

## Life history and population dynamics of the surf clam, *Mactra veneriformis* (Bivalvia: Mactridae), on an estuarine intertidal sandflat in western Kyushu, Japan

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### Abstract

*Mactra veneriformis* occurs commonly on estuarine tidal flats in temperate East Asia. Based on population sampling and recording of environmental variables over an extensive sandflat at a river mouth in Ariake Sound, southern Japan for 39 months, several reproductive traits were monitored and the recruitment, growth, and survivorship for cohorts tracked. The reproductive season ranged from May to September. Each year three to five newly-recruited cohorts appeared in June to October. A single cohort derived from adult spawning in late September occurred in December to January but disappeared by mid-May. Earlier summer recruits reached a maturation size in late September. Each year two or three cohorts survived until next February and fused into a composite cohort. High mortality in juveniles sometimes happened in the rainy period from June to July and at typhoon arrivals in July to October, with increased river discharges. Occasionally juvenile mass mortalities were observed following large wind-induced waves associated with typhoons. Despite their high mortality in the rainy period in some years, the fused adult cohorts contributed solely to the effective reproduction for the entire population. The surviving members of these cohorts died off during the following winter, with an estimated life span of 1.5 years.

**Key words:** reproduction, gonadal development, recruitment, growth, survivorship, wet monsoon, river discharge, typhoon, mass mortality, Ariake Sound

### Introduction

The surf clam, *Mactra veneriformis* Deshayes (Reeve, 1854), is a suspension-feeding infaunal bivalve commonly distributed on estuarine tidal flats along the coastline of temperate East Asia, ranging from the northern Japan Sea (Okutani *et al.* 2000), through the Yellow Sea (Chung and Ryou 2000), to the middle of the East China Sea (Hou *et al.* 2006). In Japanese waters, it occurs from northern Honshu Island to the Shikoku and Kyushu Islands (Okutani *et al.* 2000; Koga *et al.* 2005) and is one of the dominant species of the benthic community on tidal flats in large estuaries such as Tokyo Bay (Hiwatari *et al.* 2002), Ise Bay in central Honshu (Nanbu *et al.* 2006), and Ariake Sound in western Kyushu (Tamaki *et al.* 2008). Various biological or ecological traits of *M. veneriformis* have been investigated, including population genetic structure (Hou *et al.* 2006), reproduction (Iwata 1948; Chung *et al.* 1988; Chung and Ryou 2000), trematode infection (Han and Chai 2008), larval development (Hur *et al.* 2005), coupling of larval and juvenile abundances (Nanbu *et al.* 2006), recruitment, individual growth, and survivorship (Kim and Ryou 1991; Ryou and Chung 1995; Ryou 1997), food sources (Kasai *et al.* 2004; Yokoyama *et al.* 2005), body biochemical compositions (Shiraishi 2006), assimilation efficiency and benthic-pelagic coupling for nitrogen budget (Hiwatari *et al.* 2002), influences of water turbidity on survival (Chang and Chin 1978; Ahn and Choi 1998), and the effect of water salinity on burrowing, feeding, and growth (Nakamura *et al.* 2005). Of these studies, those related to population dynamics

have previously concentrated mostly on the west coast population in South Korea facing the Yellow Sea, in particular in tidal flats around Kunsan.

On an extensive intertidal sandflat located at the mouth of Shirakawa River emptying into the central part of Ariake Sound (Fig. 1; hereafter called Shirakawa sandflat), *M. veneriformis* is one of the dominant species of the benthic community, along with the venerid clam, *Ruditapes philippinarum* (Adams & Reeve, 1850), and two species of thalassinidean shrimp, *Nihonotrypaea japonica* (Ortmann, 1891) and *Upogebia major* (De Haan, 1841) (Tamaki *et al.* 2008). In summer 2004, *M. veneriformis* had the greatest population biomass of the four species over a 3.4 km<sup>2</sup> area of the sandflat, with their total estimated wet weights (without shell) being 378, 234, 304, and 111 metric tons, respectively. The single food source for these species was identified as phytoplankton, using carbon and nitrogen stable isotope analysis on the trophic structure of the benthic community (Yokoyama *et al.* 2005). They may also compete for space, partitioning the entire sandflat area by one fourth each (Tamaki *et al.* 2008). Thus the acquisition of information on life history and population dynamics of *M. veneriformis* together with possible factors regulating them would be an indispensable step toward the understanding of community structure and ecosystem functions regulated by the four dominant species of the same feeding guild in Ariake Sound. However, an integral study concerning life history and population of *M. veneriformis* in Japanese waters has yet to be conducted.

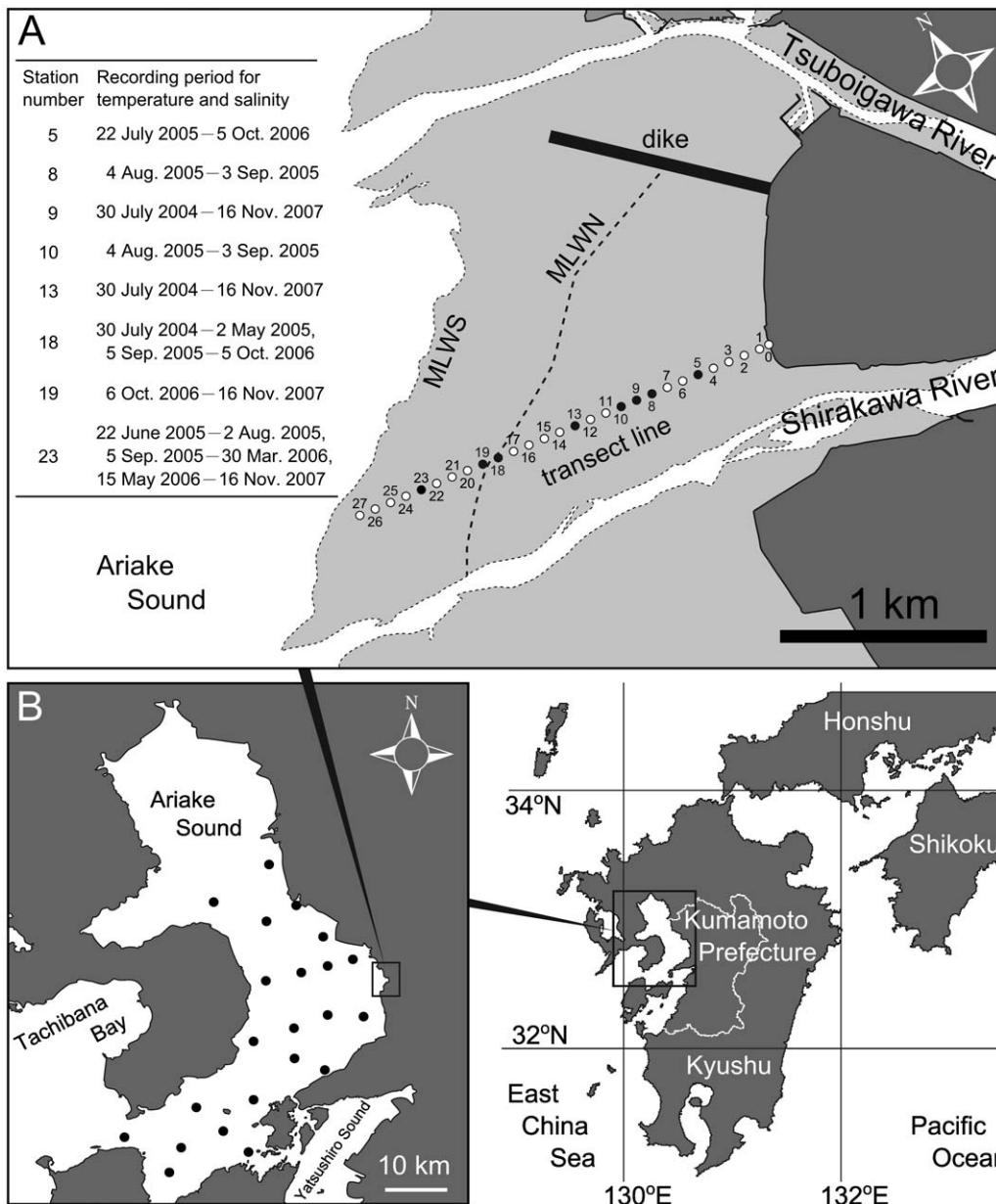
The objective of the present study is (1) to reveal the life history and population dynamics of *M. veneriformis* on the Shirakawa sandflat in relation to major environmental variables by determining the reproductive season and maturation stages based on histological analysis and by tracking recruitment, individual growth, and survivorship of multiple cohorts for over three years and (2) to compare the above traits with those reported for other conspecific populations.

**Materials and methods**

**Study site**

The Shirakawa sandflat is located between the Shirakawa and Tsuboigawa River mouths on the eastern part

of central Ariake Sound (130.60°E and 32.79°N; Fig. 1). The maximum distance from uppermost shore to lowest tide line is 2.7 km and the total area is 3.4 km<sup>2</sup> (from the dyke toward Shirakawa River). Ariake Sound is under a semi-diurnal tidal regime, with tidal amplitudes averaging 3.9 m and 2.0 m at spring and neap tides, respectively. The population of *M. veneriformis* is distributed widely on the sandflat, with its center zone situated at around the mean low water neap tide level (MLWN) and running parallel to the lowest tide line (Tamaki *et al.* 2008). One representative cross-shore transect line was established (Line B in fig. 1 in Tamaki *et al.* 2008; total length, 2130 m) across the center of the clam distribution zone, on which 28 stations (Stn 0 to Stn 27 from uppermost shore seaward) were placed at an interval of 80 m, except for 50 m between Stn 0 and Stn 1.



**FIGURE 1** Study area in Ariake Sound, western Kyushu, Japan. **A.** Light gray area stands for tidal flats in and around the Shirakawa sandflat situated between Shirakawa and Tsuboigawa River mouths. MLWS—mean low water spring tide level. MLWN—mean low water neap tide level. The collection of *Macra veneriformis* specimens and the recording of water temperature and salinity were conducted at stations along the transect line (Stn 0 to Stn 27 for clam collection; eight stations with solid circles for temperature and salinity recording, with the inset table showing periods for each station). **B.** Twenty-two stations with solid circles in Ariake Sound for monitoring of variables in the water column including temperature and chlorophyll a concentration. The monitoring has been conducted once a month by Kumamoto Prefecture Government.

