed by a minor discrete one on 26 October (Fig. 8c). Embryos and larvae for Larval Rearing Set 2 were derived from the eggs spawned on 18 October (by the adults collected 4 d earlier), in which the egg fertilization rate was 88.5 %, with the estimated time of spawning at 6:15-7:15. The directly estimated total number of spawned eggs over the monitoring period was 2,479,288 eggs (number of adults of both sexes on 18 October = 2,735). Thus the mean number of eggs per female was estimated at 1,812. The number of eggs obtained on 18 October accounted for 89.5 % of the sum total of spawned eggs, followed by the next-day value (6.3 %). The total number of eggs held by all females, as expected from the shell-width-frequency distribution (subsample's mean \pm SD shell width = 10.5 ± 1.2 mm, $N = 500$ for both sexes), was 2,883,966, which was greater than the direct-sampling-based estimate by 16.3 %.

Accompanied with their operculum and shell formation on Day 1, veliger-stage larvae in the larval tanks tended to deposit on the bottom net due to an increase in body specific gravity. These larvae undertook passive sinking and upward swimming. The

proportion of competent larvae that were ready for settlement relative to the initially fertilized eggs was 14.5 % on Day 2 and further regressed as $31.647 \times 0.664^{\text{Day}}$ % on $2 < \text{Day} \leq 9$ (Fig. 9). The availability of competent larvae during Day 9 to Day 17 declined from 0.8 % (regressed value) or 0.4 % (actual value) to 0.03 %. Later on, three larvae that were capable of settlement survived until Day 32, when the observation was terminated.

3.7. Sequential change in abundance of eggs, larvae, and settlers of U. moniliferum in the field

The seawater temperature in the field in 2008 ranged from 29.8 to 19.9°C (Fig. 7a). In the smoothed data, there was a rapid drop from 26.2 (25 September) to 23.2°C (30 September). Later the values generally increased gradually to 24.7°C (10 October) and were in a narrow range until 19 October (24.0-24.2°C), followed by a rapid drop to 22.8°C (29 October). The up-and-down shape in the smoothed data during the end of September to early November was nearly the same as that recorded in the laboratory (Section 3.6), though the field values were higher and lower by a maximum of 1.35°C during the period from 28 September to 13 October and by a maximum of 0.75°C during the period from 13 to 23 October, respectively. The seawater salinity fluctuated depending on the amount of rainfall, which sometimes dropped to near 10 (Fig. 7b). The frequency of rainfall was highest during the end of September to early October, followed by those in the middle of September and at the end of October in order. The maximum values were fairly constant between 32.5 and 33.0 over the entire period, which was lower than the laboratory constant value by 0.4 to 0.9 (Section 3.6). During the period from 2 to 21 October, when spawned eggs appeared (see below), weak

northerly winds (from northeast to northwest) prevailed, with an overall mean velocity of 3.1 m s^{-1} (Fig. 8b).

Through the field monitoring for the abundances of spawned eggs and larvae conducted during the period from 29 September to 22 October in 2008, a total of 13,802 eggs, comprised of fertilized (= embryos) and unfertilized ones, and a total of 23,948 larvae were collected. Eggs appeared first on 2 October and subsequently on all sampling occasions except for the one on 21 October (Fig. 8d). Thus eggs were spawned during both daytime and nighttime. The proportion of fertilized eggs was 95.2 % of all spawned ones. The collected embryos were at either 16-cell or 32-cell or morula stage. The 99.8 % of the larvae collected over the entire monitoring period occurred during the period from 2 to 22 October, appearing on every sampling occasion (Fig. 8e). The proportion of veligers in these larvae was 99.4 %, trochophores accounting for the rest. Larvae at the earliest sub-stage of the veliger stage, with an estimated time lapse of 8 h from the time of egg fertilization, were collected only once (during the daytime on 9 October). The other veligers were older, either at the sub-stage just prior to the appearance of opercula or at later sub-stages inclusive. The prevalence of the 16- or 32-cell and morula stages among the embryos and early-stage larvae suggests that the spawning and fertilization of eggs was synchronized in the population and that these events occurred mostly 90 or 120 min (plus 20 min) prior to the mid-point of each sampling period. The estimated egg-spawning time was 8 to 115 min before the actual high-tide time for each sampling occasion, with a mean \pm SD time-lag being 71 ± 25 min (Fig. 8a,d).

Three bouts of mass egg spawning happened during the monitoring period (Fig. 8a,d): the first one during the daytime (10:49) and nighttime (22:27) sampling occasions

on 4 October 2008 (egg spawning spike nos. 1 and 2; 4 d before neap tide); the second one on four occasions during the period from 10 to 12 October (spike nos. 3 to 6; 2 to 4 d after neap tide); and the third one during the nighttime (18:48) on 15 October (spike no. 7; 1 d before spring tide). The fertilized eggs of spike nos. 1 and 2 on 4 October accounted for 19.0 % of the sum total of the eggs spawned over the entire monitoring period. The four spikes in the second mass egg-spawning bout (spike nos. 3 to 6) occurred at 3:35 on 10 October, at 4:35 and 17:17 on 11 October, and at 5:28 on 12 October. The fertilized eggs of these spikes inclusive accounted for 61.5 % of the above-mentioned sum total. The intensity of the third mass egg spawning (spike no. 7) was much weaker, with the number of fertilized eggs accounting for 2.4 % of the sum total. The mean concentration of fertilized eggs for the four highest spawning spikes (nos. 2, 3, 5, and 6) was 4.4 eggs l^{-1} . The overall mean concentration of fertilized eggs during the period from 4 to 21 October was 0.7 eggs l^{-1} .

A tight link between egg spawning and larval appearance was most clearly ascertained by the observation that 40 and 51 % of the veliger-stage larvae occurring 1 d after the occurrence of eggs and embryos at spike nos. 2 and 3, respectively, were at the sub-stage immediately prior to operculum formation. This conformed to the developmental time course recorded in the laboratory (Harada et al., 2005; Fig. 8d,e). Furthermore, the mass egg-spawning events that took place between 10 and 12 October (spike nos. 3 to 6) appeared to be directly reflected on the highest concentrations of larvae recorded between 11 and 14 October. The mean concentration from the four highest records was 7.7 larvae l^{-1} . The occurrence of a less but still fairly large number of larvae on the nights of 16 and 19 October was immediately preceded by egg spawning spike no. 7, whose egg number was comparatively not large. By contrast, a

large number of eggs spawned on 4 October (spike nos. 1 and 2) were succeeded only by a quite low number of larvae for the subsequent 6 d. The grand mean concentration of larvae during the period from 4 to 21 October was 1.3 larvae l⁻¹.

In 2008, the density of settlers (= juveniles of the smallest shell-width class in Fig. 5) at Stn 90 along the transect on the sandflat increased sharply from 12 to 13 October, followed by the three highest values until 16 October (Fig. 8f). The mean density from the four highest records was approximately 19,000 settlers m⁻². These settler groups corresponded to the four spikes of egg spawning (nos. 3 to 6) that occurred 3 or 4 d before the appearance of each settler group (Fig. 8d). The subsequent declining pattern in settler abundance with time was more continuous than that in larval abundance (Fig. 8e). The grand mean density of settlers during the period from 10 to 22 October was approximately 8,000 settlers m⁻². Thus an estimate can be made that 0.9 % of the larvae derived from a mean of 931,000 eggs spawned by 560 females per square meter of the sandflat was successful in settlement (Sections 3.2 and 3.4).

The settler density on 29 October 2008 was based on the actual data, while those plotted on 26, 27, and 28 October (Fig. 8f) were calculated from the juvenile densities corresponding to each combined shell-width class of 0.26 and 0.27, 0.24 and 0.25, and 0.22 and 0.23 mm in the size-frequency distribution recorded on 29 October (Fig. 5). The daily juvenile growth rate (0.017 mm d⁻¹; Section 3.3) was applied to this back calculation under the assumption of no mortality. It was further assumed that the eggs leading to each of these settler groups over the four dates had been spawned 3 d (shortest PLD; Section 3.5) before the high-tide time immediately prior to the occurrence of each settler group during the low tide (cross marks in Fig. 8d). These supposed egg-spawning dates were 2 to 5 d after neap tide (on 21 October; Fig. 8a).

This situation was similar to the preceding mass egg-spawning event in the population that took place between 10 and 12 October, with a time-lag of 2 to 4 d after neap tide.

3.8. Vertical migration of larvae of U. moniliferum in the water column

All larvae collected from the 23-m deep (at low tide) water column in Tomioka Bay were of the veliger stage, with mean concentrations of 0.5 to 1.6 larvae l⁻¹ (Fig. 10a). The actual water depth of each sampling layer was within a narrow range around the respective targeted value except for sampling set no. 7, in which the deepest two layers were positioned shallower by 1 m. Larvae migrated across all depth layers, with 12.6 to 33.7 % (mean, 24.9 %) of the larvae in the water column being present at the surface 1-m deep layer. The WMDs of larvae varied from 7.0 to 12.5 m (Fig. 10b). The trajectory of WMDs appears to be of a symmetrical shape about the midnight low tide, at which time larvae reached a maximum depth. Exceptionally, the WMD at the final sampling set (no. 8) became greater than at set no. 7. The sampling station is subject to wind-induced turbulence when strong northerly winds blow (Fig. 1). Examining the wind record corresponding to the sampling period, it was confirmed that the above wind conditions took place three times, during sampling set no. 1, for a part of no. 2, and during no. 8, with mean northerly wind velocities of 2.5, 1.7, and 3.9 m s⁻¹, respectively; during the other sampling sets, the mean values were below 1.0 m s⁻¹ (Fig. 10c).

3.9. Retrieval of drift cards

The next day after the release of drift cards (28 October 2009: Day 1), 28.3 % of the total number was retrieved (Fig. 11a). Cumulatively, 51.5 % was recovered on Day 3. Furthermore, the cumulative proportion appears to have almost approached an

asymptote by Day 9, from 60.1 % on Day 4, via 71.4 % on Day 9, to 74.5 % on Day 17. For most of the sampling period, northerly winds prevailed, favoring onshore transport of drift cards (Fig. 11b). During the periods from 27 October to 1 November and from 4 to 11 November, their velocities were weak, with mean values of 3.4 m s^{-1} and 2.0 m s^{-1} , respectively, while stronger northerly winds with mean values of 6.8 m s^{-1} and 9.5 m s^{-1} blew on 2-3 and 11-12 November, respectively.

3.10. Cohorts of juveniles of U. moniliferum throughout the breeding season in 2002

Three distinct newly recruited cohorts were detected during the breeding season of 2002 (Fig. 12a-i), as in 2008 (Fig. 5). One major difference between the two years was that the abundance of the first cohort members was much greater in 2002. The larval settlement conducive to these three cohorts appeared to be concentrated at around each spring tide. On 7 October, when the first sampling was conducted in the season, there were both the first newly recruited cohort with a shell-width mode of 0.42 mm and the settler group with a truncated shell-width-frequency distribution, composed of the smallest-sized juveniles. Applying the juvenile growth-rate estimate obtained in 2008 (Section 3.3) to the 2002 data, the time of larval settlement leading to the formation of the first newly recruited cohort can be backdated to around the second spring tide in September (about 13-d time-lag between 0.42 mm and the median value of the first shell-width class). The settler group on 7 October, with a shell-width mode of 0.37 mm, had become the second newly recruited cohort on 22 October, when the last substantial settlement event in the season was in progress. The settler group on 22 October had become the third newly recruited cohort with a shell-width mode of 0.32 mm on 4 November. On 21 November, the first and second newly recruited cohorts

had merged to constitute one normal-distribution group with a shell-width mode of 0.55 mm. The presence of this fused cohort and the third newly recruited cohort was recognized until 3 January 2003, though the former was nearly absent on 21 December probably due to a sampling error. On 19 January and 2 February, the three original newly recruited cohorts had become inseparable, with the third one being the main component of the finally fused cohort with a shell-width mode of 0.72 mm (on 2 February). This overwintering juvenile cohort became the 0+ year cohort, which was clearly identified in the shell-width-frequency distribution of the adult specimens collected on 3 April 2003 (Fig. 12j).

4. Discussion

The main part of the annual breeding season of *Umbonium moniliferum* on the Tomioka sandflat was substantially confined to the period from late September through October (Tamaki, 1994; Harada et al., 2005; Figs. 8 and 12). The climatic conditions in western Kyushu over the year and their consequent influences on properties of the coastal waters are most moderate and stable in April-May and October (Wadachi, 1958). The year is divided into the “rainy” and “dry” seasons (June-September and October-May), which was reflected on the higher and largely stable salinity values of seawater in Tomioka Bay during the study period (32.5-33.0; Figs. 1 and 7b). In the rainy season, southerly winds are prevalent. In the dry season, northerly winds, which cause water turbulence in north-facing coastal locations like Tomioka Bay (Fig. 1), are dominant but are relatively weak in October (Figs. 8b, 10c, and 11b) and April-May. The water currents induced by even such weak winds would assist material including

meroplanktonic larvae, especially those present in the surface layer, to be retained within the bay. During the first 23 d in October 2008, the water temperature in the bay was stable at around 24°C, which was preceded by a rapid drop at the end of September and followed by a gradual decline through the rest of October (Fig. 7a). Furthermore, around Tomioka Bay in October, the chlorophyll *a* concentration of the water column, which is a measure of food abundance for *U. moniliferum* adults, was among the highest recorded through the year, reaching about 4 µg l⁻¹ (Shimoda et al., 2007).

