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Adaptations of subtropical Venus clams to predation and desiccation: endurance of *Gafrarium tumidum* and avoidance of *Ruditapes variegatus*

Abstract Intertidal endobenthic bivalves are often dislodged from sediments by hydrodynamic forces. As a result, they encounter the dangers of predation and desiccation, which are generally harsh near the sediment surface. To cope with such dangers, the bivalves possibly possess: (1) a strong body to endure predation and desiccation stress, (2) quick mobility to avoid the stresses, or (3) a high growth rate for attaining a size refuge. The present study examined which of these modes are adopted by the subtropical cobbled-shore Venus clams *Gafrarium tumidum* (Röding, 1798) and *Ruditapes variegatus* (Sowerby, 1852), revealing the following interspecific differences. (1) *G. tumidum* survived better than *R. variegatus* did in harsh experimental conditions, namely: the experimental cages exposed to predation and desiccation on a cobbled shore; a laboratory aquarium with a predatory crab *Scylla serrata*; and ovens with high temperatures (27°C and 34°C). (2) *R. variegatus* was more mobile than *G. tumidum* was, digging into the sediment on a cobbled shore more rapidly at both high and low tides. (3) The two species with shell lengths 20–30 mm showed similar growth rates (median: −0.2 to 44.5 μm day^{-1}) in seasonal mark–recapture surveys over 2 years. Overall, to cope with the dangers of predation and desiccation *G. tumidum* appears to have a strong body, while *R. variegatus* displays rapid mobility, and neither species seems to attain a size refuge through rapid growth. Such species-specific modes are discussed in relation to the interspecific differences found in shell morphology.

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Introduction

In the intertidal zone, endobenthic bivalves are relatively well protected from the stress of predation and desiccation compared to epibenthic bivalves. Predators are generally rarer under the sediment surface (e.g. polychaete: Kurihara et al. 2000; Seitz et al. 2001) than above the surface (gastropod, octopus, crab, starfish, fish, bird: Jangoux 1982; Rodrigues 1986; Eggleston et al. 1992; Hilgerloh 1997; Hines et al. 1997; Leonard et al. 1999; Seitz et al. 2001; for general information see Vermeij 1978; Commito and Ambrose 1985). Epibenthic predators often fail to attack prey hidden in the sediment (Blundon and Kennedy 1982b; Zwarts and Wanink 1989; Zaklan and Ydenberg 1997; Seitz et al. 2001). Desiccation is weaker in the sediment than on the sediment surface due to moisture and shading.

Even endobenthic bivalves, however, encounter intense predation and desiccation in the intertidal zone, when dislodged from the sediment by hydrodynamic forces. Such dislodgment has been reported from soft-bottom shores for the bivalves *Mya arenaria* (Matthiessen 1960; Emerson and Grant 1991), *Gemma gemma* (Commito et al. 1995) and *Macomona liliana* (Turner et al. 1997). Dislodgment presumably also occurs for many other bivalves, since many soft-bottom shores are disturbed by wave action and rainfall (Woodin 1978; Grant 1981; Berg and Alatalo 1985; Savidge and Taghon 1988; Kurihara 2002).

To adapt to such dangers, intertidal endobenthic bivalves may have evolved at least three modes. First, bivalves possibly possess morphologically and/or physiologically strong bodies. For example, the shells of some bivalves are thick enough to ward off predators and can store sufficient water to avoid desiccation (Vermeij 1973, 1978). The second mode involves being highly mobile to avoid stresses. This may be adopted by bivalves that can dig into the sediment quickly after a disturbance (Sakurai et al. 1996; Sakurai and Seto 1999). The third mode involves quick growth by which bivalves

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may rapidly exceed body sizes that are vulnerable to predation (Paine 1976; Vermeij 1978; Commito 1982; Boulding 1984; Eggleston 1990) and desiccation (Ricciardi et al. 1995). That is, bivalves that grow rapidly to exceed the vulnerable body size can avoid such types of stress quickly (Seed and Brown 1978).