#### Environmental variables in and around the sandflat

Water temperature and salinity (expressed as practical salinity unit) 30 cm above the sandflat surface were automatically recorded every 10 min using a data logger (Compact-CT, JFE Advantech Inc., Japan) at eight stations placed widely on the transect line during 30 July 2004 to 16 November 2007 (Fig. 1A). Instrument retrieval and re-installation was accomplished generally within 1 day. Fouling organisms that had attached to the sensor were removed between consecutive retrieval dates when necessary. Daily averaged values over all stations were calculated based on data recorded when each instrument sensor was submerged. In Japan, there is a rainy (or wet monsoon) period occurring usually between early June and late July, and a typhoon period most frequently between August and October. These two large meteorological events are the major cause for water salinity reductions on the tidal flats of Ariake Sound, as the amount of river discharges increase following heavy rain (Yamada *et al.* 2009, 2012). Typhoons can also generate large wind-induced waves that scour the sandflat sediment (Yamada *et al.* 2007). The records of these two events are available from Japan Meteorological Agency (<http://www.jma.go.jp/jma/index.html> [Accessed on 1 March 2012]).

As the sole food source for *M. veneriformis* was estimated to be phytoplankton (Yokoyama *et al.* 2005), chlorophyll *a* concentration at 0.5 m depth of the water column in Ariake Sound was regarded as a proxy for food abundance. The sampling of water was conducted monthly by Kumamoto Prefecture Government (around daylight high tide of spring tides) at 22 stations scattered over the lower two-thirds of the sound (Fig. 1B). The data for the period from 15 July 2004 to 11 November 2007 was available from Japan Fisheries Resource Conservation Association (<http://ay.fish-jfrca.jp/ariake/i/index.html> [Accessed on 1 March 2012]). This data source was also used to show water temperature variations with which planktonic larvae of *M. veneriformis* were encountered (depths: 0, 0.5, 10, 20, 30 m, and 1 m above bottom). For both variables, averaged values over all stations (and entire water column in the case of temperature) were calculated for each monitoring occasion.

#### Histological observation of gonads

*Macra veneriformis* is a dioecious species. Histological analysis of gonads was conducted using clams over approximately 25 mm in shell length, following the findings that half the population in Kunsan, South Korea became mature at 26.1 mm shell length (Chung and Ryou 2000). The field sampling was carried out along the transect line (Fig. 1A) once or twice a month during 11 December 2004 to 25 May 2006, with 41 or 42 clams fixed with 10% neutralized formalin solution on each occasion. A piece of gonadal tissue (a cube approximately 5–10 mm on each side) was cut off from the rear part of visceral mass. The tissue fragment was dehydrated with a series of ethyl alcohol solutions, penetrated with a xylene solution, embedded into paraffin, sliced every 4  $\mu$ m, and stained with hematoxylin and eosin. The sex and the developmental stage of each

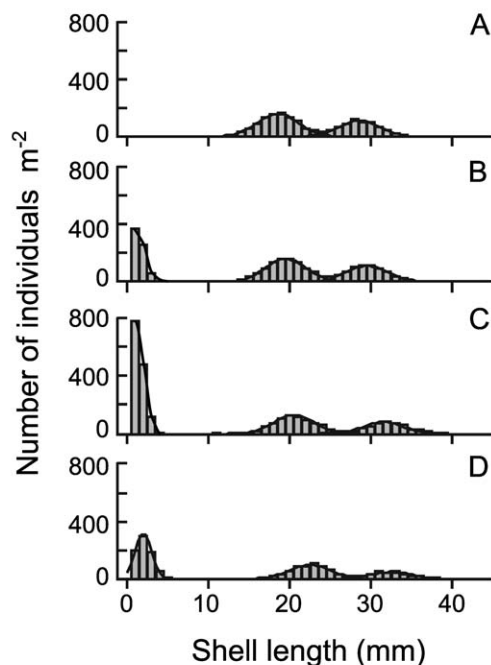
gonad were examined under an optical microscope and photographed (Olympus SP-350;  $\times 600$ ). The assignment of gonadal stages basically followed the scheme for *M. veneriformis* given in Chung *et al.* (1988) and Chung and Ryou (2000), with some modifications (see the Discussion): Pre-developmental (stage I), Follicular (stage II), Growing (stage III), Mature (stage IV), Spawning (stage V), Post-spawning (stage VI), and Degenerating (stage VII). The gonadal stage-frequency distributions were made for each sampling occasion. To examine the relationship between gonadal stage and shell length over a full size range of clams including those not covered above, smaller-sized specimens (11–30 mm shell lengths) were collected for additional histological analysis on three occasions in the reproductive season of 2005 ( $n = 18, 37,$  and  $20$  on 9 May, 22 August, and 18 September, respectively).

#### Population cohort analysis

To obtain data concerning individual growth rates and survival rates for multiple cohorts of the *M. veneriformis* population from the sandflat, a total of 42 sampling occasions were set in the period from 30 July 2004 to 26 October 2007, mostly on a monthly basis and sometimes fortnightly. Each sampling was performed during daylight low tide of spring tides. The sampling stations were placed widely on the transect line so as to cover the spatial variation in population cohort structure (Tamaki *et al.* 2008). The number of stations per sampling date varied from 15 to 28 (Fig. 1A). The lower numbers of stations were from those visited in winter, when the daylight maximum low tide is limited to around the MLWN line in this region. At each station, one to four sediment samples were separately excavated from a 25  $\times$  25 cm quadrat frame to a depth of 7 cm (maximum depth inhabited by adult clams; T. Nakano and A. Tamaki, unpublished data), sieved through a 1 mm mesh sieve, and fixed with 10% neutralized formalin solution. On any one date, the number of samples per station was the same for all stations. In the laboratory, all clams were sorted and their shell lengths measured to 0.01 mm using a digital caliper (Mitutoyo Co., Japan) for those  $\geq 5$  mm or using a stereomicroscope equipped with digital camera system (Leica, DFC 280;  $\times 8$ ) for those  $< 5$  mm. The specimens of the latter group were photographed, imported to a computer, and measured for shell length using open-access software, Image J 1.36b.

The shell-length-frequency distribution was made for each sampling occasion (range, 0.5 to 45.0 mm; size-class interval, 1 mm), with the number of individuals converted into population density (number per  $m^2$ ). In the present study, the initial date of any one recruitment event is defined as the sampling date when individuals of the smallest size class appeared for the first time (Fig. 2A, B). With time, the number of individuals of this size class should reduce due to mortality or growth to a larger size class, or increase due to continued recruitment (Fig. 2B, C). The date of completion of this recruitment event is defined as the sampling date after which the number of individuals of the smallest size class no

longer increased and steadily decreased (Fig. 2C, D). Following Aizawa and Takiguchi (1999), multiple normal-distribution curves were fitted to the entire size-frequency distribution for cohort separation. Each component normal-distribution group was regarded as one cohort, for which mean shell length and density were determined. These two parameters were used to estimate individual growth rates and survival rates. When the most left-hand group in the size-frequency distribution, including the smallest size class, showed a sign of continued recruitment, as is often evident from a truncated size-frequency distribution (Mandal *et al.* 2010), a curve simply connecting the frequency values was drawn instead of a normal-distribution curve (Fig 2B, C). For this incomplete cohort, the median value was used instead of the mean in shell length and its density was determined. The life span of a cohort was defined as the period from the date of recruitment completion to the final date of existence.



**FIGURE 2** Change in shell-length-frequency distributions with time for a putative clam population. Normal-distribution curves representing cohorts are fitted to two larger size-class groups. **A.** date with adult clams only. **B.** date with the first occurrence of a recruitment event, with the most left-hand cohort composed of a truncated size-frequency distribution. **C.** date with continued recruitment. **D.** date with the completion of this recruitment event.

Regression models describing individual growth and survivorship

To make an individual-growth curve for each cohort of *M. veneriformis*, the following three model equations were fitted to plots of mean shell length ( $y$ ) against cumulative day ( $t$ ). The starting date (Day 1) was defined as the date of recruitment completion (Fig. 2D).

Gompertz model:  $y = L_{\infty} \exp(-Ce^{-Kt})$ ,

Logistic model:  $y = L_{\infty} / (1 + e^{-K(t-C)})$ ,

von Bertalanffy model:  $y = L_{\infty} (1 - e^{-K(t-t_0)})$ .

Here,  $L_{\infty}$  is shell length on  $t = \infty$ , standing for a theoretical maximum shell length.  $K$  and  $C$  are a growth rate constant and a date of the inflection point, respectively. The latter parameter designates the date showing either the highest growth rate for a sigmoidal-type growth curve or the start of growth for a non-sigmoidal-type curve (Matsuishi *et al.* 1995). The parameter  $t_0$  is a retrospective time interval that has elapsed from Day 1 back to a date with putative 0 mm shell length ( $t_0 < 1$ ).

To make survivorship curves in terms of density or survival rate for each cohort, three model equations (Gompertz, Logistic, and Asymptotic exponential models) were fitted to plots of population density or survival rate ( $y$ ) against cumulative day ( $t$ ). For each cohort, the survival rate on each sampling date was defined as the population density relative to that on Day 1 (for the three adult cohorts on 30 July 2004, relative to respective initial densities on that date; see Fig. 7). The equation forms of Gompertz and Logistic models were the same as above, and Asymptotic exponential model was as follows:

Asymptotic exponential model:  $y = a (\exp(-e^b))^t + c$ .

The best-fit model selection was based on the smallest value of Akaike's Information Criterion (AIC) (Bozdogan 1987). However, linear regressions were applied to cohorts with the number ( $n$ ) of sampling occasions  $\leq 3$ . Furthermore, there were several cases in which linear regressions were adopted for cohorts with  $n \geq 4$  owing to smaller AIC values than those of the non-linear regressions. All regressions were carried out using R (R Development Core Team 2010).