In general, enhanced fertilization in broadcast-spawning marine invertebrates is dependent on (1) synchronous gamete release, (2) population size, density, and aggregation of spawners, and (3) sperm volume (Giese and Kanatani, 1987; Levitan, 1995). Between sexes in the present *Umbonium moniliferum* population, the synchronous spawning of both gametes was ascertained by the high egg-fertilization rates recorded in the laboratory (88.5-92.0 %; Section 3.6) and the field (95.2 %; Section 3.7). Following this, when the term, egg spawning, is used, spawning of both gametes is meant. The synchronized mass egg-spawning event in the *U. moniliferum* population within its breeding season has several characteristics that are common to those in the *U. vestiarium* population inhabiting a sandy shore in Penang, Malaysia (Section 3.7; Berry, 1986, 1987). Regarding the three points listed above, first, the synchronous spawning of both gametes was pronounced also in *U. vestiarium* (see Berry, 1987). Second, for both species, large population sizes and high densities were recorded (Fig. 6b; Berry and Zambri, 1983; Tamaki, 1994). From the mean density values for these species (1,000-2,000 adults m⁻²), the mean distance between individuals with a representative shell width of 10 mm is estimated at 1-2 cm, from which, according to figure 1 in Levitan (1995), a 90-% fertilization rate would be expected.

Third, though the sperm volume in male *U. moniliferum* was not measured, well-developed testes were as voluminous as ovaries (A. Tamaki et al., personal observation). The dry tissue weights of gonads of *U. vestiarium* were the same between sexes (Berry, 1987).

Fertilization in broadcast spawners can also be enhanced by periodic rhythms within a breeding season, including synchronized gamete release in phase with light-dark, tidal, and semilunar cycles (Morgan, 1995). Between *Umbonium moniliferum* and *U. vestiarium*, there were some differences in the former two cycles. Regarding the light-dark cycle under field conditions, the egg spawning occurred both during daytime and nighttime in *U. moniliferum* versus only during daytime in *U. vestiarium* (Section 3.7; Berry, 1986). Regarding the tidal cycle, egg spawning was estimated to occur 8 to 115 min before the time of high tide in *U. moniliferum* versus over a wider duration between 35 min before and 4.7 h after the time of high tide in *U. vestiarium* (Section 3.7; Berry, 1986). Water flows are one critical factor for enhancing gamete fertilization (Levitan, 1995). The slack water conditions around high tide with minimum advection of material might be most suitable for retaining both gametes' clouds in *U. moniliferum*. Furthermore, as embryos of *U. moniliferum* sink for 6 h in the water column before hatching out by trochophore larvae, the gamete spawning by adults densely inhabiting the lower shore timed not to low slack but to high slack tide might have an adaptive significance in that (1) settling embryos would not be inhaled by suspension-feeding, conspecific adults (cf. Woodin, 1976; André et al., 1993) and (2) early-stage swimming larvae would not be stranded on the upper shore.

Regarding the mass egg-spawning timing in phase with a semilunar cycle, there are several common characteristics between *Umbonium moniliferum* and *U. vestiarium*

(Sections 3.6 and 3.7; Berry 1986, 1987). In the laboratory in 2008, the first mass egg-spawning event in *U. moniliferum* peaked on 4 October (Fig. 8c). The direct-sampling-based estimate of the number of spawned eggs was close to the maximally available egg number expected from adult size-specific fecundity under the assumption of all females' participation in the spawning event (Section 3.6). This suggests that all females synchronously spawned all of their mature oocytes in one burst (but see Counihan et al. (2001) for spawning over two consecutive nights by the same individuals in an abalone species). A second mass egg spawning took place on 15 October (Fig. 8c), with 73 % of the maximally expected number of eggs being produced. Histological examination of ovaries of specimens from the field has detected multiple oocyte cohorts with different sizes (A. Tamaki et al., unpublished data). Thus it is suggested that with ample food supply, the spawning of the largest-oocyte cohort would be succeeded by full growth of the second largest one synchronously among the reared females in 3-d shorter than one semilunar period.

Around the neap tide on 8 October 2008 in the field, the heaviest of the first mass egg-spawning event took place 4 d earlier (spike no. 2), being coincident with that in the laboratory (Fig. 8c,d). The second mass egg-spawning event took place 2 to 4 d after that neap tide, with the heaviest one on 11 October (spike no. 5). The estimated date of the heaviest of the third mass egg-spawning event was 25 October, which was 4 d after the neap tide (Fig. 8d,f). Considering the 11-d interval between the first and second mass egg-spawning events by the same females in the laboratory (Fig. 8c), it would be safe to assume that the egg-spawning spike nos. 2 and 5 in the field with their time-lag of 7 d were assigned not to the same but to the different females. The mass egg spawning in the laboratory on 18 October was performed by the females that had

been collected from the field 4 d earlier (Fig. 8c). It is plausible that these females once took part in the mass egg-spawning event on 4 October. Synthesizing the results from laboratory and field, mass egg spawning of the *Umbonium moniliferum* population in the field appears to occur in a semilunar cycle, with two successive reproductive bouts taking place 14-d apart, beginning 2-4 d after neap tide. For the population of *U. vestiarium* in Penang, it was reported that at least three heavy egg-spawning events by the same adult members took place in a semilunar cycle between April and May, each occurring 0 to 3 d after neap tide (Berry, 1986, 1987). Moreover, the restoration of both ovary weights and number of the largest oocytes was completed within each intervening period. The three prominent recruitment groups in the population of *U. moniliferum* on the Tomioka sandflat recognized every two weeks during the breeding season of both 2002 and 2008 (Figs. 5 and 12) would have been derived from the same adult members each year. A similar iteroparous egg-spawning pattern within a single breeding season was recorded for the abalones, *Haliotis asinina* from the southern Great Barrier Reef, Australia (Jebreen et al., 2000) and *H. discus hannai* from northern Japan (Fukazawa et al., 2007). In the latter case, the quality of eggs was better in the second batch of oocytes than in the first one, suggesting an increased postlarval starvation tolerance for the juvenile cohort that comes later in the breeding season (Fukazawa et al., 2007). In the *U. moniliferum* 0+ year cohort, the increasing dominance of the third (= last) newly recruited cohort over the preceding two ones with time in the breeding season of 2002 (Fig. 12) might be ascribed to the third cohort's higher post-settlement survival rate. Fukazawa et al. (2007) also demonstrated for *H. discus hannai* that the effective accumulative temperature (EAT), a measure of the thermal integral, was one critical factor determining the time interval between the two mass egg-spawning events.

In the present study, the smoothed seawater temperatures were lower in the laboratory than in the field during the period from 4 to 25 October 2008 (Fig. 7a). Despite this, the time interval between first and second mass egg-spawning events was shorter in the laboratory than in the field by 3 d (Fig. 8c,d), suggesting that some better food conditions in the laboratory exerted their superior influence to EAT. Alternatively, the lack of ambient environmental stimuli (e.g. tidal cycles) in the laboratory may have reduced the spawning interval to 11 d.

As to the adaptive significance for semilunar periodicity of egg spawning or larval release at neap rather than spring tidal cycle, it may be a generally accepted view that the slower water movements would raise the probability of retention of larvae near their natal habitats, especially for lecithotrophic ones with short PLDs (Naylor, 1976). Other than for *Umbonium vestiarium* (see Berry, 1986), this spawning pattern in line with a local retention hypothesis has been reported for a relatively few species' populations, including corals (Babcock et al., 1986; Fan et al., 2002), oyster (Korringa, 1947), polychaetes (arenicolids – Duncan, 1960; Bailey-Brock, 1984; opheliid – Tamaki, 1985; eunicid – Caspers, 1984; serpulid – Rothlisberg, 1974), and sea urchin (Pearse, 1975). For the present *U. moniliferum* population, however, caution must be used against a simple underscoring of the advantage associated with spawning at neap rather than spring tides. Plenty of eggs spawned on 4 October 2008 (prior to the neap tide) resulted in settlement failure (Figs. 5 and 8d,f), while those spawned 2-4 d after the neap tide eventually contributed to the formation of the second newly recruited cohort in the breeding season. A large proportion of the larval assemblage derived from the “after-neap-tide” egg batch experienced the spring tide that came 4-6 d later, with some substantial members further remaining in the water column until the next neap tide.

Strong currents associated with spring tides would affect larval retention in the opposite ways; flooding currents may effectively transport competent larvae towards the Tomioka sandflat, but ebbing currents could rapidly flush them out from the sandflat to an inner shelf area off Tomioka Bay, such as observed for newly released larvae of the ghost shrimp, *Nihonotrypaea harmandi* (see Tamaki et al., 2010). The export of larvae from estuarine habitats, dispersal over the shelf, and re-invasion of estuaries by postlarvae is one typical dispersal type for decapod crustacean larvae found along the estuary to ocean gradient (Queiroga and Blanton, 2005). It is therefore suggested that some mechanism should exist for *U. moniliferum* veligers to be retained within Tomioka Bay, probably through an interaction of tidal currents, northerly-wind-induced onshore surface currents, and coastal topography, being promoted by larval vertical migration.

The shoreline configuration is one essential factor that determines the distribution and concentration of meroplanktonic larvae in nearshore waters. In particular, topographic eddies of water generated around headlands can not only entrain larvae from offshore waters but also retain them close to the shore (Alldredge and Hamner, 1980; Mace and Morgan, 2006), including abalone larvae with 3 to 12-d PLDs (McShane et al., 1988; Shepherd et al., 1992; Sasaki and Shepherd, 1995; Stephens et al., 2006). Tomioka Bay, bounded by the Tomioka headland and Tsuji-Shima Island, may act as a local sink for material (Fig. 1). The tidal currents flowing north of these topographic projections in an inner shelf area of southern Tachibana Bay are dominated by the long-shelf (= east) over cross-shelf (= north) components, with their maximum speeds different by five times (Tamaki et al., 2010). A weak clockwise residual current is observed inside Tomioka Bay, which could be regarded as a sort of topographic eddy (Suzuki et al., 1982; Fujiie et al., 2006). Upon their entry into Tomioka Bay, an

assemblage of postlarvae of *Nihonotrypaea harmandi* that is present close offshore of the bay could ride on a nighttime onshore flooding currents and further become entrained in the residual current to reach the Tomioka sandflat (Fujiie et al., 2006; Tamaki et al., 2010). Within Tomioka Bay, the concentrations of *Umbonium moniliferum* larvae appeared to be spatially constant (0.5 to 1.6 and 1.3 larvae l⁻¹ on the uppermost sandflat and a 1.5-km offshore station, respectively; Sections 3.7 and 3.8), suggesting that they are well mixed and retained inside the bay. The results of the drift-card experiment conducted to simulate the dispersal of *U. moniliferum* larvae, a quarter of which was present in the surface layer of the water column (Fig. 10a), suggest that within their shortest PLD (= 3d), at least 12.5 % (= 0.25 × 0.5) of the larvae released from the sandflat at high tide of the neap tide would be concentrated in a narrow belt close to the shoreline including the sandflat part (Fig. 1; Sections 3.5 and 3.9). Furthermore, by Day 9, 17.5 % (= 0.25 × 0.7) of the larvae would have been brought to the shore. This retention of material in surface waters could occur with relatively weak onshore currents induced by northerly winds (Fig. 11b).

The position of meroplanktonic larvae in the water column with depth-dependent current velocities determines horizontal transport trajectories (Metaxas and Saunders, 2009; Tamaki et al., 2010). When disturbed by turbulence, gastropod larvae tend to pull in their vela and sink in the water column (Fuchs et al., 2004). At set no. 8 in the sampling that examined the vertical distribution of *Umbonium moniliferum* veligers, their WMD might have been at a shallower position if it were not for water turbulence caused by the strongest northeasterly winds (Fig. 10b,c; Section 3.8). The resultant putative trajectory of WMDs over a 24-h period suggests a reverse diel vertical migration, in which larvae ascend to a minimum depth during the day and descend to a

maximum depth at night. Whether or not possible reverse diel migration for a vertical distance of 5.5 m (in WMD) undertaken by *U. moniliferum* veligers promotes their retention around the shoreline of Tomioka Bay, especially during spring-tide periods, is a future research topic.

The degree of self-recruitment in the population of *Umbonium moniliferum* on the Tomioka sandflat can be assessed by computing the ratio of the number of potentially available competent larvae to that of actually recorded settlers on a daily basis over the monitoring period for settler density (10 to 22 October 2008, excluding 17th; Fig. 8f). This ratio is similar to “Net Larval Abundance” in Yoshioka (1982) and the reciprocal of “Settlement Success Factor” in Chícharo and Chícharo (2001). For the computation, six assumptions were made as follows: (1) all larvae are retained in the water column within the sandflat; (2) there is no mortality due to predation; (3) the competent larval assemblage is a mixture of those with ages (from the time of egg fertilization) between 2 and 9 d at the time of high tide immediately prior to the low tide on each juvenile-sampling date (Section 3.6, last paragraph); (4) the exponentially decreasing function describing the availability of competent larvae with time established in the laboratory (Fig. 9) can be applied to the field circumstances, given that the difference in seawater temperature, the primary determinant of developmental rates of lecithotrophic larvae (Reitzel et al., 2004; Strathmann, 2007), was actually small between laboratory and field as well as for the difference in salinity (Fig. 7a,b); (5) the comparison between competent-larval and settler abundances can be made on an areal basis of the sandflat. The rationale is that adults (and accordingly gametes just spawned from them) and juveniles were distributed in zones parallel to the shoreline (Tamaki and Kikuchi, 1983; Tamaki, 1994; Section 3.4). As these two zones occupied different positions along the