Which of the three modes is adopted by intertidal endobenthic bivalves has been studied on some temperate and boreal shores (Seed and Brown 1978; Commito 1982; Boulding 1984; Zwarts and Wanink 1989), but rarely on subtropical shores. Compared to temperate and boreal shores, predation and desiccation appear to be more intense on subtropical shores (Vermeij 1978, 1987; Brown and Lomolino 1998). This is because, on lower latitude shores, predators have stronger weapons (e.g. crabs with large chelae and fishes with powerful jaws; Vermeij 1978, 1987); shellfish experimentally exposed to predators are more severely attacked (Zipser and Vermeij 1978; Bertness et al. 1981); sunlight is stronger; and wave splash is generally less intense, because wave action on shores is weakened by offshore coral reefs (Kurihara 2002). Therefore, to adapt to such harsh conditions, endobenthic bivalves on subtropical shores might have evolved an extremely strong body, quick mobility, or a high growth rate during their early life stages.

The present study examined which of these three modes is adopted by the Venus clams *Gafrarium tumidum* (Röding, 1798) and *Ruditapes variegatus* (Sowerby, 1852), on a subtropical cobbled shore. To compare the strength of their bodies, morphological measurements and experiments manipulating predation and desiccation stress were carried out. To compare their mobility, the digging behavior of the clams was observed. To compare their growth rates, mark–recapture surveys were conducted.

Materials and methods

Ruditapes variegatus and *Gafrarium tumidum*

The two clams inhabit subtropical cobbled shores around Japan (Kurihara et al. 2000). In preliminary sampling with quadrats, their densities peaked at 30–50 cm below the mean sea level (MSL) in the present study site. At the peak, *R. variegatus* and *G. tumidum* densities were approximately 30 and 10 m^{-2}, respectively. The two clams are often consumed by the local people.

Study site

The study site was a cobbled shore (24°30′N; 124°17′E) located in Ibaruma Bay, Ishigaki Island, Okinawa. The shore extended 20 m vertically and 200 m horizontally. The shore was hard to approach and undisturbed by beachcombers. It consisted of sandy sediment and cobbles with a mean ±SD diameter of 4.6±2.5 cm ($N=411$). The sandy sediment often moved due to storm or terrestrial run-off (Kurihara 2002), as reported in studies of other cobbled shores (Berg and Alatalo 1985). Gastropods (buccinids, muricids and naticids), crabs (portunids and xanthids), fishes and possibly polychaetes (Kurihara et al. 2000; Kurihara, personal observation) were the main predators of Venus clams at the study site. Since most predators occur on or above the sediment surface, predation

pressure appears to be highest near the sediment surface (for predation by the above-mentioned animals on Venus clams see Rodrigues 1986; Robert and Parra 1991; Saito et al. 1999).

The shore was protected by a complicated shoreline and an offshore coral reef. This leads to weak wave action (maximum wave height measured at low tide = 7 cm), resulting in limited sea spray. The shore was directly exposed to sunlight. Between July 1999 and April 2001, temperatures measured nearly every month were higher at the sediment surface (mean ±SD: 32.2±2.8°C during August–October; 21.0±1.1°C during January–March) than in the sandy sediment at 10 cm depth (29.2±2.3°C and 20.7±0.4°C) and in the air 1 m above the sediment (27.2±1.6°C and 19.8±1.5°C). Considering such conditions, desiccation appears to be very severe near the sediment surface.

Morphological measurements

To compare morphology between *G. tumidum* and *R. variegatus*, 30 individuals of each species were haphazardly collected near the study site in November 2001. In the laboratory, the shell length, height and width of each clam were measured with vernier calipers (±0.01 mm). After being dried at 60°C for 24 h, the individuals were weighed ("total dry weight" hereafter). They were then divided into flesh and shells, which were weighed separately ("flesh dry weight" and "shell dry weight"). The ratio of shell dry weight to total dry weight was calculated ("shell weight proportion"). After this, the thickness of one shell of each individual was measured near the umbo with vernier calipers ("shell thickness"). Finally, the weight of both shells of each individual was measured in water ("underwater shell weight"). Underwater shell weight is equivalent to [(shell dry weight) minus (shell volume)] according to Archimedes' principle. Using this relationship, underwater shell weight was subtracted from shell dry weight to estimate shell volume. Morphological characteristics that were not correctly measured on occasion due to instrument failure were omitted from the analyses.