## Results

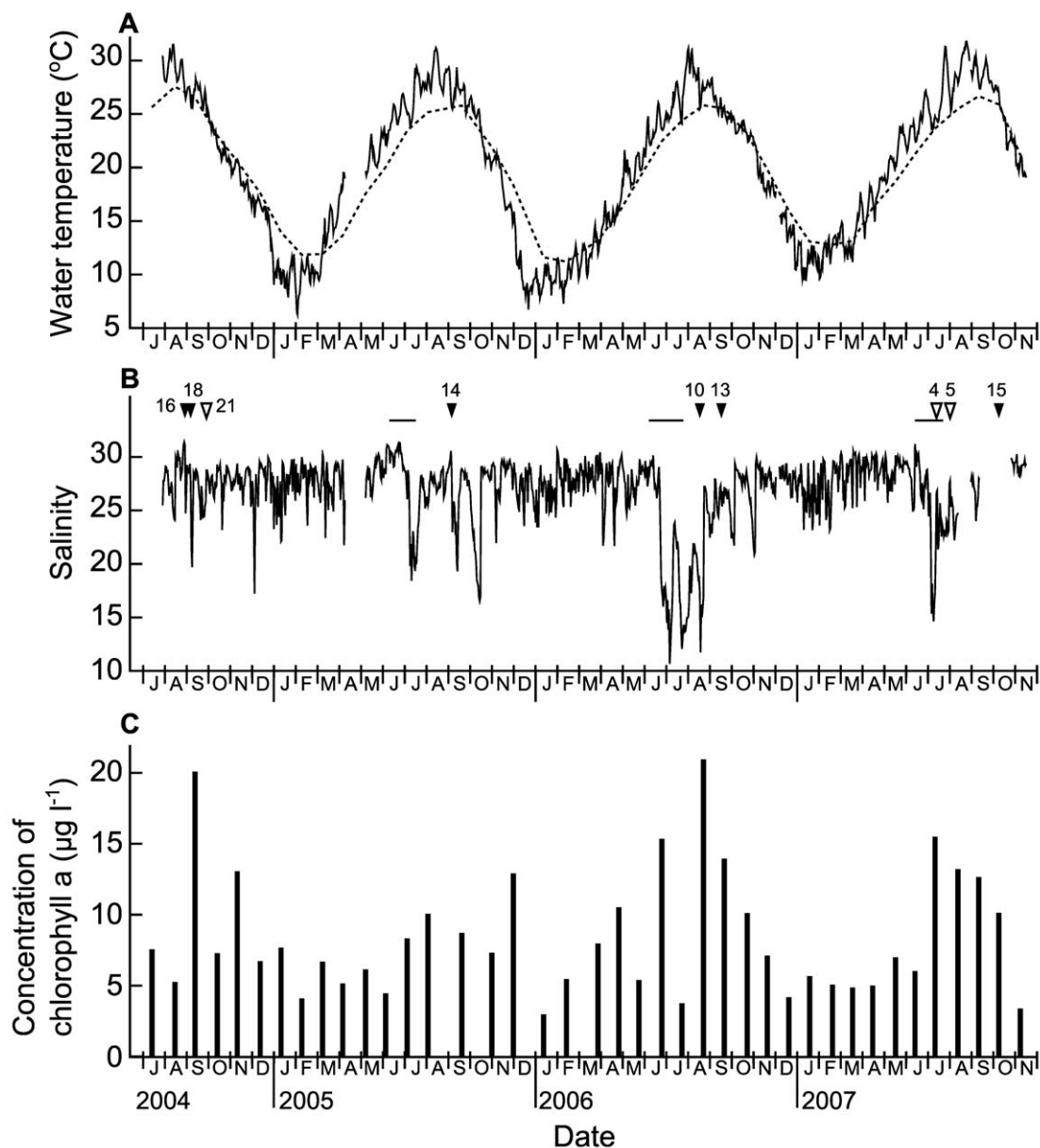
Environmental variables in and around the sandflat

The daily-averaged water temperature and salinity at 30 cm above the sandflat surface throughout the study period are shown in Figs 3A (solid line) and 3B, respectively. Water temperature varied between 6.3 and 31.8°C. The lowest and highest values were recorded in January–March and July–August, respectively. The rainy periods registered by Japan Meteorological Agency were 10 June–17 July in 2005, 8 June–26 July in 2006, and 13 June–23 July in 2007 (horizontal bars in Fig. 3B; the period in 2004 is not shown as it was over by the initial clam sampling date). Typhoons passed across Ariake Sound on 30 August and 7 September 2004 (serial numbers 16 and 18 of the year, registered by Japan Meteorological Agency; solid triangles in Fig. 3B), 6 September 2005 (no. 14), 18 August and 17 September 2006 (nos. 10 and 13), and 9 October 2007 (no. 15), and across the mainland of Kyushu on 29 September 2004 (no. 21; blank triangles) and 14 July and 2 August 2007 (nos. 4 and 5). Salinity ranged from 10.7 to 31.4, usually lying between 25 and 30. Salinity began to decrease in June, remaining unstable until as late as October. For two periods in 2007 (portions of August and September–October), salinity

records indicated extraordinary values, most probably due to fouling organisms on the sensors, and these data are omitted from the averages in Fig. 3B; the temperature sensors remained operative. The lowest salinities, of below 20, were observed during the rainy period or at the time of typhoon arrivals. In particular, both lowest salinities and longest low-salinity period were recorded during June to August of 2006, when the greatest discharges from Shirakawa River occurred (Yamada *et al.* 2012).

The averaged water temperatures through the water column over the lower two-thirds of Ariake Sound were 17.6°C (December)–27.6°C (August) in 2004, 11.8°C

(February)–25.8°C (September) in 2005, 11.2°C (February)–25.8°C (August) in 2006, and 12.8°C (February)–26.7°C (September) in 2007 (Fig. 3A, broken line). The averaged chlorophyll a concentrations at 0.5 m depth of the water column reached the highest values of 20.1, 19.5, and 15.0  $\mu\text{g l}^{-1}$  between July and September in 2004, 2006, and 2007, respectively (Fig. 3C). In 2005, it was 13.0  $\mu\text{g l}^{-1}$  recorded in December. The lowest values of the year were 4.1, 3.0, and 3.4  $\mu\text{g l}^{-1}$  recorded between December and February in 2005, 2006, and 2007, respectively, except for 5.3  $\mu\text{g l}^{-1}$  in August, 2004.



**FIGURE 3** Environmental variables in and around the Shirakawa sandflat during the study period. **A.** Solid line: daily water temperatures 30 cm above the sandflat averaged over eight stations on the transect line (Fig. 1A). Blank parts correspond to periods between data-logger retrieval and re-installation. Broken line: monthly temperatures in the water column of Ariake Sound averaged over 22 stations (Fig. 1B). **B.** Daily water salinities 30 cm above the sandflat averaged over eight stations on the transect line, with horizontal bars and triangles indicating rainy periods and typhoon arrivals during 2004 to 2007 registered by Japan Meteorological Agency (solid and blank triangles: typhoons passing across Ariake Sound and the mainland of Kyushu, respectively, with serial assigned numbers each year). Note that the extraordinary salinity values recorded during two periods in 2007 (portions of August and September–October data), most probably due to fouling organisms on the data-logger sensors, were omitted. **C.** Monthly chlorophyll a concentrations in the water column of Ariake Sound averaged over 22 stations.

### Histological observation of gonads

No hermaphroditic clams were found. The definition and state of gonadal stages are given below.

**Male.** At stage I, gonidia were scattered along the inner part of follicle epithelia (Fig. 4, M-I in upper two rows). For this stage, sexes could not be identified when based only on gonidia. However, the presence of reticula was peculiar to males, being most evident at stage VI (M-VI) and recognizable also at stage I. This feature was used to differentiate sexes at stage I. At stage II, one to three layers of spermatogonia were distributed on follicle epithelia (M-II). At stage III, aggregates of spermatids began to patchily fill in void space of follicles (M-III). At stage IV, spermatozoa became full in follicles, their aggregation forming a radial structure (M-IV). At stage V, spermatozoa were released, with their numbers around the center of the radial structure reduced, and void space of follicles increased (M-V). At stage VI, spermatozoa drastically decreased in number, with only a few remaining in follicles, and the radial structure disappeared (M-VI). Stage VII was not observed.

**Female.** At stage I, gonidia were scattered along the inner part of follicle epithelia (Fig. 4, F-I in lower three rows). At stage II, developing oocytes emerged in follicles (F-II). These were smaller than mature oocytes and clearly distinguishable from the latter, mostly attaching to follicle epithelia. At stage III, developing oocytes increased in number, filling in void space of follicles (F-III). At stage IV, mature oocytes became full in follicles, reducing void space of the latter. At stage V, mature oocytes were released, accompanied with increased void space of follicles. At stage VI, mature oocytes drastically decreased in number, with only a few left in follicles, and void space of the latter enlarged. At stage VII, the shrinkage of follicles progressed, with a few resorbing oocytes remaining.

### Temporal change in the proportion of gonadal stages

The mean trematode infection rate in the gonad was 18% overall with both sexes inclusive, which was excluded from analysis. The monthly change in the frequency of occurrence of gonadal stages is shown in Fig. 5.

**Male.** During 11 December 2004 to 11 February 2005, clams with stages I and II accounted for 75–93% of the population (Fig. 5, left-hand column). On 12 March 2005, the proportion of stage III increased, comprising 43% of the population. On 7 April, the highest proportion was replaced by stage IV, occupying 44%, and stage V began to appear. On 9 May, the proportions of stages IV and V were 52% and 39%, respectively. On 7 June, the highest proportion shifted to stage V, exceeding 70%. On 7 July, the highest proportion moved to stages VI, I, and II, indicating the termination of the first mass sperm spawning of the year. On 20 July, the proportion of stage V increased and comprised 65% of the population, indicating the beginning of the second mass spawning of the year. The proportion of stage V maintained a high value of 53–67% until 18 September. On 16 October, the dominance shifted to stage VI, indicating the termination of the second mass spawning. Subsequently until 26 April 2006, the proportion of stages I and II comprised 40–100%

of the population, with lower percentages of stages III and IV. On 25 May 2006, the proportion of stage V was 69%, indicating the beginning of spawning that year.

**Female.** During 11 December 2004 to 12 March 2005, clams with stages I and II accounted for 64–92% of the population (Fig. 5, right-hand column). On 7 April 2005, the proportion of stage III increased, comprising 60% of the population. On 9 May, the proportion of stage V occupied 81%. Between 7 June and 7 July, the highest proportions shifted from stage VI to VII, indicating the termination of the first mass egg spawning of the year. On 20 July, the proportion of stage III increased and accounted for 47% of the population, indicating the beginning of the second mass spawning. On 22 August, the proportion of stage VI was 52%, with a few percentages of stages IV and V. Subsequently until 16 October, the proportion of stage VI stayed at 36–44%, with an increase in the proportion of stages VII and I, indicating the termination of the second mass spawning of the year. Subsequently until 30 March 2006, the combined proportion of stages I–II was 75–100%. During 26 April to 25 May 2006, stages III–V appeared in low percentages, indicating the beginning of spawning that year.