elevation gradient, two strips with different lengths along the transect are correspondingly set for the comparison (160-m long strip from Stn 130 to Stn 290 and a 210-m long strip from Stn 20 to Stn 230, respectively; Fig. 6); and (6) the proportion of the settler number at a representative sampling station (Stn 90) in the sum total number from all stations containing juveniles along the transect is 5.8 % (Section 3.4). The fertilized-egg number in the water column over a unit area of the sandflat was calculated by multiplying the density of just spawned eggs by the egg-fertilization rate under field conditions (95.2 %; Section 3.7). The spawned-egg density on each sampling occasion in the egg-concentration monitoring period (2 to 21 October 2008; Fig. 8d) was calculated under three assumptions as follows: (1) any one of all females spawned its eggs at full strength only once at any high tide during the period between the two consecutive neap tides (Section 4, fourth paragraph); (2) the total number of eggs spawned from the population existing on a unit area of the sandflat during this period can be estimated from the shell-width-frequency distribution of adults and their size-specific fecundity on a representative date just prior to the initial neap-tide date (956,000 eggs m⁻² on 29 September 2008; Section 3.2); and (3) the number of spawned eggs corresponding to each high tide during the period can be estimated by allocating the total number of spawned eggs to each sampling occasion in proportion to the ratio of the actually recorded concentration of spawned eggs to the sum total concentrations over the period (Fig. 8d). The computed outcomes for the competent-larva-to-settler ratio on each of the 12 consecutive dates during the middle of October 2008 were 49.2 (October 10th), 2.4 (11th), 2.2 (12th), 0.5 (13th), 0.9 (14th), 1.1 (15th), 0.7 (16th), 1.1 (18th), 0.7 (19th), 1.2 (20th), 1.8 (21st), and 5.0 (22nd). Except for the highest values on October 10th and 22nd, the ratios were fairly stable in a narrow range, with six dates

exceeding 1.0 and four dates less than 1.0. Except for a small peak in the egg spawning on the 15th, no mass egg spawning took place on the eve of the occurrence of settlers in the last one third of the monitoring period (18th-22nd), yet those settlers could be explicable by the surviving larvae derived from the four egg-spawning spikes in the first one-third period (10th-12th; spike nos. 3 to 6 in Fig. 8d). Even with the most conservative estimates of larval supply to the Tomioka sandflat possible (i.e. complete retention of spawned larvae and no predation on those larvae), the population would still appear to be falling short, and hence there must be subsidies of larvae coming from other nearby tidal flats. The candidates for such local populations are those residing on seven major intertidal sandflats along the east coast of Amakusa-Shimoshima Island, which are located 20-30 km eastwards alongshore from the Tomioka sandflat (Fig. 1). These local populations would most probably have acted as a larval source in the late 1990s to replenish the Tomioka sandflat population that had been driven to extinction by an increased bioturbating activity of the *Nihonotrypaea harmandi* population during the early to middle 1980s (Flach and Tamaki, 2001). In order to assess the degree of self-recruitment in the *U. moniliferum* population on the Tomioka sandflat, it is especially required to know the degree of synchronization between autochthonous and allochthonous egg spawnings, and the amount and speed of transport of those allochthonous competent larvae.

The dispersal distance of meroplanktonic larvae for 1-20 km has been least documented in the larval ecology literature, which may stem from an artifact simply due to a kind of available data set and to our poorer knowledge on nearshore larval transport processes associated with complex local hydrodynamics in irregular topographic settings (Pineda, 2000; Cowen and Sponaugle, 2009; Shanks, 2009; Tamaki et al., 2010).

Local populations of abalone species with 3 to 12-d PLDs are supposed to have a potential connectivity mostly at a maximum distance of 10-30 km, but the usual larval transport distance could be on the order of 0-10 km presumably related to self-recruitment (McShane, 1995; Sasaki and Shepherd, 1995; Stephens et al., 2006). For the present *Umbonim moniliferum*, an extended PLD with 2 wk to 1 mo was recorded for a few larvae in the laboratory (Section 3.6). In the field, such aged larvae could be transported for a much longer distance than usual (Kinlan et al., 2005), as recorded for planulae or embryos of brooding corals (Richmond, 1987) and gamete-spawning ones (Babcock and Heyward, 1986) in surface slicks, which have potencies to prolong their larval competence length far beyond the shortest PLD of hours to days.

In the present study, the settlers available per day during the daily monitoring and the newly recruited cohort in the shell-width-frequency distribution of *Umbonium moniliferum* were defined as juveniles belonging to the smallest size class and to the most left-hand normal distribution group, respectively (Section 2.3; Fig. 5). The presence of the juvenile group to the left of that newly recruited cohort, including settlers, means that the process from settlement to recruitment is still underway. Once so defined, the ambiguity about discriminating settlers and recruits has disappeared. As operational definitions of settlers and recruits are deemed inevitable in marine benthic ecology (Booth, 1991; Michener and Kenny, 1991; Gosselin and Qian, 1997; Pineda, 2000), our definition would serve as one feasible way to avoid the uncertainty between these two terms especially for those macrobenthos that release their gametes or larvae (1) with a relatively short PLD, (2) in a (semi) lunar cycle, and (3) en masse over a short period of time for each. The local population of *U. moniliferum* in the present

study area satisfies all above conditions, enabling the link from egg spawning, via competent larval occurrence, to larval settlement and juvenile recruitment to be tracked quantitatively. One cycle from mass egg spawning to juvenile recruitment has been completed basically from one neap tide to the next, which was repeated three times, most probably by the same adult members within a short annual breeding season (Sections 3.3, 3.7, and 3.10). The consequently formed three distinct newly recruited cohorts have eventually fused into a single young-of-the-year cohort in the adult population (Fig. 12j). If sediment samples were treated with a 0.5- or 1-mm mesh sieve through, for instance, a monthly sampling schedule, true processes underlying that cohort formation would have been missed. Even a fortnightly sampling schedule with sediment samples unsieved (Fig. 12a-i) could neither present these processes nor give explicit quantities to the terms with double quotation marks listed in the first paragraph of the Introduction (Section 1), except for the size of recruits. At least for one semilunar cycle, the daily monitoring for settler density with one or two samplings per day will be necessary (Figs. 5 and 8f; Connell, 1985; Gosselin and Qian, 1997; Pineda, 2000). Furthermore, the daily monitoring for egg spawning and larval abundance patterns have strengthened our grasp of the entire flow of sequential events (Fig. 8d,e), into which results from the laboratory rearing experiments (Figs. 8c and 9; Section 3.5) and other information from the field (Figs. 3, 4, and 6) were incorporated. Although the present study has successfully demonstrated the process of newly recruited cohort formation, only suggestions were available concerning the mechanism of local retention or regional-scale allochthonous subsidies of larvae (Figs. 10 and 11; Section 4, ninth paragraph). To evaluate the degree of self-recruitment, future research on the nearshore hydrodynamics responsible for larval dispersal and transport, including the

construction of an appropriate biophysical transport model, will be needed (cf. Pineda, 2000; Cowen and Sponaugle, 2009; Metaxas and Saunders, 2009). As *U. moniliferum* and *U. vestiarium* act as key dominant suspension feeders supporting a number of associated species on each local benthic community in intertidal sandflats or sandy shores scattered along a vast stretch of the coastline from middle to low latitudes of the Indo-West Pacific Province (Fretter, 1975; Berry and Zambri, 1983; Morton and Morton, 1983; Reise, 1991; Tamaki 1994; Abdul-Salam and Sreelatha, 1998; Ogaya, 2004), the understanding of their meta- and local population dynamics will be crucial to elucidate the dynamics of coastal communities and ecosystems there.

5. Conclusions

For the understanding of processes of initial cohort formation in populations of benthic macro-invertebrates with a meroplanktonic larval phase in soft-sediment habitats, the present study has highlighted the importance of (1) giving clear definitions for settlers and recruits, depending on the specific circumstances, (2) setting a fine resolution in time and space in the sampling program to differentiate settlers and recruits, and (3) tracking released propagules (i.e. eggs/larvae), competent larvae, settlers, and recruits in a comprehensive framework. The trochid gastropod, *Umbonium moniliferum*, with its short PLD, high population abundance, and cyclic, synchronous, and pulsed mass gamete-spawning pattern in the population within a limited breeding season of the year, would provide us with one of the most appropriate case-study organisms for revealing a mechanism of distinct cohort formation in soft-sediment benthic systems.

Acknowledgements

We would like to express our appreciation to the following persons for their assistance: Y. Saito, S. Sen-jyu, and W. Jinno for sandflat sampling and laboratory rearing experiments, K. Kawamura for laboratory rearing experiments, the captain and crew of the RV “Kakuyo-Maru”, A. Manda, M. Matsuo, and Y. Inouye for sampling on board the ship, T. Kawamoto and S. Sen-jyu for drift card release and retrieval, and Y. Maeno, T. Yurimoto, and T. Nakano for histological analysis. M. Tokimatsu (Kumamoto Prefecture Government) kindly compiled the local wind data set. We also thank two anonymous reviewers for constructive comments. S. Mandal is grateful to the Ministry of Education, Culture, Sports, Science and Technology, Japan for his scholarship. This study was partly supported by the Japan Society for the Promotion of Science Grant-in-Aid for Scientific Research 19310148 to AT.

References

- Abdul-Salam, J., Sreelatha, B.S., 1998. Studies on Cercariae from Kuwait Bay. IX. Description and surface topography of *Cercaria kuwaitae* IX sp. n. (Digenea: Zoogonidae). Comp. Parasitol. 65, 141-146.
- Aizawa, Y., Takiguchi, N., 1999. Consideration of the methods for estimating the age-composition from the length frequency data with MS-Excel. Bull. Jpn. Soc. Fish. Oceanogr. 63, 205-214. (in Japanese).
- Akaike, H., 1973. Information theory and an extension of the maximum likelihood

- principle. In: Petrov, B.N., Csáki, F. (Eds.), Second International Symposium on Information Theory. Akadémiai Kiadó, Budapest, pp. 267-281.
- Allredge, A.L., Hamner, W.M., 1980. Recurring aggregation of zooplankton by a tidal current. *Estuar. Coast. Mar. Sci.* 10, 31-37.
- André, C., Jonsson, P.R., Lindegarth, M., 1993. Predation on settling bivalve larvae by benthic suspension feeders: the role of hydrodynamics and larval behaviour. *Mar. Ecol. Prog. Ser.* 97, 183-192.
- Asakura, A., 1995. Sexual differences in life history and resource utilization by the hermit crab. *Ecology* 76, 2295-2313.
- Babcock, R.C., Heyward, A.J., 1986. Larval development of certain gamete-spawning scleractinian corals. *Coral Reefs* 5, 111-116.
- Babcock, R.C., Bull, G.D., Harrison, P.L., Heyward, A.J., Oliver, J.K., Wallace, C.C., Willis, B.L., 1986. Synchronous spawnings of 105 scleractinian coral species on the Great Barrier Reef. *Mar. Biol.* 90, 379-394.
- Bailey-Brock, J.H., 1984. Spawning and development of *Arenicola brasiliensis* (Nonato) in Hawaii (Polychaeta; Arenicolidae). In: Hutchings, P.A. (Ed.), Proc. First Internat. Polychaete Confer. The Linne. Soc. New South Wales, Sydney, pp. 439-449.
- Berry, A.J., 1986. Daily, tidal, and two-weekly spawning periodicity and brief pelagic dispersal in the tropical intertidal gastropod *Umbonium vestiarium* (L.). *J. Exp. Mar. Biol. Ecol.* 95, 211-223.
- Berry, A.J., 1987. Reproductive cycles, egg production and recruitment in the Indo-Pacific intertidal gastropod *Umbonium vestiarium* (L.). *Estuar. Coast. Shelf Sci.* 24, 711-723.

- Berry, A.J., Zambri bin Othman., 1983. An annual cycle of recruitment, growth and production in a Malaysian population of the trochacean gastropod *Umbonium vestiarium* (L.). Estuar. Coast. Shelf Sci. 17, 357-363.
- Booth, D.J., 1991. The effect of sampling frequency on estimates of recruitment of the domino damselfish *Dascyllus albisella* Gill. J. Exp. Mar. Biol. Ecol. 145, 149-159.
- Bownes, S.J., McQuaid, C.D., 2009. Mechanisms of habitat segregation between an invasive and an indigenous mussel: settlement, post-settlement mortality and recruitment. Mar. Biol. 156, 991-1006.
- Caley, M.J., Carr, M.H., Hixon, M.A., Hughes, T.P., Jones, G.P., Menge, B.A., 1996. Recruitment and the local dynamics of open marine populations. Annu. Rev. Ecol. Syst. 27, 477-500.
- Caspers, H., 1984. Spawning periodicity and habitat of the palolo worm *Eunice viridis* (Polychaeta: Eunicidae) in the Samoan Islands. Mar. Biol. 79, 229-236.
- Chícharo, L., Chícharo, M.A., 2001. A juvenile recruitment prediction model for *Ruditapes decussatus* (L.) (Bivalvia: Mollusca). Fish. Res. 53, 219-233.
- Connell, J.H., 1985. The consequences of variation in initial settlement vs. post-settlement mortality in rocky intertidal communities. J. Exp. Mar. Biol. Ecol. 93, 11-45.
- Counihan, R.T., McNamara, D.C., Souter, D.C., Jebreen, E.J., Preston, N.P., Johnson, C.R., Degnan, B.M., 2001. Pattern, synchrony and predictability of spawning of the tropical abalone *Haliotis asinina* from Heron Reef, Australia. Mar. Ecol. Prog. Ser. 213, 193-202.
- Cowen, R.K., Sponaugle, S., 2009. Larval dispersal and marine population connectivity. Annu. Rev. Mar. Sci. 1, 443-466.