Shell weight proportion, which was the only measurement not significantly correlated with shell length (see "Results"), was compared between species by a Mann–Whitney test (Zar 1999). The other measurements were compared by analyses of covariance (ANCOVAs), with shell length being a covariate (Zar 1999). In total, data from the same individuals were tested six times (i.e. one Mann–Whitney test and five ANCOVAs). Thus, to avoid excessive type-I errors, the significance level was lowered from the widely used 0.05 to 0.0085 (Dunn–Sidák procedure; Underwood 1997). Before these six tests were performed, 20 individuals with a shell length of 23–35 mm were re-sampled from each species. This procedure was necessary because the sample included extremely small *R. variegatus* (minimum: 19.4 mm) and large *G. tumidum* (maximum: 44.5 mm), which led to extreme, and possibly erroneous, extrapolations in ANCOVAs.

Caging experiments

Two runs of caging experiments were conducted. The experiments examined whether *G. tumidum* survive better than *R. variegatus* do in cages exposed to both predation and desiccation. Each run used lidless cages (37 cm length×25 cm width×9 cm height; made of 0.5 cm×0.5 cm resin mesh), set randomly at 40 cm below MSL and at a mean distance of 70 cm apart. The open side of cages faced upward. Half the cages were chosen randomly, and sediment from the study site was added. These cages were covered with a 0.2 cm×0.2 cm black mesh ("netted cage"). The other half of the cages were not netted and contained no sediments ("no-net cage"). Clams collected near the study site were placed into each cage. Clams were more safely protected from predation and desiccation in the netted than in the no-net cages due to the net and sediments. In run 1, two netted and two no-net cages were prepared. Ten marked *G. tumidum* were put into one cage of each type, and ten

marked *R. variegatus* were placed into the remaining cages on 16 April 2002. Ten days later the survivors were counted by checking whether they closed their shells together tightly. In a preliminary experiment, it had been confirmed that clams could not emigrate from the cages. In run 2, ten netted and ten no-net cages were prepared. Six marked individuals of either *G. tumidum* or *R. variegatus* (mean ± SD shell length = 30.1 ± 3.5 mm and 31.4 ± 2.3 mm, respectively) were put into each cage on 26 April 2002 in a similar manner to run 1. Then, 13 days later, the survivors were counted. Counts were compared between cage types for each species, using a Mann–Whitney test (Zar 1999).

At the end of each run, predators at each cage were identified at low tide. During run 2, for some cages, maximum temperatures were measured by two maximum thermometers (Nihon Keiryoki Kogyo, Tokyo), and downwelling light intensity by four micro data-recorder systems for light ("MDSL"; Alec Electronics, Kobe). Half of these recorders were randomly set in netted cages, while the remaining half were placed in no-net cages. The MDSL underestimated irradiance due to fouling on the sensor and thus assessed only relative intensity of irradiance for each cage. Because a netted cage holding a MDSL with *G. tumidum* was broken by an animal, the data on irradiance and survival in this cage were excluded from analyses.