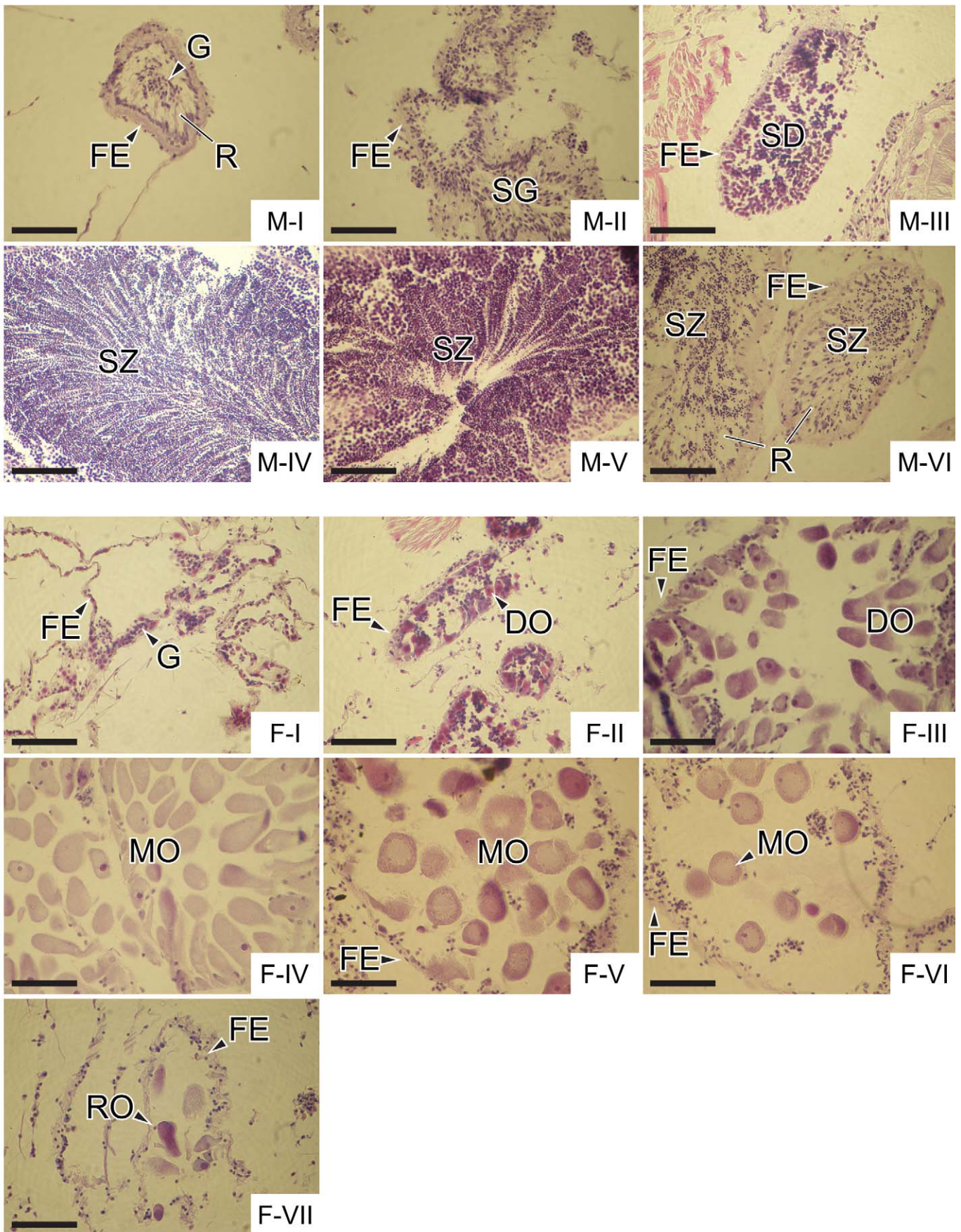
To summarize above, the reproductive season ranged from May to September each year, in which the mass spawning of gametes largely coincided between sexes. The water temperatures on the sandflat in May, September, and October averaged over respective months of the entire study period were 20.6, 27.1, and 23.5°C (Fig. 3A, solid line). The latter part of the reproductive season (July to September) accorded with the period with maximum concentrations of chlorophyll *a* in the water column through the year (Fig. 3C).

### Clam size at gonadal stages IV to VII

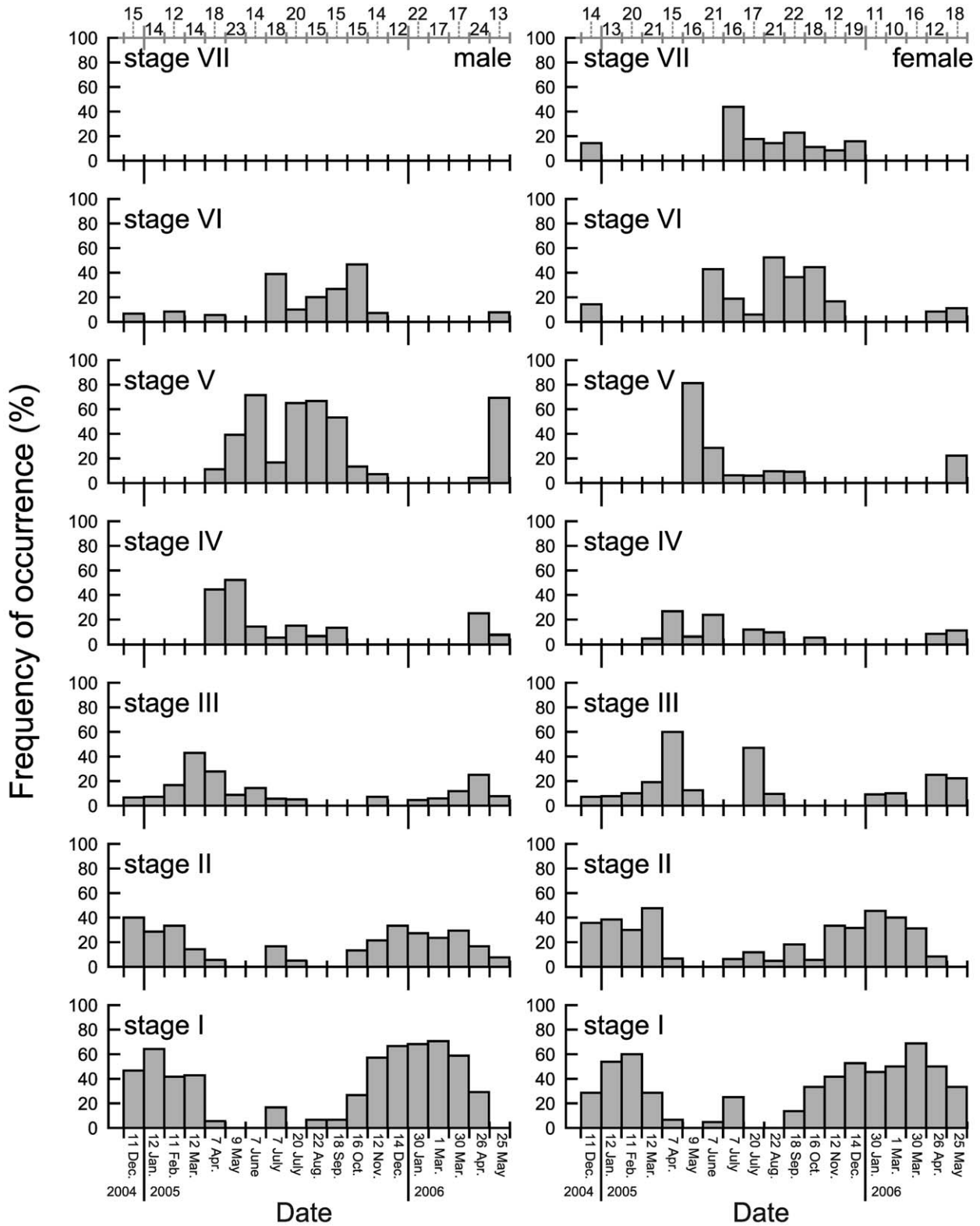
The relationship between gonadal stage and shell length for clams of both sexes collected in May, August, and September inclusive is shown in Fig. 6. In a group with clams < 25 mm, only two females, with the smallest value of 16.7 mm (hereafter referred to 'smallest mature shell length'), were found at stages IV to VII (actually in this case, both at stage VI), which accounted for only 3.5% of the group. The proportion increased to 56% in the group ≥ 25 mm but < 30 mm (four males and six females) and to 86% in the group ≥ 30 mm (49 males and 47 females). The minimum shell length in the latter two groups was 26.0 mm, which is hereafter referred to as 'standard mature shell length'.

### Separation of cohorts in the population

The maximum shell length of clams collected through the population sampling period was 44.7 mm. On the initial date of sampling (30 July 2004), three cohorts existed, to which serial numbers were assigned from large to small in shell length (Cohorts 1–3; Fig. 7). On 4 August, one newly-recruited cohort joined the population (Cohort 4). A total of 16 newly-recruited cohorts were identified by the final sampling occasion on 26 October 2007 (last one = Cohort 19; note that the smallest size-class clams to the left of this cohort were excluded from analysis). The newly-recruited cohorts were categorized into the summer and winter



**FIGURE 4** *Mactra veneriformis*. Seven gonadal stages for males (upper two rows) and females (lower three rows). M-I and F-I. Pre-developmental stage (stage I). M-II and F-II. Follicular stage (stage II). M-III and F-III. Growing stage (stage III). M-IV and F-IV. Mature stage (stage IV). M-V and F-V. Spawning stage (stage V). M-VI and F-VI. Post-spawning stage (stage VI). F-VII. Degenerating stage (stage VII); no stage-VII male specimens were found. Abbreviations: FE—follicle epithelium; G—gonium; R—reticulum; SG—spermatogonium; SD—spermatid; SZ—spermatozoon; DO—developing oocyte; MO—mature oocyte; RO—resorbing oocyte. All scale bars: 50  $\mu$ m.



**FIGURE 5** *Mactra veneriformis*. Monthly change in the frequency of occurrence of gonadal stages throughout the year for males (left-hand column) and females (right-hand column). For the definition and state of stages, see Fig. 4. No stage-VII male specimens were found. The numerals on the top row indicate the total number of specimens examined for each sampling occasion.