- Dubois, S., Comtet, T., Retière, C., Thiébaud, E., 2007. Distribution and retention of *Sabellaria alveolata* larvae (Polychaeta: Sabellariidae) in the Bay of Mont-Saint-Michel, France. *Mar. Ecol. Prog. Ser.* 346, 243-254.
- Duncan, A., 1960. The spawning of *Arenicola marina* (L.) in the British Isles. *Proc. Zool. Soc. Lond.* 134, 137-156.
- Ebert, T.A., 1999. Plant and animal populations: Methods in demography. Academic Press, San Diego, 312 pp.
- Eckman, J.E., 1996. Closing the larval loop: linking larval ecology to the population dynamics of marine benthic invertebrates. *J. Exp. Mar. Biol. Ecol.* 200, 207-237.
- Eggleston, D.B., Armstrong, D.A., 1995. Pre- and post-settlement determinants of estuarine Dungeness crab recruitment. *Ecol. Monogr.* 65, 193-216.
- Ellien, C.E., Thiébaud, E., Dumas, F., Salomon, J.-C., Nival, P., 2004. A modelling study of the respective role of hydrodynamic processes and larval mortality on larval dispersal and recruitment of benthic invertebrates: example of *Pectinaria koreni* (Annelida: Polychaeta) in the Bay of Seine (English Channel). *J. Plankton Res.* 26, 117-132.
- Fan, T.-Y., Li, J.-J., Ie, S.-X., Fang, L.-S., 2002. Lunar periodicity of larval release by pocilloporid corals in southern Taiwan. *Zool. Stud.* 41, 288-294.
- Feller, R.J., Stancyk, S.E., Coull, B.C., Edwards, D.G., 1992. Recruitment of polychaetes and bivalves: long-term assessment of predictability in a soft-bottom habitat. *Mar. Ecol. Prog. Ser.* 87, 227-238.
- Flach, E., Tamaki, A., 2001. Competitive bioturbators on intertidal sand flats in the European Wadden Sea and Ariake Sound in Japan. In: Reise, K. (Ed.), *Ecological Studies. Ecological comparisons of sedimentary shores*, vol. 151. Springer, Berlin,

pp. 149-171.

- Fretter, V., 1975. *Umbonium vestiarius*, a filter-feeding trochid. J. Zool., Lond. 177, 541-552.
- Fuchs, H.L., Mullineaux, L.S., Solow, A.R., 2004. Sinking behavior of gastropod larvae (*Ilyanassa obsoleta*) in turbulence. Limnol. Oceanogr. 49, 1937-1948.
- Fujiie, W., Yanagi, T., Tamaki, A., 2006. Numerical simulation for larval connection network of the ghost shrimp *Nihonotrypaea harmandi* population among intertidal sandflats in Tachibana Bay and Ariake Sound, western Kyushu, Japan. La Mer 44, 67-84.
- Fukazawa, H., Kawamura, T., Takami, H., Watanabe, Y., 2007. Oogenesis and relevant changes in egg quality of abalone *Haliotis discus hannai* during a single spawning season. Aquaculture 270, 265-275.
- Gaines, S.D., Bertness, M.D., 1992. Dispersal of juveniles and variable recruitment in sessile marine species. Nature 360, 579-580.
- Giese, A.C., Kanatani, H., 1987. Maturation and spawning. In: Giese, A.C., Pearse, J.S., Pearse, V.B. (Eds.), Reproduction of marine invertebrates, vol. IX. Blackwell Scientific, Palo Alto, and Boxwood Press, Pacific Grove, CA, pp. 251-329.
- Gosselin, L.A., Qian, P.-Y., 1997. Juvenile mortality in benthic marine invertebrates. Mar. Ecol. Prog. Ser. 146, 265-282.
- Grosberg, R.K., 1987. Limited dispersal and proximity-dependent mating success in the colonial ascidian *Botryllus schlosseri*. Evolution 41, 372-384.
- Harada, K., Ohashi, S., Fujii, A., Tamaki, A., 2005. Embryonic and larval development of the trochid gastropod *Umbonium moniliferum* reared in the laboratory. Venus (Jpn. J. Malacol.) 63, 135-143.

- Harii, S., Kayanne, H., 2003. Larval dispersal, recruitment, and adult distribution of the brooding stony octocoral *Heliopora coerulea* on Ishigaki Island, southwest Japan. *Coral Reefs* 22, 188-196.
- Hughes, T.P., Baird, A.H., Dinsdale, E.A., Moltschaniwskyj, N.A., Pratchett, M.S., Tanner, J.E., Willis, B.L., 2000. Supply-side ecology works both ways: the link between benthic adults, fecundity, and larval recruits. *Ecology* 81, 2241-2249.
- Hunt, H.L., Scheibling, R.E., 1997. Role of early post-settlement mortality in recruitment of benthic marine invertebrates. *Mar. Ecol. Prog. Ser.* 155, 269-301.
- Incze, L.S., Wahle, R.A., Palma, A.T., 2000. Advection and settlement rates in a benthic invertebrate: recruitment to first benthic stage in *Homarus americanus*. *ICES J. Mar. Sci.* 57, 430-437.
- Ishii, R., Sekiguchi, H., Nakahara, Y., Jinnai, Y., 2001. Larval recruitment of the Manila clam *Ruditapes philippinarum* in Ariake Sound, southern Japan. *Fish. Sci.* 67, 579-591.
- Jebreen, E.J., Counihan, R.T., Fielder, D.R., Degnan, B.M., 2000. Synchronous oogenesis during the semilunar spawning cycle of the tropical abalone *Haliotis asinina*. *J. Shellfish Res.* 19, 845-851.
- Jenkins, S.R., Marshall, D., Fraschetti, S., 2009. Settlement and recruitment. In: Wahl, M. (Ed.), *Ecological Studies. Marine hard bottom communities*, vol. 206. Springer, Berlin, pp. 177-190.
- Keough, M.J., Downes, B.J., 1982. Recruitment of marine invertebrates: the role of active larval choices and early mortality. *Oecologia (Berl.)* 54, 348-352.
- Kinlan, B.P., Gaines, S.D., Lester, S.E., 2005. Propagule dispersal and the scales of marine community process. *Diversity Distrib.* 11, 139-148.

- Korringa, P., 1947. Relations between the moon and periodicity in the breeding of marine animals. *Ecol. Monogr.* 17, 347-381.
- LeBlanc, S., Miron, G., 2006. Benthic-pelagic distribution of early stages of softshell clams (*Mya arenaria*) in tidally contrasted regimes. *Can. J. Zool.* 84, 459-472.
- Levitan, D. R., 1995. The ecology of fertilization in free-spawning invertebrates. In: McEdward, L. (Ed.), *Ecology of marine invertebrate larvae*, CRC Press, Boca Raton, pp. 123-156.
- López, S., Turon, X., Montero, E., Palacín, C., Duarte, C.M., Tarjuelo, I., 1998. Larval abundance, recruitment and early mortality in *Paracentrotus lividus* (Echinoidea). Interannual variability and plankton-benthos coupling. *Mar. Ecol. Prog. Ser.* 172, 239-251.
- Mace, A.J., Morgan, S.G., 2006. Larval accumulation in the lee of a small headland: implications for the design of marine reserves. *Mar. Ecol. Prog. Ser.* 318, 19-29.
- McGuinness, K.A., Davis, A.R., 1989. Analysis and interpretation of the recruit-settler relationship. *J. Exp. Mar. Biol. Ecol.* 134, 197-202.
- McShane, P.E., 1995. Recruitment variation in abalone: its importance to fisheries management. *Mar. Freshw. Res.* 46, 555-570.
- McShane, P.E., Black, K.P., Smith, M.G., 1988. Recruitment processes in *Haliotis rubra* (Mollusca: Gastropoda) and regional hydrodynamics in southeastern Australia imply localized dispersal of larvae. *J. Exp. Mar. Biol. Ecol.* 124, 175-203.
- Metaxas, A., Saunders, M., 2009. Quantifying the “bio-“ components in biophysical models of larval transport in marine benthic invertebrates: advances and pitfalls. *Biol. Bull.* 216, 257-272.
- Michener, W.K., Kenny, P.D., 1991. Spatial and temporal patterns of *Crassostrea*

- virginica* (Gmelin) recruitment: relationship to scale and substratum. J. Exp. Mar. Biol. Ecol. 154, 97-121.
- Minchinton, T.E., Scheibling, R.E., 1991. The influence of larval supply and settlement on the population structure of barnacles. Ecology, 72: 1867-1879.
- Moksnes, P.-O., Wennhage, H., 2001. Methods for estimating decapod larval supply and settlement: importance of larval behavior and development stage. Mar. Ecol. Prog. Ser. 209, 257-273.
- Morgan, S.G., 1995. The timing of larval release. In: McEdward, L. (Ed.), Ecology of marine invertebrate larvae, CRC Press, Boca Raton, pp. 157-191.
- Morton, B., Morton, J., 1983. The sea shore ecology of Hong Kong, Hong Kong Univ. Press. Hong Kong, 350 pp.
- Naylor, E., 1976. Rhythmic behaviour and reproduction in marine animals. In: Newell, R.C. (Ed.), Adaptation to environment: Essays on the physiology of marine animals. Butterworths, London, pp. 393-429.
- Ogaya, C., 2004. Presence or absence of the shell aperture: a criterion to identify shell breakage induced by durophagy in *Umbonium* (Mollusca: Gastropoda: Trochidae). Paleontol. Res. 8, 311-324.
- Ólafsson, E.B., Peterson, C.H., Ambrose Jr., W.G., 1994. Does recruitment limitation structure populations and communities of macro-invertebrates in marine soft sediments: the relative significance of pre- and post-settlement processes. Oceanogr. Mar. Biol. Annu. Rev. 32, 65-109.
- Olson, R.R., 1985. The consequences of short-distance larval dispersal in a sessile marine invertebrate. Ecology 66, 30-39.
- Olson, R.R., Olson, M.H., 1989. Food limitation of planktotrophic marine invertebrate

- larvae: does it control recruitment success? *Annu. Rev. Ecol. Syst.* 20, 225-247.
- Onitsuka, T., Kawamura, T., Horii T., Takiguchi, N., Takami, H., Watanabe, Y., 2007. Synchronized spawning of abalone *Haliotis diversicolor* triggered by typhoon events in Sagami Bay, Japan. *Mar. Ecol. Prog. Ser.* 351, 129-138.
- Pearre Jr., S., 2003. Eat and run? The hunger/satiation hypothesis in vertical migration: history, evidence and consequences. *Biol. Rev.* 78, 1-79.
- Pearse, J.S., 1975. Lunar reproductive rhythms in sea urchins. A review. *J. Interdiscipl. Cycle Res.* 6, 47-52.
- Pedersen, T.M., Hansen, J.L.S., Josefson, A.B., Hansen, B.W., 2008. Mortality through ontogeny of soft-bottom marine invertebrates with planktonic larvae. *J. Mar. Sys.* 73, 185-207.
- Pineda, J., 2000. Linking larval settlement to larval transport: assumptions, potentials, and pitfalls. *Oceanogr. East. Pac.* 1, 84-105.
- Porri, F., McQuaid, C.D., Radloff, S., 2006. Spatio-temporal variability of larval abundance and settlement of *Perna perna*: differential delivery of mussels. *Mar. Ecol. Prog. Ser.* 315, 141-150.
- Queiroga, H., Blanton, J., 2005. Interactions between behaviour and physical forcing in the control of horizontal transport of decapod crustacean larvae. *Adv. Mar. Biol.* 47, 107-214.
- Queiroga, H., Almeida, M.J., Alpuim, T., Flores, A.A.V., Francisco, S., González-Gordillo, I., Miranda, A.I., Silva, I., Paula, J., 2006. Tide and wind control of megalopal supply to estuarine crab populations on the Portuguese west coast. *Mar. Ecol. Prog. Ser.* 307, 21-36.
- R Development Core Team, 2008. *R: A language and environment for statistical*

- computing. R Foundation for Statistical Computing, Vienna.
- Reise, K., 1991. Macrofauna in mud and sand of tropical and temperate tidal flats. In: Elliott, M., Ducrotoy, J.-P. (Eds.), *Estuaries and coasts: Spatial and temporal intercomparisons*. Olsen & Olsen, Fredensborg, pp. 211-216.
- Reitzel, A.M., Miner, B.G., McEdward, L.R., 2004. Relationships between spawning date and larval development time for benthic marine invertebrates: a modeling approach. *Mar. Ecol. Prog. Ser.* 280, 13-23.
- Richmond, R.H., 1987. Energetics, competency, and long-distance dispersal of planula larvae of the coral *Pocillopora damicornis*. *Mar. Biol.* 93, 527-533.
- Rilov, G., Dudas, S.E., Menge, B.A., Grantham, B.A., Lubchenco, J., Schiel, D.R., 2008. The surf zone: a semi-permeable barrier to onshore recruitment of invertebrate larvae? *J. Exp. Mar. Biol. Ecol.* 361, 59-74.
- Rothlisberg, P.C., 1974. Reproduction in *Spirorbis* (*Spirobella*) *marioni* Caullery & Mesnil (Polychaeta: Serpulidae). *J. Exp. Mar. Biol. Ecol.* 15, 285-297.
- Rumrill, S.S., 1990. Natural mortality of marine invertebrate larvae. *Ophelia* 32, 163-198.
- Sasaki, R., Shepherd, S.A., 1995. Larval dispersal and recruitment of *Haliotis discus hannai* and *Tegula* spp. on Miyagi coasts, Japan. *Mar. Freshw. Res.* 46, 519-529.
- Shanks, A.L., 2009. Pelagic larval duration and dispersal distance revisited. *Biol. Bull.* 216, 373-385.
- Shepherd, S.A., Lowe, D., Partington, D., 1992. Studies on southern Australian abalone (genus *Haliotis*) XIII: larval dispersal and recruitment. *J. Exp. Mar. Biol. Ecol.* 164, 247-260.
- Shimoda, K., Aramaki, Y., Nasuda, J., Yokoyama, H., Ishihi, Y., Tamaki, A., 2007. Food