Predation experiments

Laboratory experiments were conducted to examine whether *G. tumidum* is more resistant to predation than *R. variegatus* is. Crabs possibly preying upon clams were caught near the study site in December 2002. They consisted of four *Scylla serrata*, four *Thalamita sima* and one *Eriocheir japonicus*, with carapace widths of 66–145 mm. Each crab was put into a separate aquarium (38 cm length×26 cm width×24 cm height, but 51 cm length×36 cm width×30 cm height for the largest crab) with running seawater (mean ± SD: 23.6 ± 1.0°C; $N=31$). Ten individuals of each clam species taken from the study site were placed in each aquarium. Within each aquarium the shell lengths of *G. tumidum* (mean ± SD: 30.2 ± 4.4 mm) and *R. variegatus* (30.0 ± 4.7 mm) were not significantly different (*t*-tests: $t = 0.074$ to 0.83, $P = 0.417$ to 0.941). None of the aquaria held sediment, so the clams were directly exposed to the crabs. After 3 days of exposure, eaten clams were counted. The ratio of the numbers of individuals eaten versus not eaten was compared between *G. tumidum* and *R. variegatus* for each aquarium by a Fisher exact test (Zar 1999).

Desiccation experiments

Two runs of laboratory experiments were conducted to examine whether *G. tumidum* is more resistant to desiccation than *R. variegatus* is. For each run ten individuals of each clam species were collected from the study site in December 2002. They were brought into a drying oven in the laboratory. The oven was regulated to 34°C for the first run and 27°C for the second. These values approximated

the annual maximum and mean temperatures, respectively, on the sediment surface in the study site. In the oven, clams were put on a saucer with no sediment, so that they were directly exposed to the dry air. After 44 h of exposure, individuals whose valves were gaping were counted. Such gaping appears to indicate damage to clams, since nine out of ten gaping clams died 1 day after being placed in an aquarium with running seawater after the experiment, whereas only one out of ten non-gaping clams died. For each run the ratio of gaping and non-gaping individuals was compared between *G. tumidum* and *R. variegatus* by a Fisher exact test.

Observations of digging behavior

Four runs of observations were made to determine whether *R. variegatus* digs into the sediment faster than *G. tumidum* does. Runs 1 and 2 were conducted at low tide on 3 November 2001 and 8 February 2002, respectively (air temperatures recorded at http://www.data.kishou.go.jp/index90.htm: 23.3°C and 19.1°C). Runs 3 and 4 were conducted at high tide on 12 and 15 December 2002, respectively (19.6°C and 23.3°C). Weather conditions during run 3 were exceptionally harsh, with heavy rain and strong wave action. For each run, 10–20 individuals of each species were collected near the study site. These individuals were placed onto the sandy sediment among cobbles at 40 cm below MSL. Individuals that extended their foot to dig into the sediment were then counted intermittently over 15 min. The count just after each run was analyzed by a Fisher exact test, which compared the ratio of the numbers of digging/non-digging individuals between *R. variegatus* and *G. tumidum*.

On the same days as runs 1 and 2, observations under natural conditions were made to examine whether *R. variegatus* lay on the sediment surface less frequently than *G. tumidum* did. For each species, living individuals whose whole body was exposed to the air were counted along a transect of approximately 200 m length at 40 cm below MSL. Whether individuals were alive or dead was determined by examining whether they closed their shells firmly.

Surveys of growth patterns

To examine whether *R. variegatus* grows faster than *G. tumidum* does, eight sets of mark–recapture surveys (four seasons×two years) were conducted between July 1999 and May 2001. For each set different individuals were collected, released and recaptured (Table 1). Both species were randomly collected from near the study site, and 86–90 individuals of each were numbered with paint in the laboratory. Their shell lengths were measured with slide calipers (± 0.01 mm). For each species, individuals were divided into six groups of 14–15 individuals. Among the six groups, shell lengths were not significantly different (one-way analyses of variance; $df_1 = 5$ to 8; $df_2 = 84$ to 126; $F = 0.011$ to 0.098, $P > 0.992$). Each of the 12 groups (six groups×two species) was released into 1 of 12 plots of 0.5×0.5 m² that had been placed within a 50×1 m²

Table 1 *Ruditapes variegatus* and *Gafrarium tumidum*. Eight sets of mark–recapture surveys