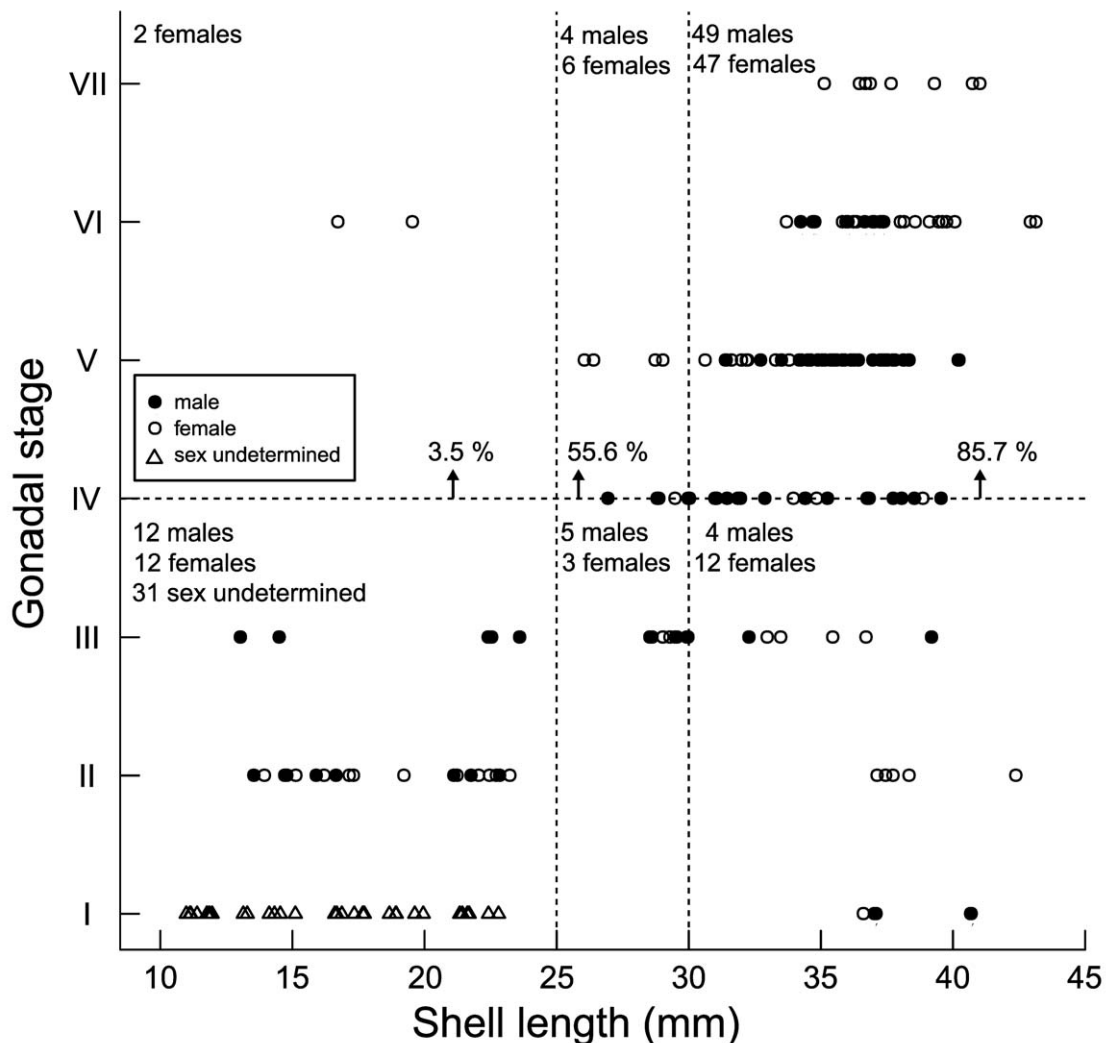
recruitment groups. The former group consisted of those cohorts that were recruited at intervals of 1 or 0.5 month from the preceding recruitment during June to October each year (Cohorts 4, 6–8, 10–14, and 16–19), while the latter one was comprised of a single cohort that was recruited in low

densities after mid-November (dates of recruitment completion in December to January: Cohorts 5, 9, and 15). Throughout the entire sampling period, the fusing of multiple cohorts was recognized three times, all of which were derived from cohorts of the summer recruitment group. The



fusion actually means that the preceding component cohorts expressed as normal-distribution curves became inseparable in the shell-length-frequency distribution. The first fusion occurred from 12 January to 11 February 2005, during which

time Cohorts 2 and 3 joined to bring about a composite cohort, referred to as Cohort (2+3). The second and third fusions took place on 1 March 2006 and 23 January 2007, generating Cohorts (6+7+8) and (11+12+13), respectively.

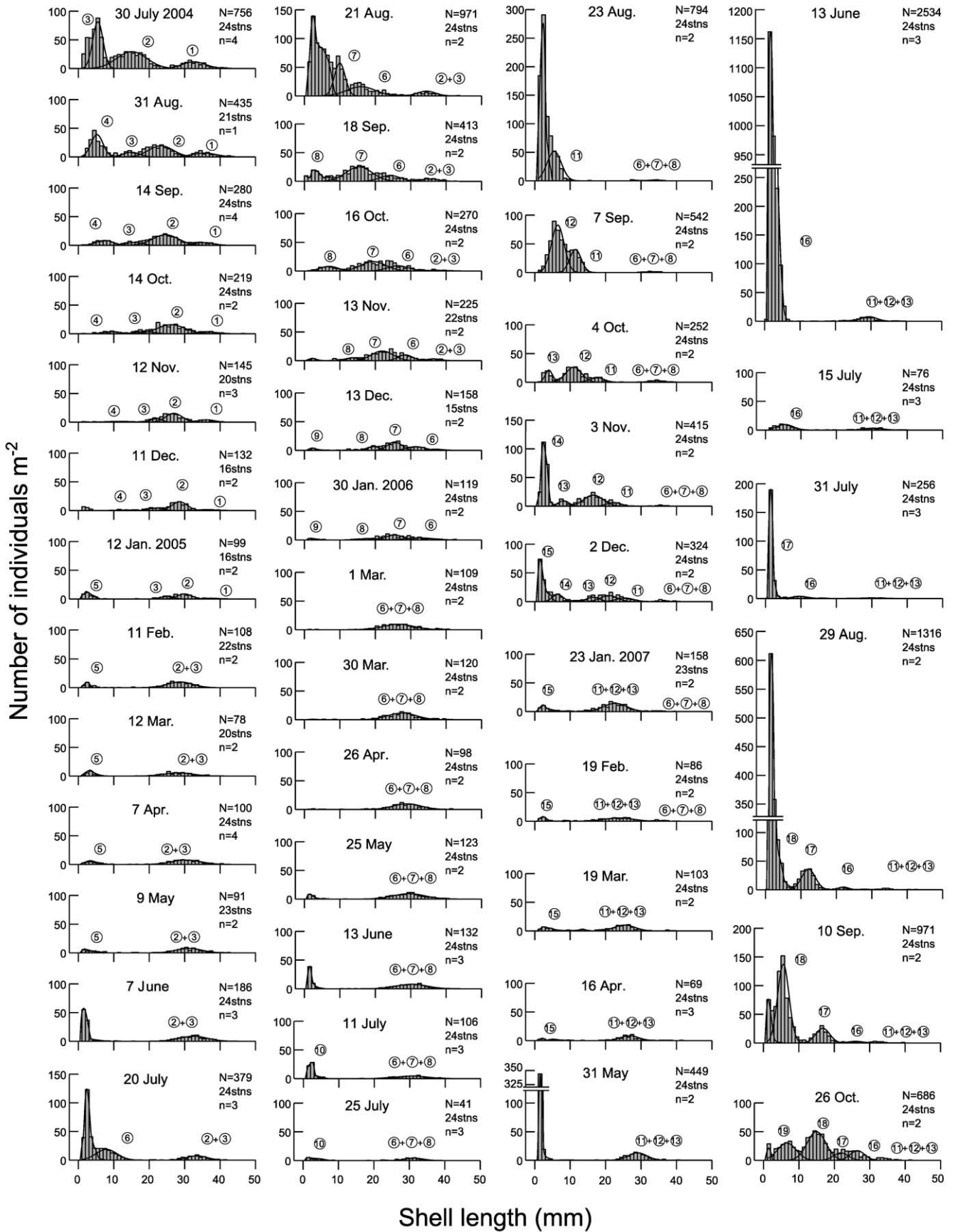


**FIGURE 6** *Mactra veneriformis*. Relationship between gonadal stage and shell length for both sexes of clams collected in May (in 2005 and 2006) and August and September (in 2005) inclusive. Gonadal stage IV is Mature stage (Fig. 4). The percentage proportion of clams with stages IV to VII in each of the three size ranges is given.

#### Change in individual growth rates with time

The daily individual-growth rate in any one cohort of clams is defined as an increment in mean shell length between two consecutive sampling dates divided by their interval in days on the individual-growth curve (Fig. 8A). The parameter values in each curve are given in Table 1. Clams of Cohorts 6–8, 11–13, and 16–18, which were recruited earlier in the reproductive season each year, grew rapidly during their initial 3–4 months. The minimum, maximum, and mean daily growth rates were 0.01–0.21, 0.21–0.47, 0.12–0.21 mm d<sup>-1</sup>, respectively (the common value, 0.21 mm d<sup>-1</sup>, came from Cohort 13, with a linear regression equation fit to plots). Of these cohorts, Cohorts 6–8, 11, 12, 16, and 17 attained the smallest mature shell length 35–76 days after recruitment completion. This was accomplished within the reproductive season each year, particularly evident for Cohorts 6, 7, 11, 16, and 17. Furthermore, around the end of the season (late September),

99–100% of the members in Cohorts 6 and 16 had reached the standard mature shell length. The daily growth rates in Cohorts 4, 10, and 14 were low for the summer recruitment group, being 0.05–0.1 mm d<sup>-1</sup> (mean value, 0.08 mm d<sup>-1</sup>), 0.04 mm d<sup>-1</sup> (linear regression), and 0.1 mm d<sup>-1</sup> (linear regression), respectively. Cohorts 4 & 14 and Cohort 10 were recruited last and first in each reproductive season, respectively. The daily growth rates in the winter recruitment group were much lower, with 0.01 and 0.02 mm d<sup>-1</sup> for Cohorts 5 and 15 (linear regressions), respectively, and undetected for Cohort 9. The relationship between daily growth rates and water temperatures for all cohorts with their shell lengths ≤ 16.7 mm is shown in Fig. 9. Very little growth was observed for the group at ≤ 15°C, while a positive correlation was detected for the group at ≥ 18°C ( $r = 0.55$  for mean values), in which the grand mean daily growth rate was 0.20 mm d<sup>-1</sup>. The non-linear regression equation over all plots of mean values was expressed as a power function.



**FIGURE 7** *Mactra veneriformis*. Temporal change in the shell-length-frequency distributions of clams with both sexes combined throughout the sampling period. N—total number of clams. Number prior to stns—number of visited stations on each sampling date. n—number of 25 × 25-cm quadrat samples collected at each station. Normal-distribution curves representing cohorts are fitted to the distributions wherever possible. In the case of the occurrence of continued recruitment, the curve for the most left-hand cohort with a truncated size-frequency distribution is drawn by simply connecting the frequency values (Fig. 2B, C; sometimes no curves are shown for simplicity). The circled numbers designate the serial cohort numbers, with plus marks indicating the fusion of two or three preceding cohorts.

The daily growth rates in the cohorts that were recruited earlier in the reproductive season slowed in October and November with decreasing water temperatures (Figs 3A and 8A), and two or three of these cohorts fused in January to February the next year. In each of these three fused cohorts, all preceding component cohorts had reached the smallest or standard mature shell length prior to fusing. The mean shell lengths at the beginning of the reproductive season (1 May) were 30.6 mm, 28.4 mm, and 27.0 mm in Cohorts (2+3), (6+7+8), and (11+12+13), respectively. The members of the fused cohorts continued to grow slowly at relatively constant rates of 0.01–0.03 mm d<sup>-1</sup> (minimum values), 0.04–0.05 mm d<sup>-1</sup> (maximum), and 0.03–0.04 mm d<sup>-1</sup> (mean), with no apparent retardation throughout the reproductive season until disappearance.