- sources for three species of *Nihonotrypaea* (Decapoda: Thalassinidea: Callianassidae) from western Kyushu, Japan, as determined by carbon and nitrogen stable isotope analysis. J. Exp. Mar. Biol. Ecol. 342, 292-312.
- Shimoyama, S., 1985. Size-frequency distribution of living populations and dead shell assemblages in a marine intertidal sand snail, *Umbonium* (*Suchium*) *moniliferum* (Lamarck), and their palaeoecological significance. Palaeogeogr., Palaeoclimatol., Palaeoecol. 49, 327-353.
- Stephens, S.A., Broekhuizen, N., Macdiarmid, A.B., Lundquist, C.J., McLeod, L., Haskew, R., 2006. Modelling transport of larval New Zealand abalone (*Haliotis iris*) along an open coast. Mar. Freshw. Res. 57, 519-532.
- Strathmann, R.R., 2007. Three functionally distinct kinds of pelagic development. Bull. Mar. Sci. 81, 167-179.
- Suzuki, H., Hirayama, A., Kikuchi, T., Goto, I., Samejima, T., 1982. The bottom current system of Tomioka Bay, west Kyushu. Publ. Amakusa Mar. Biol. Lab., Kyushu Univ. 6, 95-104.
- Systat Software, 2006. SigmaPlot version 10.0. New York.
- Tamaki, A., 1985. Zonation by size in the *Armandia* sp. (Polychaeta: Opheliidae) population on an intertidal sand flat. Mar. Ecol. Prog. Ser. 27, 123-133.
- Tamaki, A., 1987. Comparison of resistivity to transport by wave action in several polychaete species on an intertidal sand flat. Mar. Ecol. Prog. Ser. 37, 181-189.
- Tamaki, A., 1994. Extinction of the trochid gastropod, *Umbonium* (*Suchium*) *moniliferum* (Lamarck), and associated species on an intertidal sandflat. Res. Popul. Ecol. 36, 225-236.
- Tamaki, A., Kikuchi, T., 1983. Spatial arrangement of macrobenthic assemblages on an

- intertidal sand flat, Tomioka Bay, west Kyushu. Publ. Amakusa Mar. Biol. Lab., Kyushu Univ. 7, 41-60.
- Tamaki, A., Mandal, S., Agata, Y., Aoki, I., Suzuki, T., Kanehara, H., Aoshima, T., Fukuda, Y., Tsukamoto, H., Yanagi, T., 2010. Complex vertical migration of larvae of the ghost shrimp, *Nihonotrypaea harmandi*, in inner shelf waters of western Kyushu, Japan. Estuar. Coast. Shelf Sci. 86, 125-136.
- Thorson, G., 1950. Reproductive and larval ecology of marine bottom invertebrates. Biol. Rev. 25, 1-45.
- Todd, C.D., 1998. Larval supply and recruitment of benthic invertebrates: do larvae always disperse as much as we believe? Hydrobiologia 375/376, 1-21.
- Turon, X., Codina, M., Tarjuelo, I., Uriz, M.J., Becerro, M.A., 2000. Mass recruitment of *Ophiothrix fragilis* (Ophiuroidea) on sponges: settlement patterns and post-settlement dynamics. Mar. Ecol. Prog. Ser. 200, 201-212.
- van der Meer, J., Heip, C.H., Herman, P.J.M., Moens, T., van Oevelen, D., 2005. Measuring the flow of energy and matter in marine benthic animal populations. In: Eleftheriou, A., McIntyre, A. (Eds.), Methods for the study of marine benthos, 3rd ed. Blackwell Science, Oxford, pp. 326-407.
- Verdier-Bonnet, C., Carlotti, F., Rey, C., Bhaud, M., 1997. A model of larval dispersion coupling wind-driven currents and vertical larval behaviour: application to the recruitment of the annelid *Owenia fusiformis* in Banyuls Bay, France. Mar. Ecol. Prog. Ser. 160, 217-231.
- Wadachi, K., 1958. Climate of Japan. Tokyodo, Tokyo, 492 pp. (in Japanese).
- Wardiatno, Y., Shimoda, K., Koyama, K., Tamaki, A., 2003. Zonation of congeneric callianassid shrimps, *Nihonotrypaea harmandi* (Bouvier, 1901) and *N. japonica*

- (Ortmann, 1891) (Decapoda: Thalassinidea), on intertidal sandflats in the Ariake-Sound estuarine system, Kyushu, Japan. *Benthos Res.* 58, 51-73.
- Woodin, S.A., 1976. Adult-larval interactions in dense infaunal assemblages: patterns of abundance. *J. Mar. Res.* 34, 25-41.
- Yoshioka, P.M., 1982. Role of planktonic and benthic factors in the population dynamics of the bryozoan *Membranipora membranacea*. *Ecology* 63, 457-468.
- Yoshioka, P.M., 1986. Chaos and recruitment in the bryozoan, *Membranipora membranacea*. *Bull. Mar. Sci.* 39, 408-417.
- Young, C.M., Chia, F.-S., 1987. Abundance and distribution of pelagic larvae as influenced by predation, behavior, and hydrographic factors. In: Giese, A.C., Pearse, J.S., Pearse, V.B. (Eds.), *Reproduction of marine invertebrates*, vol. IX. Blackwell Scientific, Palo Alto, and Boxwood Press, Pacific Grove, CA, pp. 385-463.

Figure captions

Fig. 1. Study area in the estuarine system ranging from Ariake Sound, via Tachibana Bay, to the coastal waters of the East China Sea, western Kyushu, Japan, with contours representing 10-m depth changes. The main intertidal sandflats are indicated in black along the coastline. On the Tomioka sandflat located at the northwestern corner of Amakusa-Shimoshima Island, the collection of *Umbonium moniliferum* juveniles and adults was made along one representative shore-normal transect within a long-term monitoring area of the sandflat during low tide (inset panel; Sections 2.3-2.6 in text). The collection of spawned eggs and larvae was done at the uppermost point of the transect during high tide (Section 2.2). The larval sampling on board the ship and drift-card release (Sections 2.7 and 2.8) were performed off the sandflat within Tomioka Bay lying between Tomioka headland and Tsuji-Shima Island. The retrieval of drift cards was conducted along the upper shoreline indicated in thick line in the inset panel. The wind velocity data were recorded every 10 min at the meteorological observation station run by the Kumamoto Prefecture Government (<http://cyber.pref.kumamoto.jp/bousai/>).

Fig. 2. Laboratory setup for accommodating adults (adult tank), collecting spawned eggs (egg tank), and maintaining embryos and larvae (larval tank) of *Umbonium moniliferum* in running ambient seawater within a large tub (dimension of each component not to scale; Sections 2.9, 2.10, 3.5, and 3.6 in text). Black arrows designate the direction of seawater flow.

Fig. 3. Scatter plots of ripe egg numbers versus shell width in *Umbonium moniliferum* collected from the Tomioka sandflat in 2002. The best-fitted regression equation presented with the superimposed curve is: $No. \text{ eggs} = 2588.98 [1 + 1807.98 \exp (-0.955 \text{ Shell width})]^{-1}$. The two points circled with broken lines were excluded from regression analysis as outliers (Sections 2.5 and 3.1 in text).

Fig. 4. Shell-width-frequency distributions of *Umbonium moniliferum* with fitted normal-distribution curves for the combined samples collected with a 100-cm² corer on 18 August and 29 October 2008 (a) and with a 625-cm² quadrat frame on 3 August 2008 (b) on the Tomioka sandflat. The vertical axis in panel (a) indicates the frequency of individuals for each size class per core. The normal-distribution curve with a broken line in panel (b) is a supposed one for 29 September 2008, as extrapolated from the 3 August curve (solid line), based on the daily individual growth rate and mortality rate for each of the two cohorts, which were derived from panel (a) (Sections 2.6 and 3.2 in text).

Fig. 5. Shell-width-frequency distributions of juveniles of *Umbonium moniliferum* per 200 cm² at Stn 90 along the transect on the Tomioka sandflat during September to October 2008 (Figs. 1 and 6). Note the different scales on the y-axes. A value to the third decimal place was set at the boundary between two adjacent classes. Normal-distribution curves were fitted to the supposed newly recruited cohorts (Sections 2.3 and 3.3 in text).

Fig. 6. Variation in the density of *Umbonium moniliferum* along the transect on the Tomioka sandflat, with a mean and range ($n = 2$) for juveniles on 14 October 2008 (a) and for two different year-cohorts of adults ($n = 1$) on 3 August 2008 (b) (Sections 2.3 and 3.4 in text). The two adult cohorts were separated at a shell width of 10 mm (Fig. 4).

Fig. 7. Variations in seawater temperature (a) and salinity (b) in the water column on the Tomioka sandflat and in the laboratory tank at Nagasaki Prefectural Institute of Fisheries (Fig. 2) during the period of monitoring for spawned eggs, larvae, and juveniles of *Umbonium moniliferum* in 2008. The intermittent missing data in the laboratory record was due to the daily procedure to check for spawned eggs in the adult tank. Smoothing of temperature data was done with a Loess regression (Sections 2.2, 2.9, 3.6, and 3.7 in text).

Fig. 8. Sequential change in the densities of spawned eggs (d) and larvae (e) at the uppermost point of the transect during high tide, and settlers at Stn 90 along the transect during low tide (f) of *Umbonium moniliferum* on the Tomioka sandflat in relation to the variations in tidal height at Stn 230 with lunar phases and spring/neap tides (a), in wind velocity (b), and in the mean \pm SD density (no. of samples beside bars) of spawned eggs in laboratory Larval Rearing Sets 1 and 2 (c) during the period from 2 to 29 October 2008. The seven highest spikes of egg spawning in the field are given serial numbers in order of dates (panel (d)). The settler densities on 26-28 October, indicated as blank columns, were back calculated from the juvenile shell-width-frequency distribution recorded on 29 October (Fig. 5). The dates of the egg spawning corresponding to

those settlers on 26-29 October (cross marks in panel (d)) were estimated based on the shortest PLD (= 3 d; Section 3.5). The tidal height values on 28-29 October were extrapolated from the data measured with the pressure gauge deployed at Stn 230 up to 0:00 on 28 October. See Sections 2.2, 2.3, 2.9, 3.3, 3.4, 3.6, and 3.7 in text.

Fig. 9. Change in the proportion of the number of surviving larvae relative to that of initially fertilized eggs of *Umbonium moniliferum* with the lapse of days in Larval Rearing Sets 1 and 2 combined. The estimated initial egg numbers in Sets 1 and 2 are 1,879,001 and 2,084,461, respectively. The superimposed broken line indicates the regression curve for $2 < \text{Day} \leq 9$ given as an exponential function (Sections 2.9 and 3.6 in text).

Fig. 10. Sequential change in the concentrations of veligers of *Umbonium moniliferum* (no. of larvae 450 l^{-1}) along water depth in the course of eight sets of pump sampling at a station in Tomioka Bay (star mark in inset panel of Fig. 1) conducted for 22 h between 22 and 23 October 2007 (a) and in the weighted mean depth (WMD) of those larvae in the course of diel- and tidal-phase shifts (b) in relation to wind velocity variation (c). The definition of WMD is given in Section 2.7 in text (see also Section 3.8). The WMD values are plotted at the mid-point of the period for each sampling set.

Fig. 11. Cumulative retrieval rates of drift cards released at a station in Tomioka Bay (cross mark in inset panel of Fig. 1; $N = 800$) on 27 October 2009, collected along the upper shoreline (thick line in inset panel of Fig. 1) over the subsequent 17 d (a) in relation to wind velocity variation (b) (Sections 2.8 and 3.9 in text).

Fig. 12. Shell-width-frequency distributions of *Umbonium moniliferum* in the combined samples for each date, which were collected along the transect on the Tomioka sandflat for juveniles every spring tide during the period from October 2002 to February 2003 (a-i) and for adults on 3 April 2003 (j). Normal-distribution curves were fitted to supposed cohorts including the newly recruited ones (a-g). The two cohorts in panel (j) stand for 0+, and 1+ and older, respectively (Sections 2.4 and 3.10 in text).

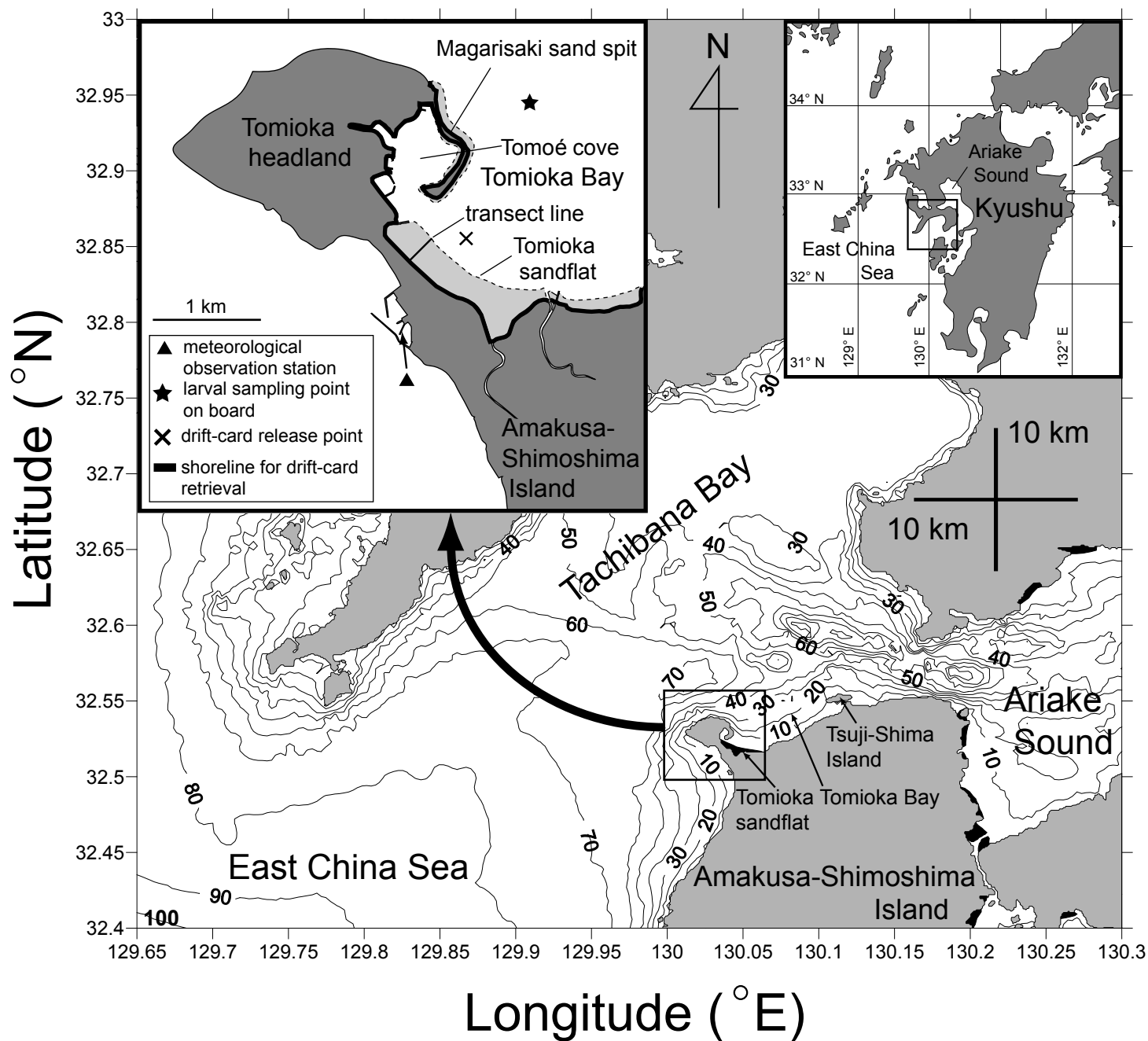


Fig. 1 (S. Mandal *et al.*)