Release day	Recapture day	Days	No. of plots for releasing each species	R. variegatus		G. tumidum	
				Median recapture rate (%) (min.–max.)	No. of released indivudals	Median recapture rate (%) (min.–max.)	No. of released indivudals
4 Jul 1999	11 Aug 1999	38	6	34.5 (28.6–66.7)	87	27.6 (7.1–33.3)	86
10 Oct 1999	28 Nov 1999	49	6	23.3 (20.0–33.3)	90	50.0 (26.7–73.3)	90
12 Jan 2000	23 Feb 2000	42	6	33.3 (20.0–53.3)	90	86.7 (73.3–100.0)	89
9 Apr 2000	22 May 2000	43	9	33.3 (13.3–60.0)	135	73.3 (40.0–93.3)	135
6 Jul 2000	30 Aug 2000	55	6	36.7 (6.7–46.7)	90	36.7 (6.7–60.0)	90
12 Oct 2000	29 Nov 2000	48	6	20.0 (6.7–26.7)	90	30.0 (6.7–46.7)	90
13 Jan 2001	25 Feb 2001	43	6	20.0 (6.7–60.0)	90	46.7 (13.3–53.3)	90
12 Apr 2001	28 May 2001	46	6	26.7 (6.7–46.7)	90	41.4 (26.7–53.3)	89

area at 40 cm below MSL. For the fourth set, three additional groups were prepared for each species (i.e. six additional groups in total), and each group was released into one of six additional plots. The positions of all plots were randomly determined, and no two plots were placed in the same position during the study period. Because plots were marked with a lone stake, marked individuals could emigrate freely. From 38 to 55 days after release, marked individuals were recaptured by sieving the sediment in each plot through 6 mm×6 mm mesh. Shell lengths of clams recaptured alive were measured again. Increase in shell length between release and recapture was divided by the number of days to estimate growth rate.

Growth rates of both species were generally smaller for larger individuals (see "Results"). Thus, growth rates were compared between species within each of 20–30 mm and 30–40 mm shell length classes. Comparisons were made only visually. None of the widely used statistic tests (e.g. ANOVA, ANCOVA) was performed, due to excessive violation of the assumptions of such tests (i.e. balanced data and homoscedasticity; Zar 1999) ($P < 0.05$ in Cochran's tests).