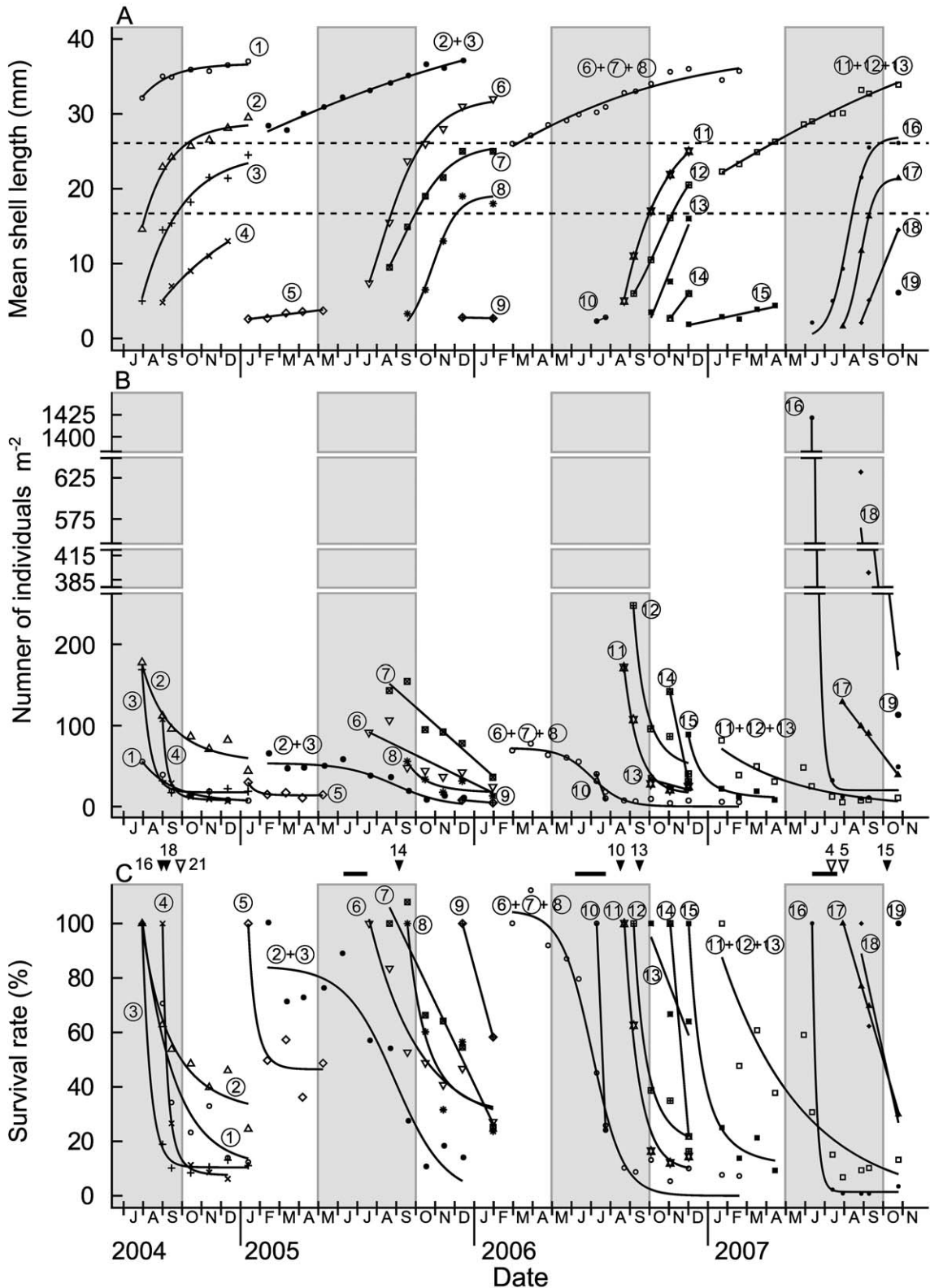
#### Change in population densities with time and survivorship

At the time of recruitment completion, the population densities of cohorts of the summer recruitment group were 33.5–1423 m<sup>-2</sup> (mean, 263.5 m<sup>-2</sup>), and those of the winter recruitment group were 8.0–89 m<sup>-2</sup> (mean, 42.3 m<sup>-2</sup>) (Fig. 8B). The parameter values in the population density- and survivorship curves are given in Tables 2 and 3, respectively. The survivorship shortly after recruitment completion was rather poor in all cohorts of the summer recruitment groups, falling to a survival rate value of 50% in 6–115 days (grand mean, 39 days; Fig. 8C). In Cohort 4 in 2004, the value fell below 50% in 8 days, which coincided with the arrival of Typhoon 18 of the year (from 51 to 42% in 1 day with the typhoon passage, as estimated from the survival rate curve; Figs 3B and 8C). In Cohorts 6, 7, and 8 in 2005, the values fell below 50% in 89, 116, and 43 days, respectively.

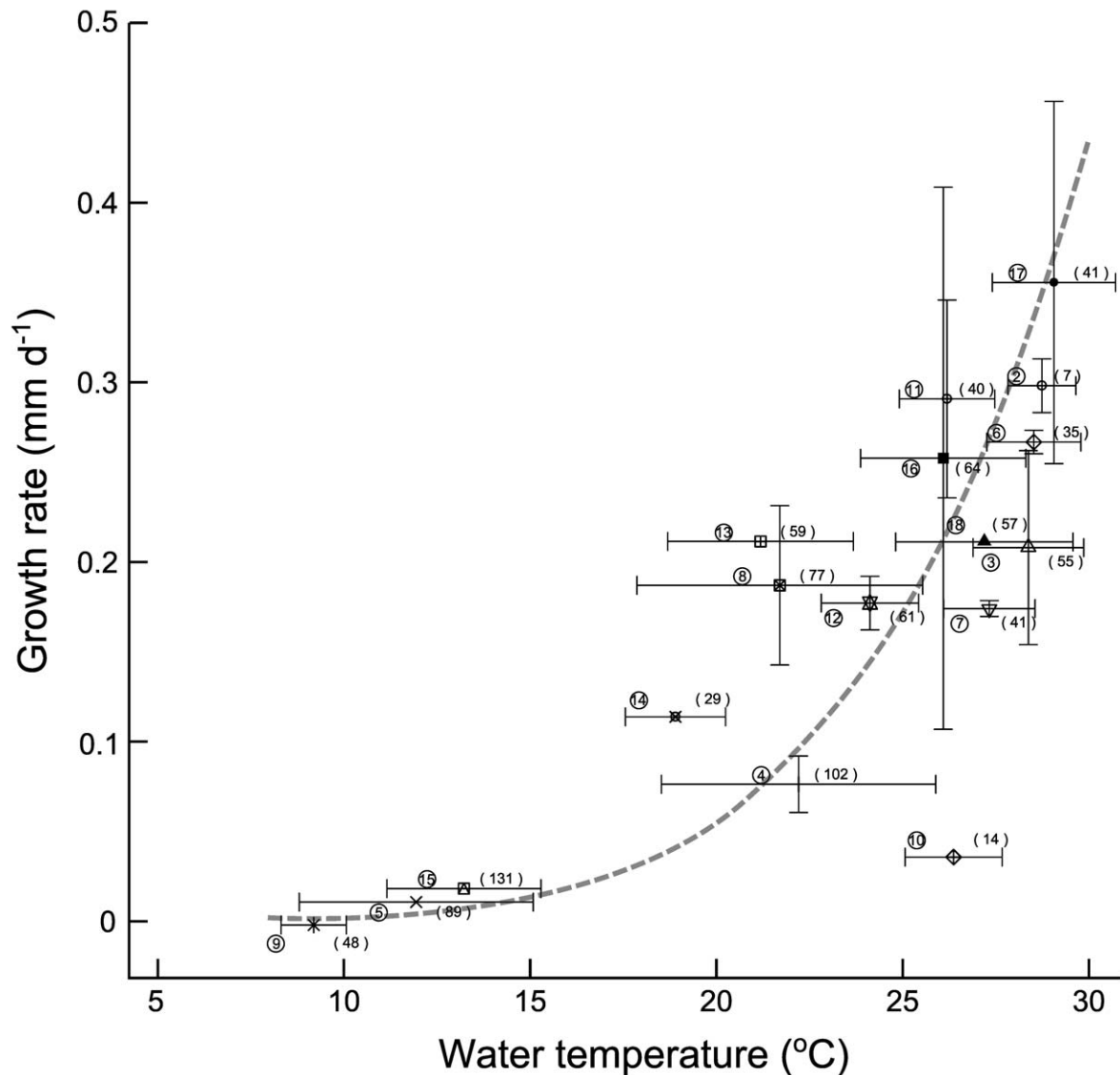
Typhoon 14 of the year arrived 48 days and 16 days after the date of recruitment completion in Cohorts 6 and 7, respectively, with no influence detected. A marked reduction in the survival rate value occurred for Cohort 8 in the low-salinity period subsequent to the arrival of Typhoon 14, from 95 to 59% during 20 September to 16 October. In 2006, the values in Cohorts 10, 11, and 12 fell below 25% in 14, 41, and 65 days, respectively. Cohorts 10 and 11 markedly declined in the low-salinity periods (the former completely disappeared in the rainy period; the survival rate value of the latter decreased from 98 to 63% during 24 August to 4 September, following the arrival of Typhoon 10 on 18 August). The reduction in Cohort 12 coincided with the arrival of Typhoon 13, from 70 to 65% in 1 day with its passage. Cohort 13 maintained a value higher than 50% for 60 days before disappearance. In Cohorts 16, 17, and 18 in 2007, the values fell below 50% in 6, 65, and 38 days, respectively. The value in Cohort 16 markedly decreased in the low-salinity period, from 47% to 2% during 18 June to 14 July. The value in Cohort 18, with its recruitment completion date of 29 August, fell to 74% on 12 September and finally to 27% on 26 October. No influences of Typhoon 15 that arrived on 9 October were detected for these two cohorts. Regarding the winter recruitment groups, the survival rate values fell below 50% in 37 and 20 days from the dates of recruitment completion in Cohorts 5 and 15, respectively (no value was available for Cohort 9). The life spans of these cohorts were 49–136 days, having disappeared by the beginning of the reproductive season each year (dates of disappearance, 9 May 2005, 30 January 2006, and 16 April 2007 for Cohorts 5, 9, and 15, respectively).

**TABLE 1** *Mactra veneriformis*. Parameter values in the selected model equation representing the individual-growth curve for each cohort of the population. For cohort serial numbers, see Figs 7 and 8A. Plus marks indicate the fusion of two or three preceding cohorts.