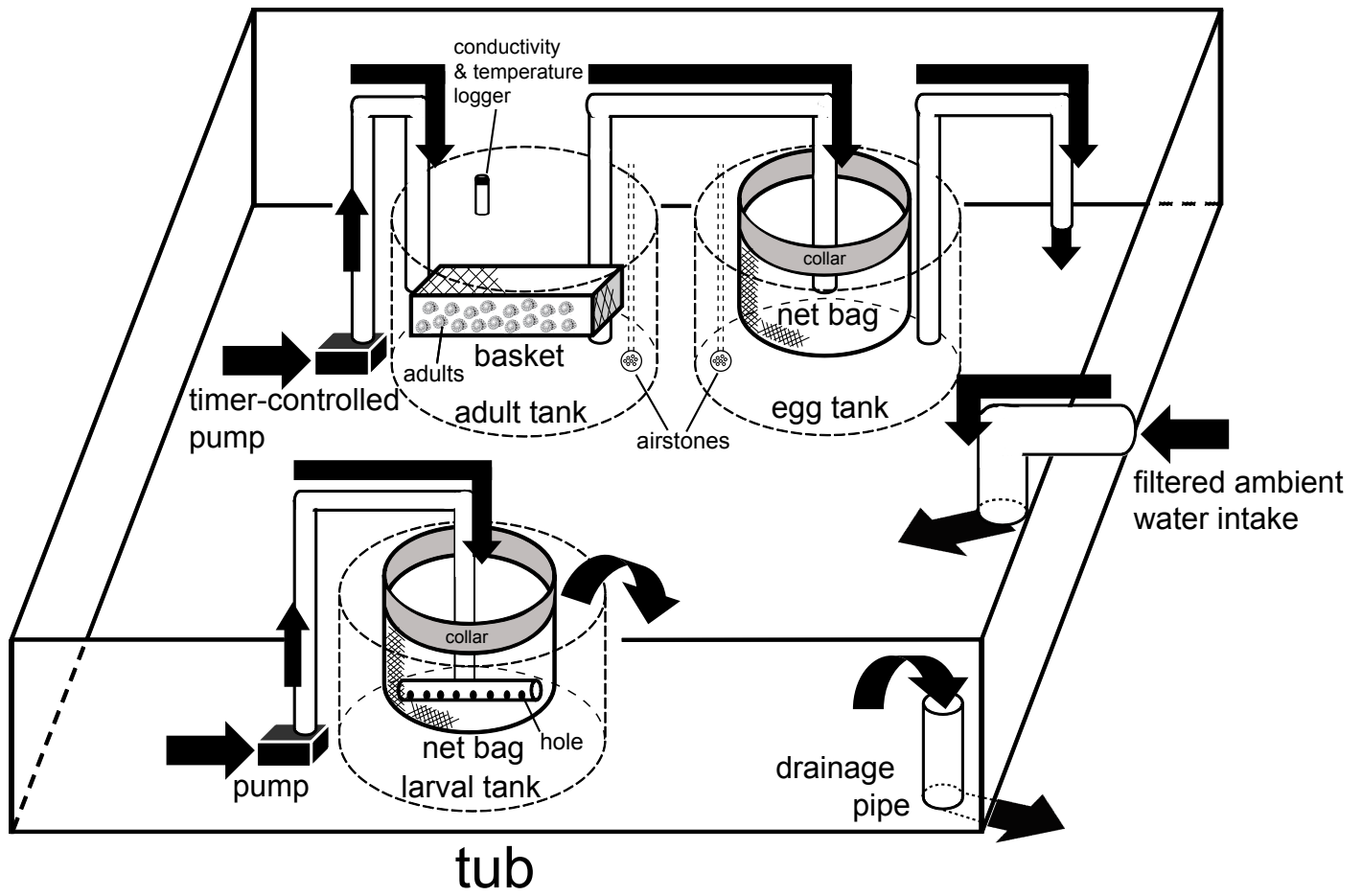


Fig. 2 (S. Mandal *et al.*)

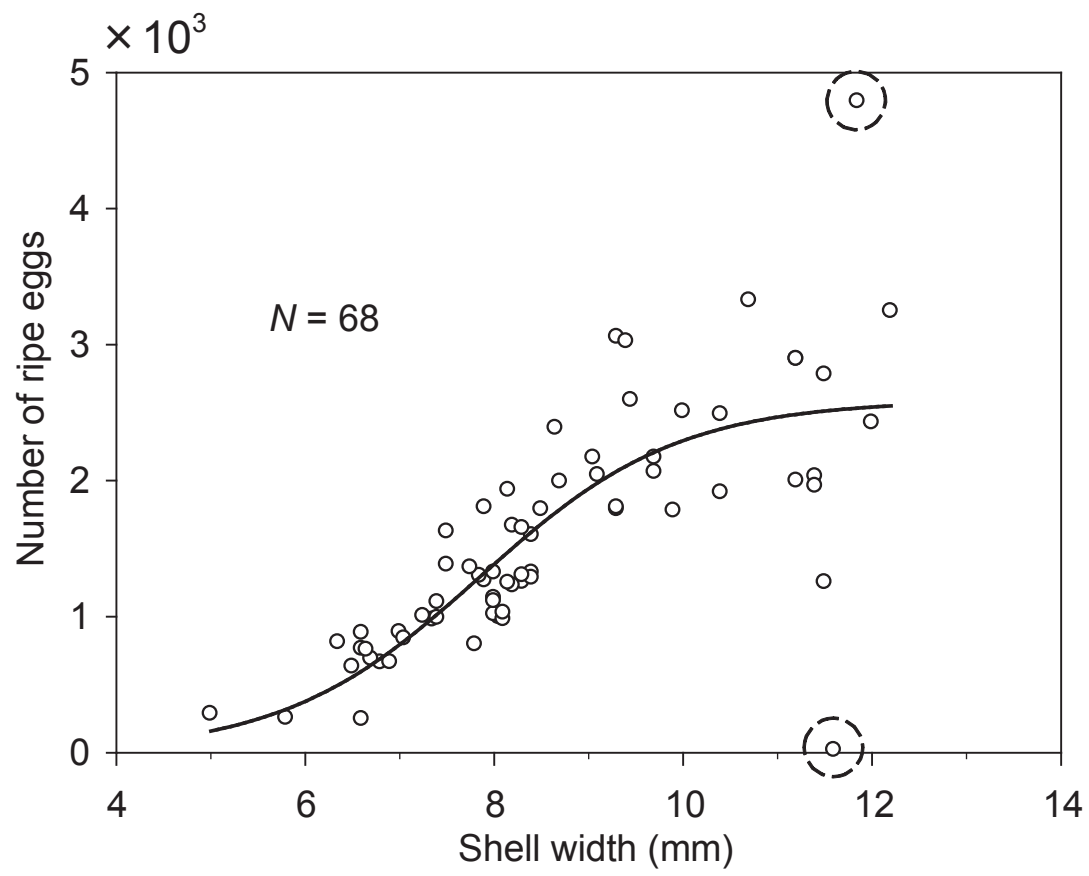


Fig. 3 (S. Mandal *et al.*)

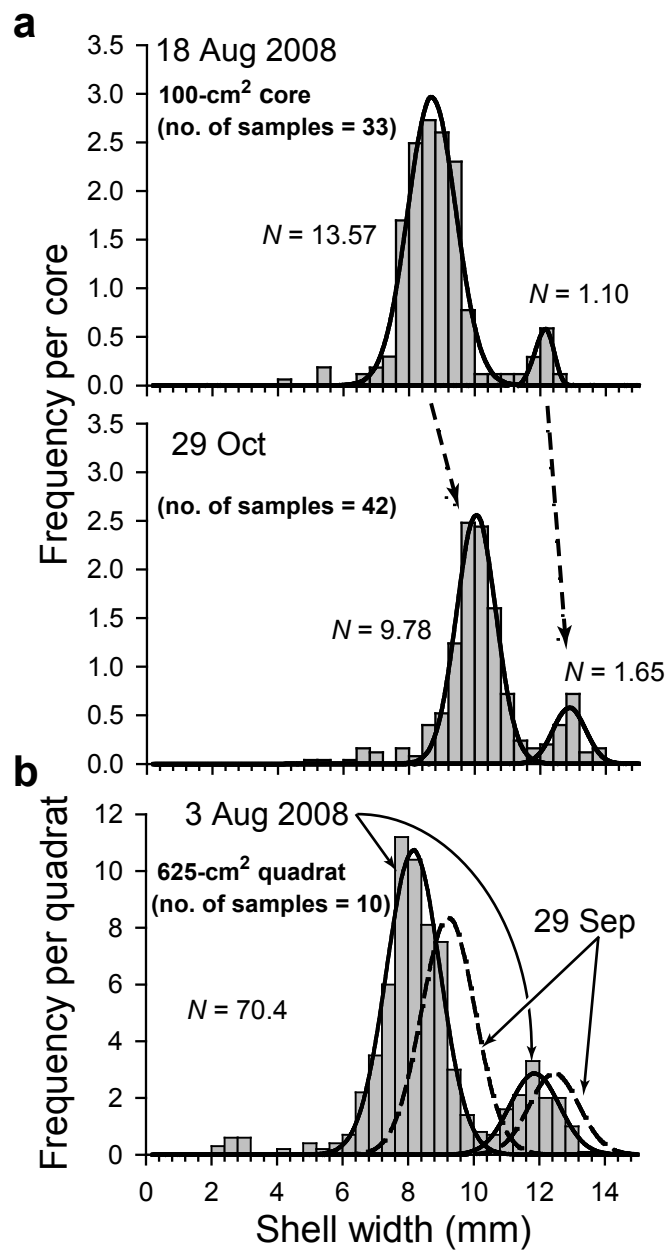


Fig. 4 (S. Mandal *et al.*)

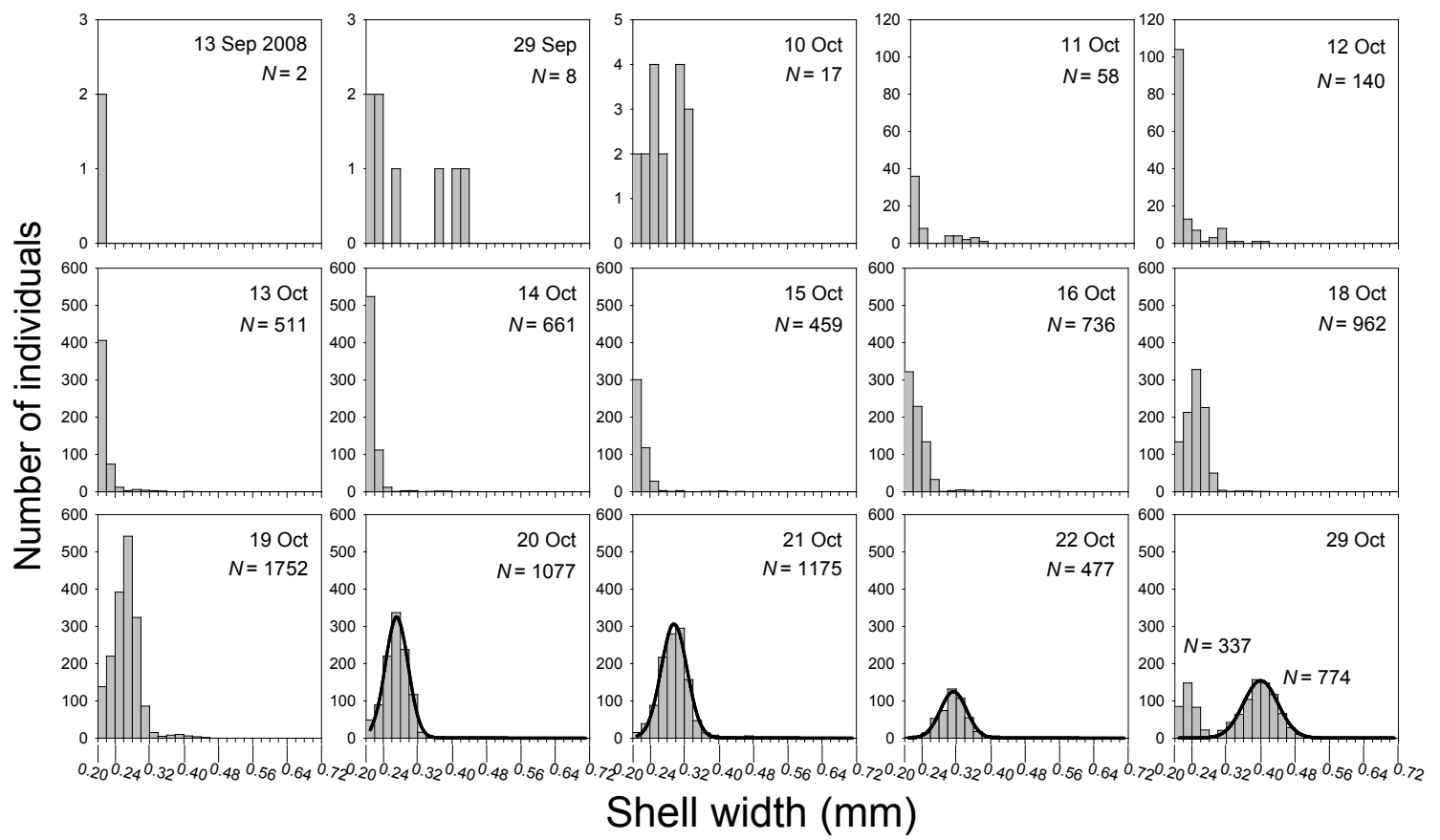


Fig. 5 (S. Mandal et al.)