Results
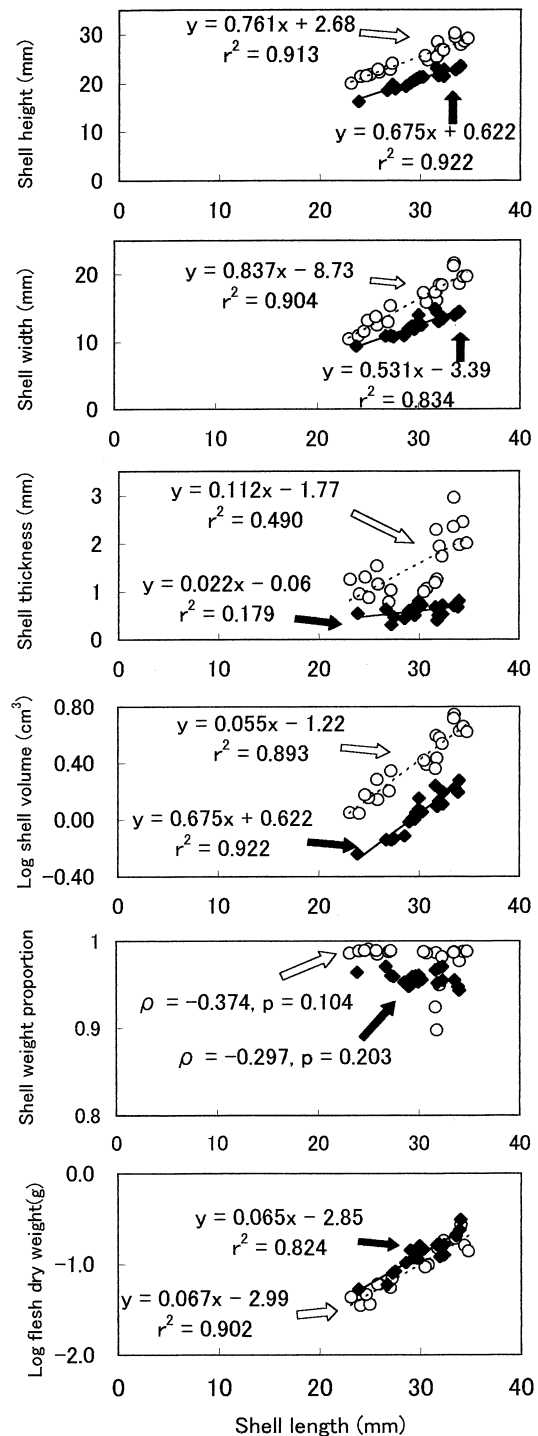
Morphology

Most of the morphological measurements were significantly larger in *Gafrarium tumidum* than in *Ruditapes variegatus* (Fig. 1). Shell height, shell thickness, log shell volume and log flesh dry weight significantly differed, not regarding slopes (ANCOVAs with shell length being the covariate, modified by a Dunn–Sidák procedure; $P = 0.015$ to 0.890; see Table 2 for df_1, df_2 and F-ratios), but regarding elevation ($P \leq 0.001$). All elevations were higher for *G. tumidum* than for *R. variegatus*, except for log flesh dry weight. Shell width significantly differed regarding slope (ANCOVA; $P = 0.003$), which made interspecific comparison of elevation difficult (Zar 1999). In the range of shell lengths examined, however, *G. tumidum* had a higher elevation (Fig. 1). Shell weight proportion was not significantly correlated with shell length for either species (Spearman rank correlation tests; $P = 0.104$ to 0.203) and was significantly higher for *G. tumidum* (Mann–Whitney test; $P = 0.001$).

Survival in caging experiments

Environments greatly differed between cage types, at least during run 2. Daytime irradiance was more intense in the no-net cages (mean ± SD: 479.6 ± 283.2 µE m^{-2} s^{-1}; $N = 2026$) than in the netted cage (300.6 ± 341.9 µE m^{-2} s^{-1}; $N = 1013$). The maximum temperature was higher in the no-net cage (36.0°C) than in the netted cage (30.4°C). Predators (muricid gastropods and portunid crabs) were found only around no-net cages.

During both runs 1 and 2, all *G. tumidum* except for one missing individual survived, whereas two to six *R. variegatus* died in the no-net cage (Table 3). As a result, only for *R. variegatus*, the median numbers of surviving individuals were lower in the no-net than in the netted cages. After each run shells of marked *R. varieg-*

Fig. 1 *Ruditapes variegatus* and *Gafrarium tumidum*. Morphological measurements and regression lines for *R. variegatus* (*filled diamonds* and *solid lines*) and *G. tumidum* (*open circles* and *dotted lines*), together with regression equations and correlation coefficients (r^2). Note that no regression lines are presented for shell weight proportion because this measurement was not significantly correlated with shell length ($P > 0.05$), as shown by the low Spearman rank correlation coefficients (ρ)

atus that had died were found in the vicinity of the no-net cages. Some consisted of a pair of uninjured valves with a hinge, while others were broken into pieces.

Table 2 *Ruditapes variegatus* and *Gafrarium tumidum*. Interspecific comparisons regarding morphology. ANCOVAs with shell length as a covariate (for all tests, $df1 = 1$) and non-parametric tests (ρ, Spearman rank correlation coefficient; U, statistic in a Mann–Whitney test)

ANCOVAs

Measurement	Slope					Elevation				
	MS1	MS2	$df2$	F-ratio	P	MS1	MS2	$df2$	F-ratio	P
Shell height	0.647	0.572	36	1.132	0.294	211.86	0.574	37	369.03	< 0.001
Shell width	8.332	0.796	36	10.469	0.003	No test was performed				
Shell thickness	0.724	0.111	36	6.508	0.015	9.78	0.128	37	76.56	< 0.001
Log (shell volume)	0.000258	0.00421	36	0.061	0.806	1.42	0.004	37	346.20	< 0.001
Log(flesh dry weight)	0.000146	0.00754	33	0.019	0.890	0.09	0.007	34	12.58	0.001