Cohort no.	model	L <sub>∞</sub>	K	C	t <sub>0</sub>	d	y-intercept
1	Bertalanffy	36.696	0.023		-91.770		
2	Bertalanffy	28.760	0.023		-30.277		
3	Bertalanffy	24.704	0.016		-14.088		
4	Bertalanffy	20.346	0.007		-40.192		
5	Linear					0.011	2.568
6	Gompertz	32.143	0.023	1.499			
7	Logistic	25.815	0.028	19.612			
8	Logistic	19.116	0.051	39.884			
9	Linear					-0.002	2.802
10	Linear					0.036	2.264
11	Bertalanffy	29.574	0.016		-10.998		
12	Logistic	25.413	0.030	39.763			
13	Linear					0.211	2.549
14	Linear					0.114	2.586
15	Linear					0.018	1.765
16	Logistic	26.935	0.068	56.808			
17	Logistic	21.452	0.088	28.336			
18	Linear					0.211	2.095
2+3	Logistic	44.612	0.004	-132.519			
6+7+8	Logistic	38.486	0.006	-120.799			
11+12+13	Logistic	43.198	0.005	-10.180			



**FIGURE 8** *Mactra veneriformis*. **A.** Individual-growth curves for the mean shell lengths of 19 cohorts identified through the sampling period, with shaded columns indicating reproductive seasons. The circled serial numbers of cohorts correspond to those given in Fig. 7, in which plus marks indicate the fusion of two or three preceding cohorts. The parameters describing the best-fit curve for mean shell lengths in each cohort are given in Table 1. The lower and upper horizontal broken lines designate the smallest and standard mature shell lengths (16.7 mm and 26.0 mm), respectively. **B.** Survivorship curves for 19 cohorts in terms of population density. The parameters describing the best-fit curve for densities in each cohort are given in Table 2. **C.** Survivorship curves for 19 cohorts in terms of survival rate relative to the density at the time of recruitment completion for each cohort (for Cohorts 1–3, relative to the initial densities on 30 July 2004). The parameters describing the best-fit curve for survival rates in each cohort are given in Table 3. Horizontal bars and triangles on the top row designate rainy periods and typhoon arrivals during 2004 to 2007 registered by Japan Meteorological Agency (solid and blank triangles: typhoons passing across Ariake Sound and the mainland of Kyushu, with serial assigned numbers each year).



**FIGURE 9** *Mactra veneriformis*. Relationship between growth rate for clams  $\leq 16.7$  mm shell length (smallest mature shell length) and water temperature 30 cm above the sandflat, based on Figs 3A and 8A. The mean  $\pm$ SD ranges are shown for both axes. The circled number and number within parenthesis for each bar group indicate the serial cohort number given in Fig. 7 and the number of days for that cohort to reach 16.7 mm from the date of recruitment completion, respectively. The regression equation fitted to plots with mean values:  $y = 1.029 \times 10^{-8} x^{5.162}$  ( $n = 17$ ,  $R^2 = 0.76$ ,  $p < 0.001$ ; gray broken line).

Having passed the initial high-mortality phases in the summer recruitment groups, the surviving cohorts largely turned into stable plateau phases (Fig. 8B, C). However, two cohorts disappeared by December (Cohorts 4 and 14). Although the longest persistent period was 195 days for a single cohort from its recruitment completion (Cohort 6), the life span of the respective cohorts could have been extended after joining one of the three fused cohorts in mid-January to February. The largest component cohort in each of these fused cohorts was Cohort 2 in 2005 (percentage proportions prior to the fusion in Cohorts 2 and 3: 77 and 23%), Cohort 7 in 2006 (Cohorts 6, 7, and 8: 23, 52, and 25%), and Cohort 12 in 2007 (Cohorts 11, 12, and 13: 19, 58, and 23%). The densities of the fused cohorts decreased gradually for a while subsequent to the fusion of component cohorts. The mean density values at the beginning and end of the reproductive

season (number of individuals  $m^{-2}$  on 1 May and 30 September) were 51.3 and 16.7 in 2005, 67.5 and 1.9 in 2006, and 32.3 and 8.4 in 2007. Relative to the density on the date of fusion of component cohorts, the survival rate values corresponding to the above dates were 81% and 26% in 2005, 98% and 3% in 2006, and 40% and 10% in 2007. The difference in the survival rates at the end of the reproductive season among years was parallel to the difference in the amount of discharges from Sirakawa River in the rainy period from June to July (2006 > 2007 > 2005; Yamada *et al.* 2012), which was reflected in the degree of salinity reductions (Fig. 3B). The abruptly lowered salinity values indicate the occurrence of large discharges from Shirakawa and Tsuboigawa Rivers and their floods over the tidal flat at low tide (Yamada *et al.* 2009, 2012), which was actually seen (F. Yamada and A. Tamaki, personal observation).

Assemblages of fresh dead shells colored the sediment surface whitish at low tides immediately after a flood over the sandflat (T. Nakano and A. Tamaki, personal observation). In Cohort (2+3), the survival rate value fell from 75% on 10 June (beginning of rainy period) to 60% on 25 July (end of low-salinity period extended from the end of rainy period on 17 July). In Cohort (6+7+8), the value fell from 78% on 8 June (beginning of rainy period) to 30% on 26 July (end of rainy period), and finally to 12% on 23 August (extended low-salinity period). In Cohort (11+12+13), the value fell from 28% on 13 June (beginning of rainy period) to 20% on 23 July (end of rainy period). The

three fused cohorts contributed solely to the effective reproduction by the entire population each year, as juveniles derived from the spawning by precocious clams of the 0+ year class in September disappeared by the next May. Cohorts (2+3) and (6+7+8) disappeared on 13 December 2005 and 19 February 2007, respectively. Cohort (11+12+13) persisted until the final population sampling occasion on 26 October 2007. If the survivorship after cohort fusion can be simply added to that of each component cohort prior to the fusion, the total life spans of Cohorts 6–8 and 11–13 could be 337–551 days (mean, 440 days).

**TABLE 2** *Macra veneriformis*. Parameter values in the selected model equation representing the survivorship curve (in terms of density) for each cohort of the population. For cohort serial numbers, see Figs 7 and 8B. Plus marks indicate the fusion of two or three preceding cohorts.

Cohort no.	model	$L_{\infty}$	K	C	a	b	c	d	y-intercept
1	Asymptotic exponential				51.03	-3.89	5.89		
2	Gompertz	52.99	0.01	-1.22					
3	Asymptotic exponential				164.02	-2.53	17.66		
4	Gompertz	8.14	0.05	-2.72					
5	Gompertz	13.95	0.07	-0.82					
6	Linear							-0.39	92.31
7	Linear							-0.70	152.59
8	Gompertz	17.01	0.02	-1.21					
9	Linear							-0.07	8.07
10	Linear							-2.15	41.85
11	Asymptotic exponential				166.28	-3.12	15.74		
12	Gompertz	44.89	0.03	-1.75					
13	Linear							-0.22	33.77
14	Linear							-3.83	145.97
15	Gompertz	9.92	0.02	-2.24					
16	Asymptotic exponential				1635.21	-1.88	20.18		
17	Linear							-1.03	130.54
18	Linear							-6.79	570.64
2+3	Logistic	53.64	-0.03	200.73					
6+7+8	Logistic	72.19	-0.04	126.18					
11+12+13	Asymptotic exponential				74.40	-4.86	-2.20		

## Discussion

Regarding the gonadal stages of the population of *M. veneriformis* on the Shirakawa sandflat in Ariake Sound, western Kyushu, Japan, Degenerating stage (stage VII) was confirmed only for females, with the shrinkage of follicles accompanied by the collapse of mature oocytes inside (Fig. 4). Yurimoto *et al.* (2005) regarded Degenerating stage of the female pen shell, *Atrina pectinata* (Linnaeus, 1767), collected from Ariake Sound as the stage at which unreleased mature oocytes in follicles were resorbed. This stage was not detected for males. Conceivably, resorption process might be taking place too rapidly in sperms to be

captured on time, with their much smaller size. For male specimens of *M. veneriformis* collected from Kunsan, western South Korea, our Degenerating stage and Pre-developmental stage (stage I) were described inclusively as Degenerating and resting stage (Chung *et al.* 1988, plate 2, fig. 15) or as Spent/Inactive stage (Chung and Ryou 2000, fig. 8F). On closer inspection, however, the latter two stages appear to be equivalent to our Post-spawning stage (stage VI).

The two separate mass gamete-spawning events for both sexes of *M. veneriformis* in their reproductive season, taking place from May to early July and from late July to September on the Shirakawa sandflat (Fig. 5), had also been

recorded for the Tokyo Bay population, with one from May to June and the other from late September to early October (Iwata 1948). On the Shirakawa sandflat, the first mass spawning appears to begin as temperature on the sandflat exceeds 20°C (averaged value of 20.6°C for May in 2005–2007; Fig. 3A). The second mass spawning coincided with the season with maximum water temperatures and generally highest water-column chlorophyll a concentrations (Fig. 3A, C). The reproductive season of the conspecific

population from Kunsan, which is located at a higher latitude than the Shirakawa sandflat (by 3.15°), ranged from June to September, also beginning at water temperature of 20°C (year-round values, 2.5 to 26.2°C; Chung *et al.* 1988) or 22°C (year-round values, 5 to 26.4°C; Chung and Ryou 2000). The maximum and minimum water temperatures through the year on the Shirakawa sandflat were higher than those in Kunsan by 5.4°C and 3.8°C, respectively.

**TABLE 3** *Mactra veneriformis*. Parameter values in the selected model equation representing the survivorship curve (in terms of survival rate) for each cohort of the population. For cohort serial numbers, see Figs 7 and 8C. Plus marks indicate the fusion of two or three preceding cohorts.

Cohort no.	model	$L_{\infty}$	K	C	a	b	c	d	y-intercept
1	Asymptotic exponential				92.90	-3.89	10.60		
2	Gompertz	29.93	0.01	-1.21					
3	Asymptotic exponential				97.00	-2.53	10.43		
4	Gompertz	7.56	0.05	-2.72					
5	Gompertz	46.44	0.07	-0.82					
6	Asymptotic exponential				77.13	-4.35	25.51		
7	Linear							-0.49	106.48
8	Gompertz	30.43	0.02	-1.21					
9	Linear							-0.87	100.87
10	Linear							-5.42	105.42
11	Asymptotic exponential				96.87	-3.11	9.20		
12	Gompertz	18.15	0.03	-1.75					
13	Linear							-0.61	95.70
14	Linear							-2.70	102.70
15	Gompertz	11.06	0.02	-2.25					
16	Asymptotic exponential				115.04	-1.87	1.41		
17	Linear							-0.81	101.54
18	Linear							-1.07	90.09
2+3	Logistic	84.38	-0.03	200.63					
6+7+8	Logistic	104.82	-0.04	126.11					
11+12+13	Asymptotic exponential				91.00	-4.86	-2.66		

The standard mature shell length of *M. veneriformis* for the Shirakawa population (26.0 mm; Fig. 6) is close to that recorded for the Kunsan population (26.1 mm) in which half the members became mature (Ripe stage in Chung and Ryou 2000). In the latter case, 36% of males and 25% of females had reached Ripe stage at shell lengths of 21–25 mm. Higher percentages (64% of males and 58% of females with 21–25 mm) were recorded on another sampling occasion in Kunsan (Mature stage in Chung *et al.* 1988). The smallest mature shell length in the Shirakawa population (16.7 mm) is comparable to that in the Kunsan population in which 33% of males and 12.5% of females with 15–20 mm shell lengths were at Mature stage (Chung *et al.* 1988).