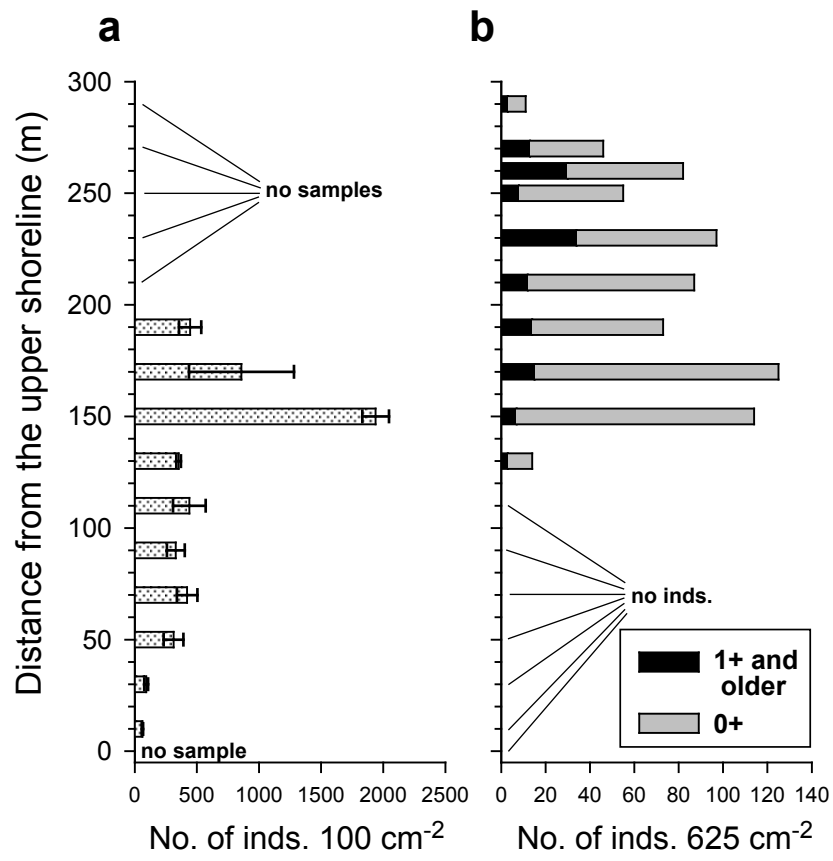


Fig. 6 (S. Mandal et al.)

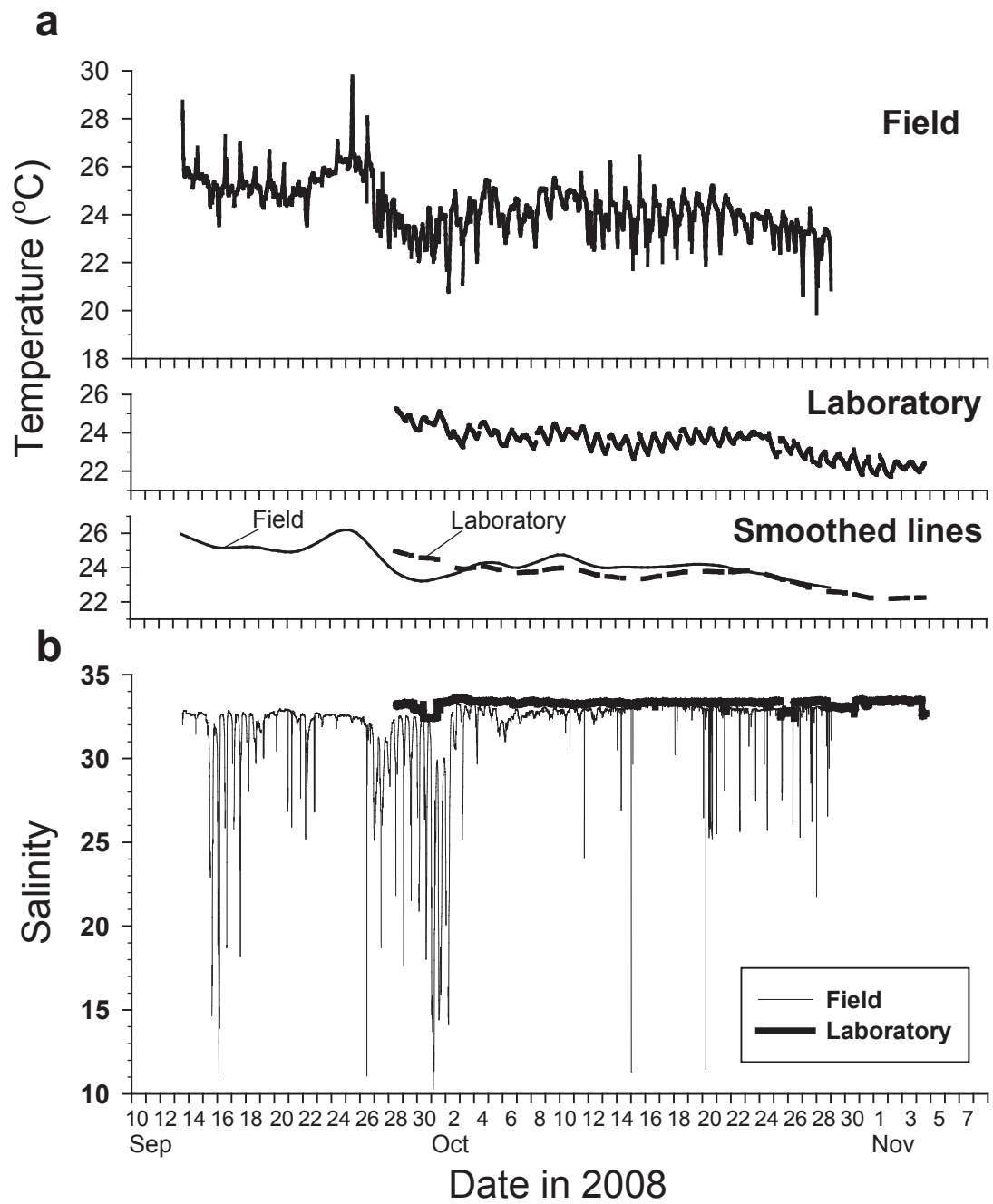


Fig. 7 (S. Mandal *et al.*)

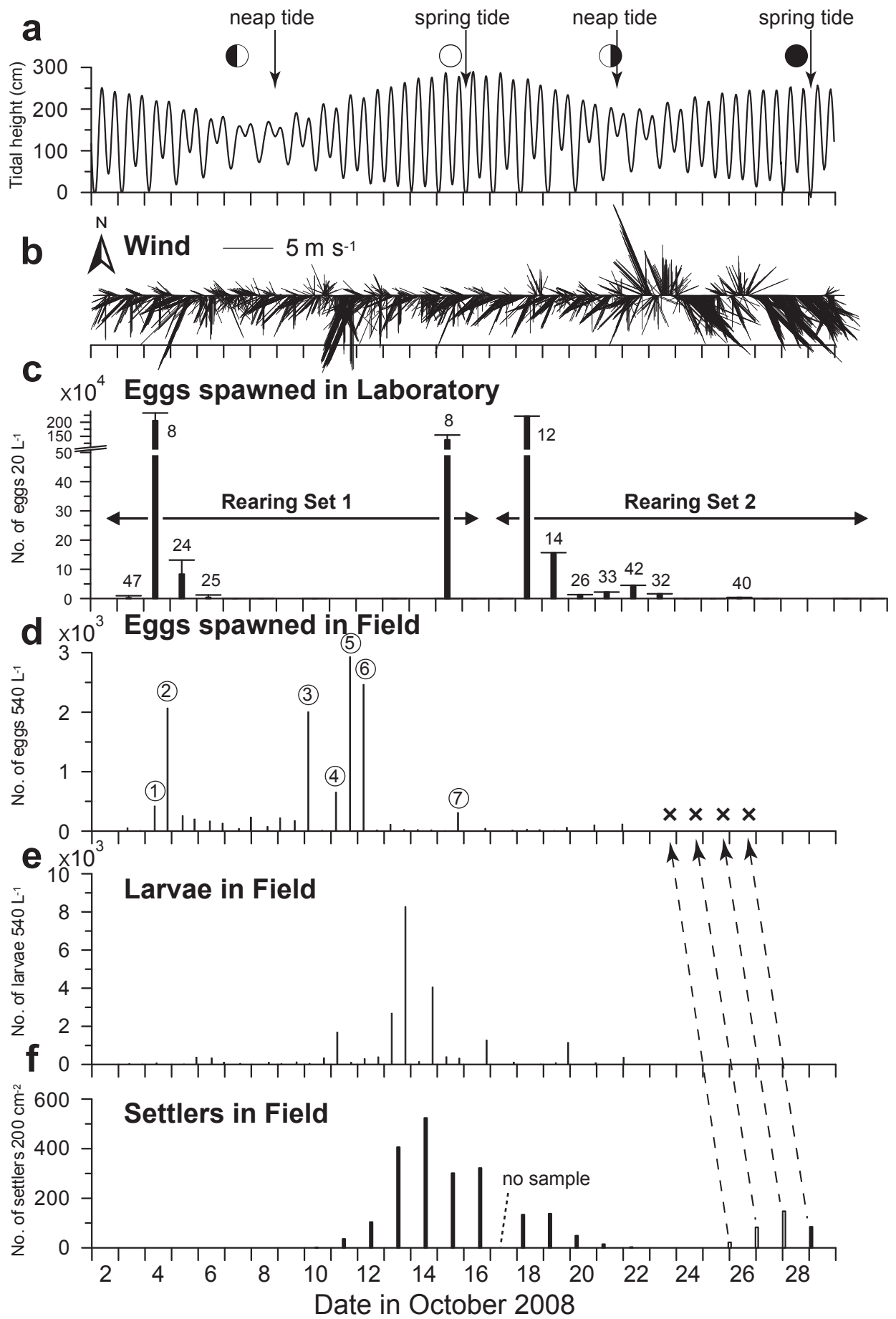


Fig. 8 (S. Mandal *et al.*)

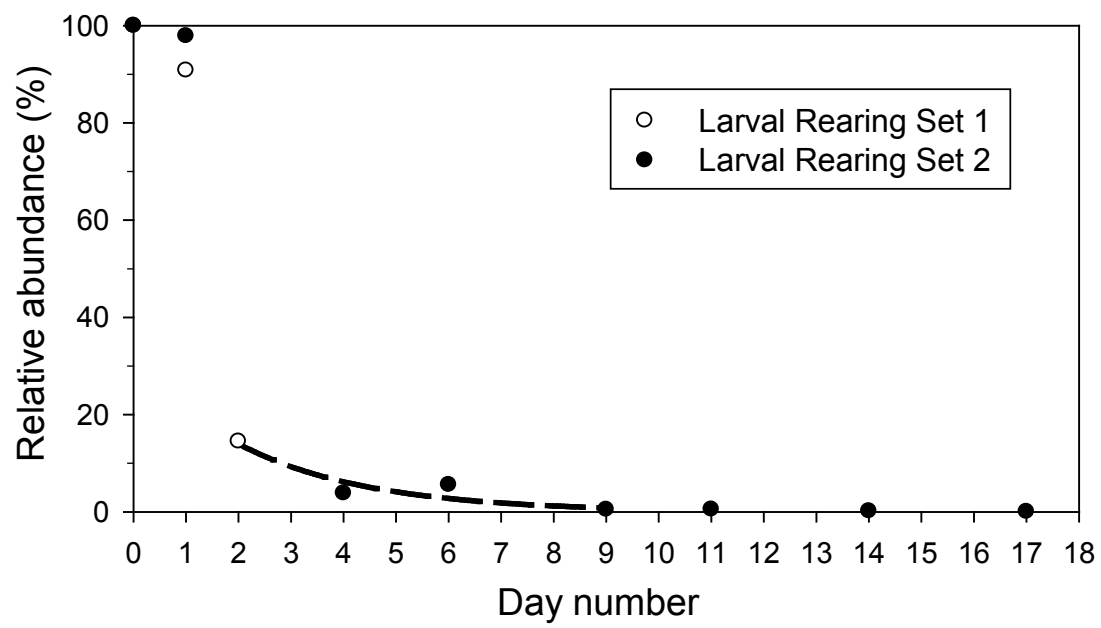


Fig. 9 (S. Mandal *et al.*)