Non-parametric tests

Measurement	Species	Correlation with shell length		Interspecific comparison	
		ρ	P	U	P
Shell weight proportion	*R. variegatus*	−0.297	0.203	57.0	< 0.001
	G. tumidum	−0.374	0.104		

Table 3 *Ruditapes variegatus* and *Gafrarium tumidum*. Caging experiments. Note that for *G. tumidum* in run 2 a netted cage was broken and thus excluded from the analysis

Species	Run	Cage type	No. of cages	No. of individuals released (per cage)	Median no. of surviving individuals (min.–max.)	Mann–Whitney test	
						U	P
R. variegatus	1	Netted	1	10	10 (10–10)	Not performed	
		No-net	1	10	8 (8–8)		
	2	Netted	5	6	6 (5–6)	0.0	0.007
		No-net	5	6	1 (0–3)		
G. tumidum	1	Netted	1	10	10 (10–10)	Not performed	
		No-net	1	10	10 (10–10)		
	2	Netted	4	6	6 (6–6)	8.0	0.371
		No-net	5	6	6 (5–6)		

Survival in predation experiments

Of the nine predatory crabs, only the largest and secondly largest individuals (both *Scylla serrata*) foraged on clams (Table 4). Of the two *S. serrata*, the larger crab foraged on the same number of *G. tumidum* and *R. var-iegatus*, while the smaller crab ate a significantly larger number of *R. variegatus* (Fisher exact test; $P = 0.011$).

Heat coma in desiccation experiments

At the end of both runs of the desiccation experiments, no *G. tumidum* but five *R. variegatus* fell into heat coma, showing a significant interspecific difference (Fisher exact test: $P = 0.033$ for each run).

Digging behavior

During runs 1, 2 and 4, the numbers of *R. variegatus* digging into the sandy sediment gradually increased, while the numbers of digging *G. tumidum* remained low (Table 5; $P \leq 0.011$ in Fisher exact tests at the end of each run). During run 3, although there was no such significant difference ($P > 0.999$), a greater number of *R. variegatus* dug into the sediment. Under natural conditions, only *G. tumidum* individuals were found to lie on the sediment surface: seven and nine individuals for runs 1 and 2, respectively.

Table 4 *Ruditapes variegatus* and *Gafrarium tumidum*. Numbers of individuals eaten by crabs (arranged according to carapace width) and significance levels (P) in Fisher exact tests

Crab	Carapace width (mm)	No. of individuals eaten		P
		R. variegatus	*G. tumidum*	
Thalamita sima	66	0	0	> 0.999
Scylla serrata	67	0	0	> 0.999
Eriocheir japonicus	70	0	0	> 0.999
T. sima	71	0	0	> 0.999
T. sima	72	0	0	> 0.999
T. sima	76	0	0	> 0.999
S. serrata	112	0	0	> 0.999
S. serrata	121	6	0	0.011
S. serrata	145	6	6	> 0.999

Table 5 *Ruditapes variegatus* and *Gafrarium tumidum*. Numbers of individuals digging sediments 5, 10 and 15 min after being artificially put on the sediment surface (*P* significance levels in Fisher exact tests)

Tide	Run	Species	No. of inds	No. of inds digging			*P*
				5 min	10 min	15 min	
Low	1	*R. variegatus*	14	5	9	9	< 0.001
		G. tumidum	13	0	0	0	
	2	*R. variegatus*	10	3	5	6	0.011
		G. tumidum	10	0	0	0	
High	3	*R. variegatus*	15	3	0	1	> 0.999
		G. tumidum	15	0	0	0	
	4	*R. variegatus*	20	9	15	17	< 0.001
		G. tumidum	20	3	3	6	