The maximum recruitment-event number recorded for

the summer recruitment group of *M. veneriformis* on the Shirakawa sandflat was five, occurring every month from June to October in 2006 (Figs 7 and 8). In the Kunsan population, South Korea, there seems to be three recruitment events during June to July (fig. 4 in Ryou and Chung 1995), but no firm records are found for the period from August to September despite the documented reproductive season lasting until September (Chung *et al.* 1988; Chung and Ryou 2000). The time interval between gamete spawning by adults and newly-settled juveniles reaching the smallest size class (class's median shell length, 1 mm) on the Shirakawa sandflat could be 1 month, as estimated from the first date of egg spawning in 2005 (9 May; Fig. 5) and the first appearance date of a newly-recruited cohort in that year (7

June; Fig. 7). The duration of planktonic larvae to reach the competent pediveliger stage at 22.0°C was reported to be 14 days (Hur *et al.* 2005). Around the head of Ise Bay, central Honshu, Japan, a high-density larval assemblage was followed by an assemblage of high-density newly-settled juveniles with a 0.3 mm shell length, with time-lags varying from 0.6 month (from beginning to end of August) to 3.1 months (beginning of August to beginning of November) (Nanbu *et al.* 2006). Using the shortest larval duration estimate from above, the time interval for newly-settled juveniles to reach the smallest size class could be estimated at 0.5 month on the Shirakawa sandflat. In Kunsan, the duration for newly-settled juveniles with 0.25–0.35 mm shell lengths to reach about 0.8 mm can be estimated at 28 days (from fig. 4 in Ryou and Chung 1995). The juveniles recruited during December to January on the Shirakawa sandflat (winter recruitment group) were most probably derived from gametes that had been spawned around late September, having passed 2–3.5 months before reaching the smallest size class. Those larvae appearing subsequent to this spawning were encountered with water temperatures in the water column with a mean value of 24°C in early October (Fig. 3A, broken line). In this period the larval developmental rate could be the same as in the summer recruitment. Thereafter, juveniles derived from larvae that had settled in mid-October exhibited progressively lower initial individual-growth rates with decreasing water temperatures on the sandflat, with mean daily growth rates of 0.094 mm at 22°C in late October, 0.042 mm at 19°C in November, and 0.007 mm at 13°C in December (Fig. 3A, solid line and Fig. 9, regression curve; see also Ryou and Chung 1995; Ryou 1997). It is estimated that at this rate, the mean shell length of the cohort with the smallest-size clams in early December could be 3.0 mm, agreeing well with the actual values (Cohorts 5, 9, and 15; Figs 7 and 8A). Such temperature dependencies in both larval and juvenile developmental rates would have led to the separation of the summer- and winter recruitment groups. The lower food abundance in the wintertime could have acted as a stress to members of the latter group, which disappeared by mid-May (Fig. 3C).

The high initial individual-growth rates recorded for the summer recruitment group of *M. veneriformis* on the Shirakawa sandflat, with a grand mean value of 0.20 mm d<sup>-1</sup> at monthly mean water temperatures of 24–29°C during June to September (Fig. 9), is much higher than in the Kunsan population of South Korea. The daily growth rate constant values (K) were 0.007–0.008 in Shirakawa and 0.0015 in Kunsan (calculated from Kim and Ryou 1991). On the Shirakawa sandflat, cohorts that were recruited during June to July constituted a major component of the population in terms of density in late September, having reached the standard mature shell length (Cohorts 6 and 16) or the smallest mature shell length (Cohorts 7 and 17) (Figs 6 and 8A, B). However, considering the eventual disappearance of the newly-recruited cohorts of the winter recruitment group that were derived from gametes spawned around late

September (Fig. 8B, C), the contribution of these precocious clams to the recruitment for the entire population should be non-existent. For the Kunsan population, it can be estimated from an individual-growth curve (Kim and Ryou 1991) that it would take 279 or 397 days for newly-settled juveniles to reach the smallest mature shell length (17.5 mm in Chung *et al.* 1988; 23 mm in Chung and Ryou 2000). Thus cohorts that were recruited in July (Ryou and Chung 1995) would have reached these sizes as late as April or August the next year.

Throughout the study period on the Shirakawa sandflat, typhoons and/or heavy rain could have caused mass mortalities in six newly-recruited cohorts of the summer recruitment group of *M. veneriformis* (Cohorts 4, 8, 10, 11, 12, and 16; Figs 3B and 8B, C). Typhoons can generate large wind-induced waves and/or lowered water salinities to various degrees. Two typhoons that passed across Ariake Sound sent the largest surges over the sandflat, disturbing its substrate considerably. Typhoon 18 in September, 2004 caused a 2.7 m significant wave height at a location 2 km south of the sandflat, which was 16 times higher than the value averaged over 10 years from 2001 to 2011 (F. Yamada, unpublished data). Typhoon 13 in September, 2006 caused a 1.2 m significant wave height on the sandflat, with a large quantity of surface sediments resuspended in the water column (Yamada *et al.* 2007), when a concomitant mass mortality of juveniles of *R. philippinarum* due to sediment scouring was recorded from a tidal flat situated in the northwestern part of Ariake Sound (Mizuta *et al.* 2011). Cohorts 4 and 12 of *M. veneriformis* on the present sandflat were encountered with the above two influential typhoons 7 and 10 days after their recruitment completion, when their mean shell lengths were 5.8 and 7.5 mm, respectively (Fig. 8A). They were most likely to have been washed out of the surface sediment. The other typhoons caused at most around 0.2 m significant wave heights (Yamada *et al.* 2007; F. Yamada, unpublished data). Cohort 7 and Cohorts 17 & 18 were encountered with Typhoon 14 in September 2005 and Typhoon 15 in October 2007 passing across Ariake Sound, respectively, when no substantial immediate mortalities were detected. This might be owing to not only the smaller wave heights but also the clams' greater shell lengths at these times (mean values: 12.4, 21.0, and 11.0 mm, respectively), when some deeper position could have been reached in the sediment column. The mass mortalities of Cohorts 8, 10, 11, and 16 took place during low-salinity periods associated with either rainy periods (Cohorts 10 and 16) or typhoon arrivals (Cohorts 8 and 11) (Figs 3B and 8B, C). Nakamura *et al.* (2005) have demonstrated in the laboratory that both juveniles and adults of *M. veneriformis* from the present sandflat were more tolerant of reduced salinity (6–11) than either *R. philippinarum* or *Meretrix lusoria* (Röding, 1798), suggesting that some other variables might be responsible for the highest mortality of *M. veneriformis* observed in the field. Higher suspended silt-clay loads with increased river discharges could be one factor (Lohrer *et al.* 2004; Yokoyama *et al.* 2005; Yamada *et al.* 2009, 2012). Chang and Chin (1978) have experimentally shown for *M. veneriformis* that silt-clay particles in high concentrations



(1000 ppm) caused 50% mortality in 37 days from gill clogging. This mechanism could explain a high mortality rate of this species exposed to turbid waters over a tidal flat in western South Korea (Ahn and Choi 1998). In conclusion, except for vagaries of typhoon arrivals, the best recruitment period in the reproductive season on the Shirakawa sandflat would be the end of July–August after the rainy period, with relatively high salinities, high temperatures, and high phytoplankton abundance in the water column available for fairly high growths and moderate survivals in recruits, as evident for Cohorts 7 and 17 (Figs 3, 8, and 9).

On the Shirakawa sandflat, some major newly-recruited cohorts of the summer recruitment group of *M. veneriformis* have managed to survive to form a fused cohort, which contributed solely to the effective reproductive output by the population each year (Fig. 8). This cohort's members suffered from more or less high mortalities in the rainy period, as in juveniles. This was most pronounced for Cohort (6+7+8) as for Cohort 10 in the summer of 2006, with the lowest water salinities in the study period recorded (Fig. 3B). Although the maximum life span of members of the fused cohorts (from recruitment completion) was estimated at 1.5 years, with mean shell lengths of 36.1–37.1 mm (Figs 7 and 8), the theoretical life span could be longer; for example, 4.6 years for Cohort (6+7+8) to reach an asymptotic mean shell length of 38.5 mm and 5.6 years for Cohort (11+12+13) to reach 43.2 mm (calculated from parameters given in Table 1). Actually, the abundance of these 2+ and older clams would have been very low if present. The recurrent freshwater flood events might preclude most members of the population from realizing their potential maximum life span. For the Kunsan population of South Korea, a 6-year life span for clams with a maximum shell length of 46 mm was suggested from the results of monthly collections for one year (Kim and Ryou 1991; Ryou 1997). The authors' conclusion was based on (1) a distinct shell growth line which is marked once a year in March to April (first one: 9 months after recruitment), (2) a maximum of five distinct lines was found, and (3) von Bertalanffy growth model depicted an asymptote shell length at the sixth year from recruitment. No other studies on the Korean populations of *M. veneriformis* have explicitly mentioned its life span and reproductive contributions by the 2+ and older year classes. Generally, caution must be used concerning apparent growth line markers in bivalves, as they could be formed in response to not only lower temperatures in the wintertime but also reduced salinities caused by freshwater runoff in the summertime (Richardson 1987; Debenay *et al.* 1994). Further investigation using growth lines as reliable yearly signatures will be needed for *M. veneriformis* populations from different regions.

### Acknowledgements

We thank the staff of Oshima Fisheries Cooperative Association, Kumamoto City for allowing access to the Shirakawa sandflat. Y. Aramaki, K. Koyama, A. Nakaoka, H.

Maekawa, H. Hayase, H. Yokoyama, H. Tanoue, K. Shimatani, M. Matsuo, S. Mandal, S. Kawachi, and A.M. Lohrer assisted in the field sampling. Two anonymous reviewers provided constructive comments. This study was supported by the Japan Society for the Promotion of Science Grant-in-Aid for Scientific Research 15570018, 19310148, and 22510015, and the Environment Research and Technology Development Fund (D-1104) of the Ministry of the Environment, Japan to AT.

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