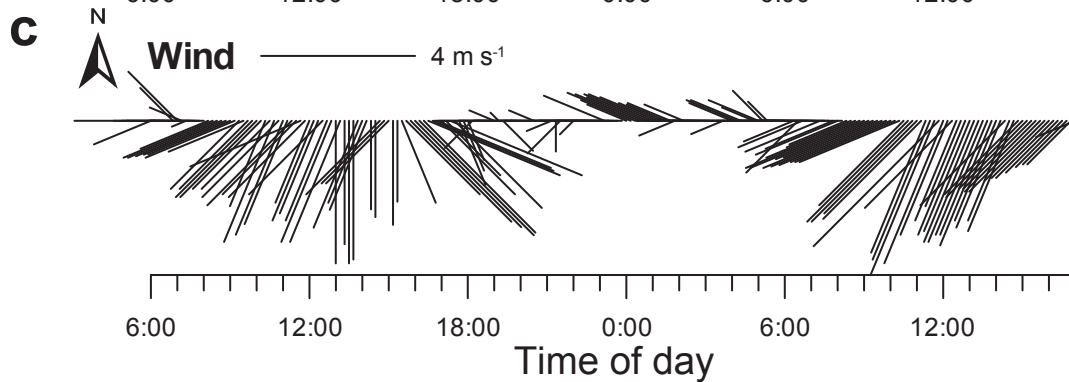
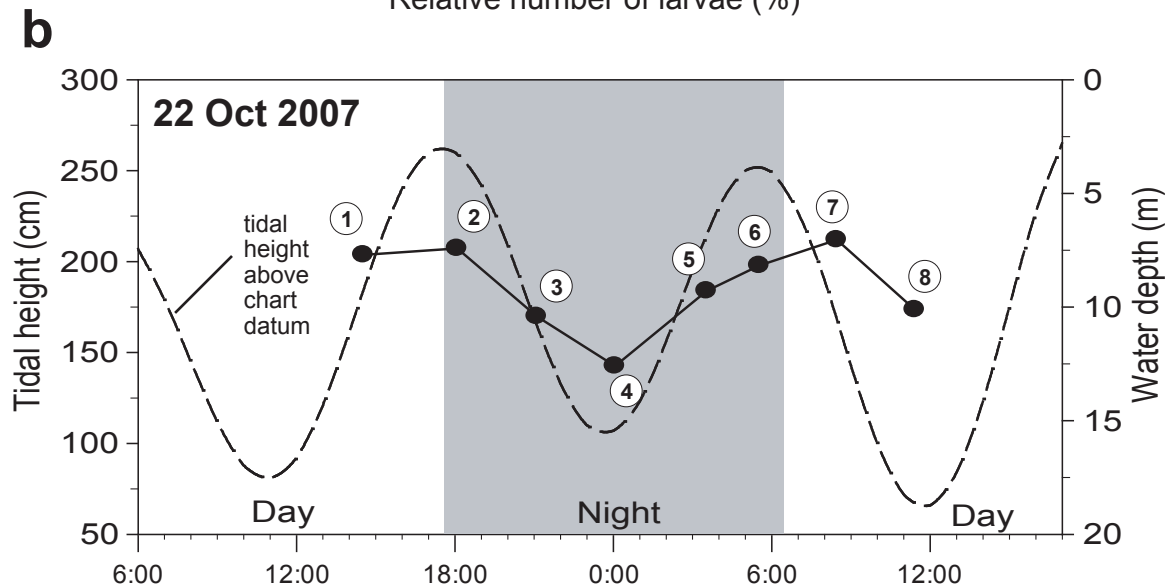
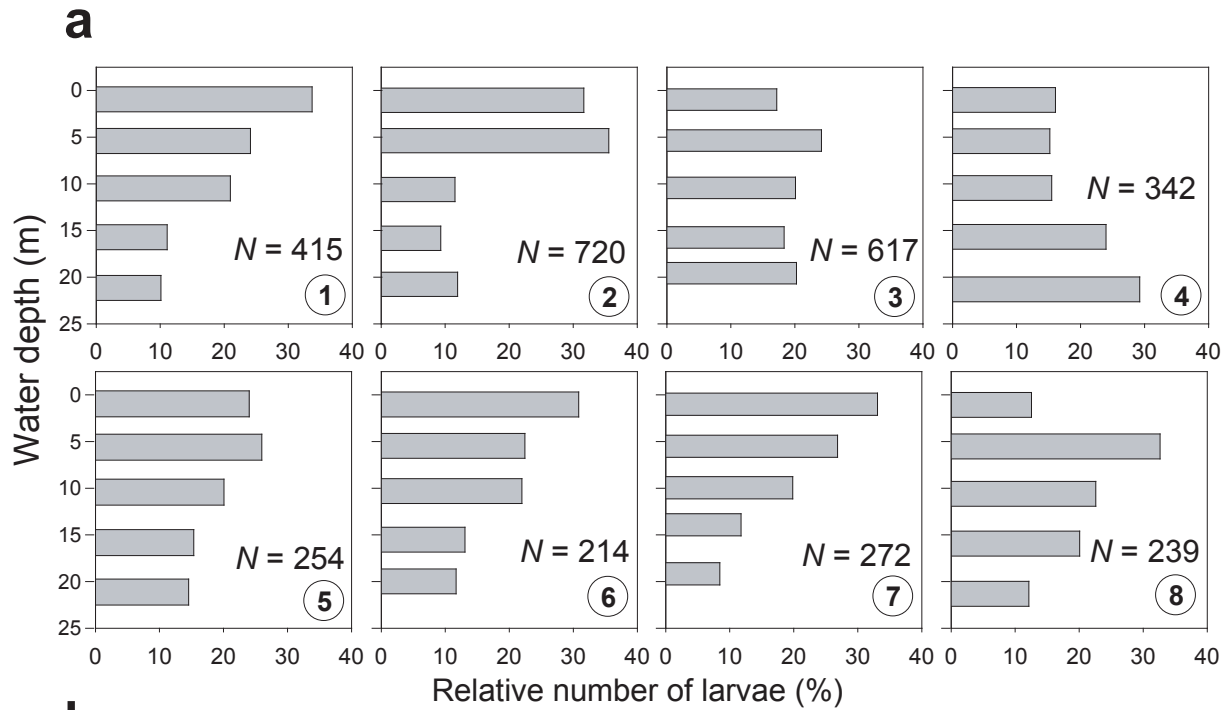


Fig. 10 (S. Mandal *et al.*)

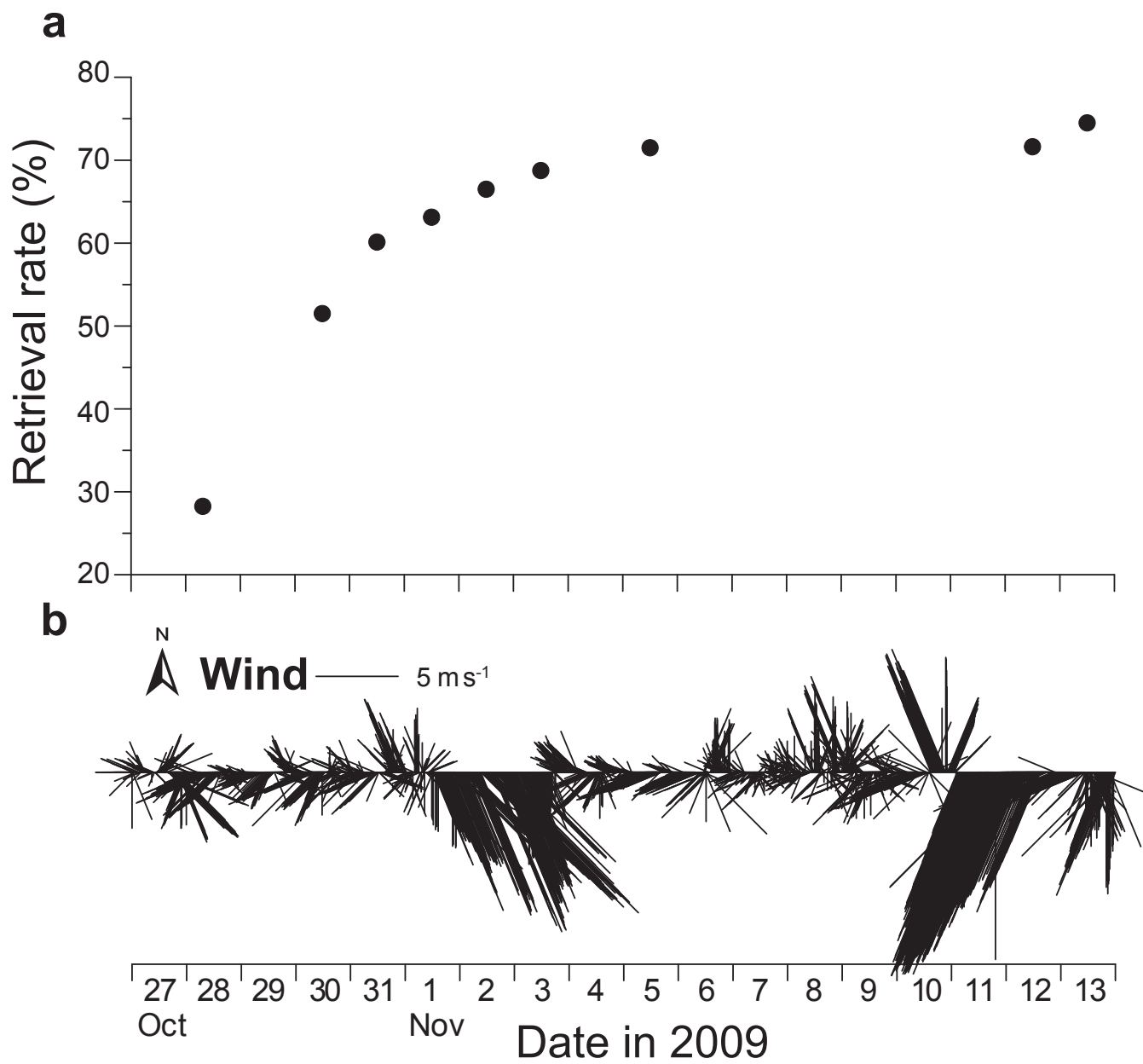


Fig. 11 (S. Mandal *et al.*)

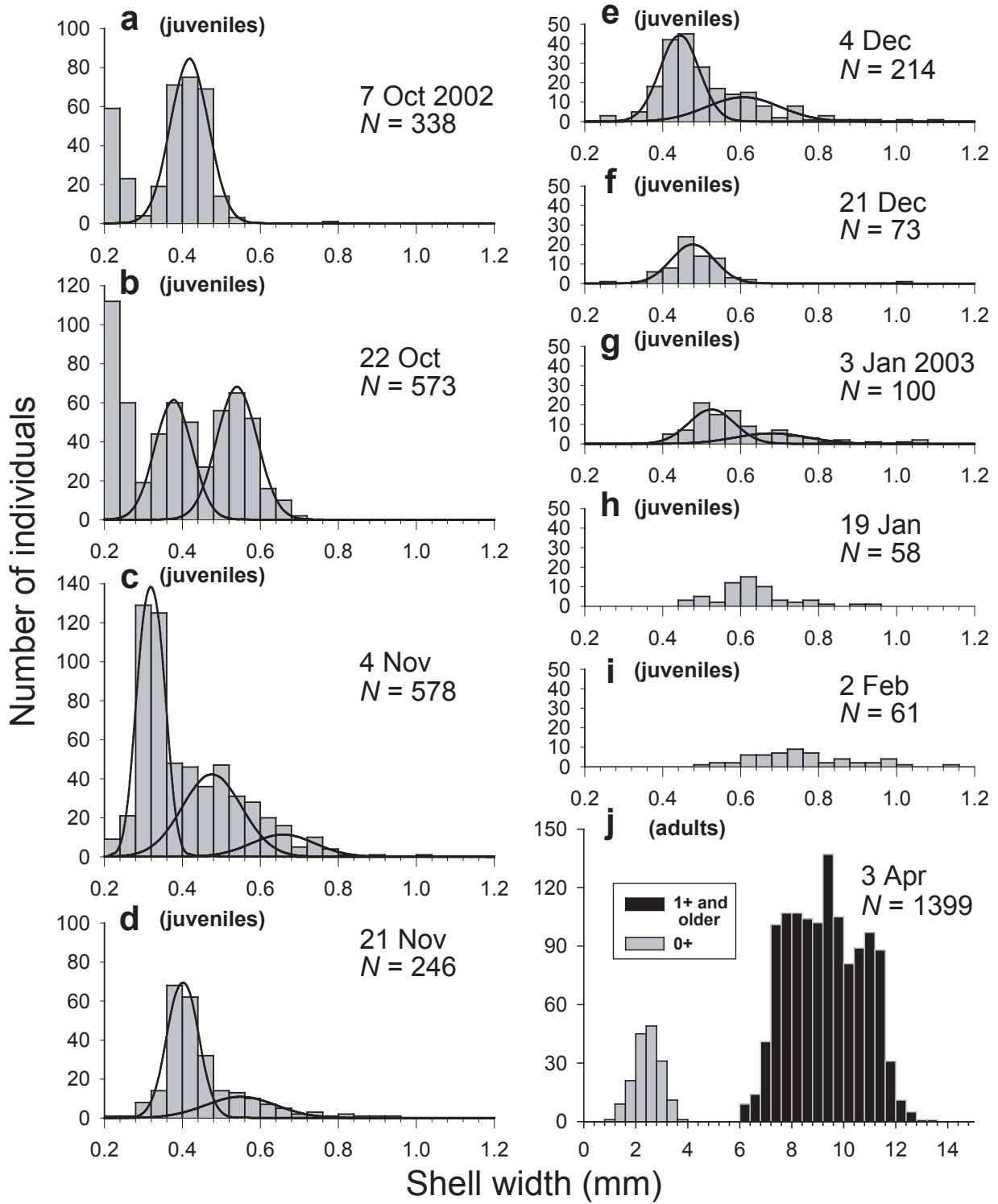


Fig. 12 (S. Mandal *et al.*)

Table 1
Initial growth rates in shell width of *Umbonium moniliferum* for six time intervals in October 2008. The shell-width values are the modes of either the truncated distribution groups composed of the smallest juveniles or the normal-distribution groups forming a newly recruited cohort (Fig. 5).

date in October		shell width (mm)		growth rate (mm d ⁻¹)
initial	final	initial	final	
16	18	0.205	0.245	0.020
18	19	0.245	0.265	0.020
19	20	0.265	0.271	0.006
20	21	0.271	0.296	0.025
21	22	0.296	0.314	0.018
22	29	0.314	0.400	0.012

Table 1 (S. Mandal *et al.*)