Fig. 2 *Ruditapes variegatus* and *Gafrarium tumidum*. Growth rates of mark–recaptured clams with medians for shell-length classes of 20–30 mm and 30–40 mm for *R. variegatus* (*filled diamonds* and *solid lines*) and *G. tumidum* (*open circles* and *dotted lines*)
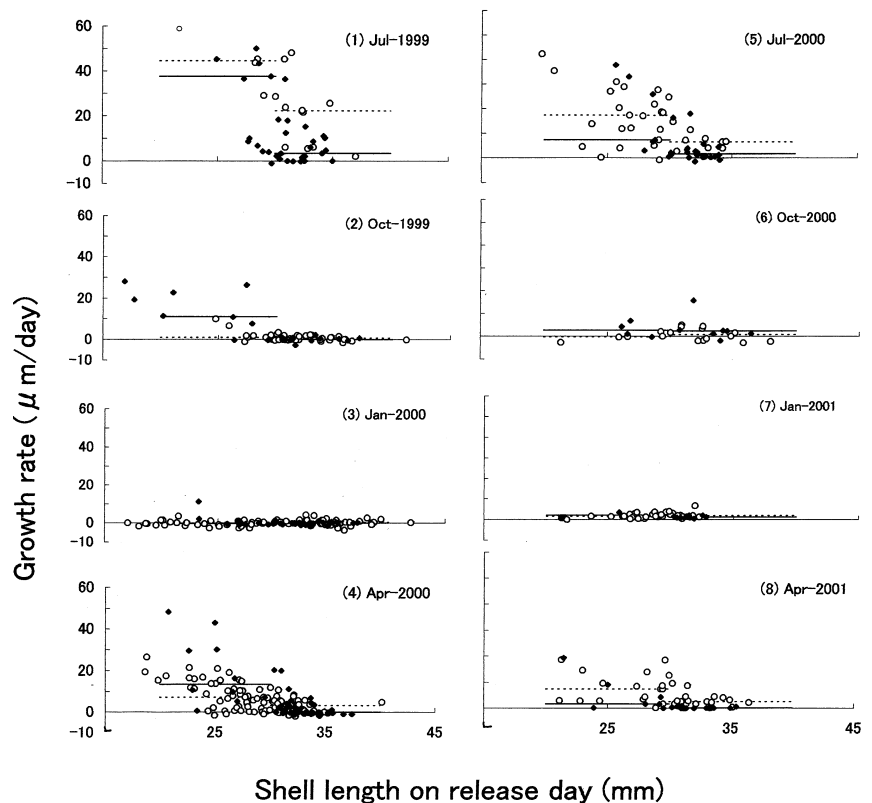
Growth patterns

In all but the first survey, the median recapture rate of *R. variegatus* (20.0–36.7%) did not exceed that of *G. tumidum* (30.0–86.7%; Table 1). Small *R. variegatus*, with shell lengths of 20–30 mm, showed no clear difference in growth rate from small *G. tumidum* (Fig. 2). That is, the median growth rate of small *R. variegatus* was greater by > 1.0 μm day^{-1} than that of small *G. tumidum* for the October 1999, April 2000 and October 2000 surveys, while the former was smaller by > 1.0 μm day^{-1} for the July 1999, July 2000 and April 2001 surveys. For the remaining four surveys, the median growth rates of small clams did not much great interspecific difference. Large *R. variegatus*, with shell lengths of 30–40 mm, grew more slowly than large *G. tumidum* did. That is, only during the October 2000 survey was the median growth rate of large *R. variegatus* greater than that of large *G. tumidum* by > 1.0 μm day^{-1}, while for four other surveys (July 1999, April 2000, July 2000 and April 2001) the latter was greater by > 1.0 μm day^{-1}.

Growth rates varied not only between species, but also among seasons and between years. Generally, growth rates were the lowest in January in each year and in the second year for each season. However, the causes of such temporal fluctuations are beyond the scope of this study and will be discussed elsewhere.

Discussion and conclusions

Resistance of *Gafrarium tumidum* to predation and desiccation

Ruditapes variegatus is likely to be more susceptible to predation than *G. tumidum* is. This is suggested by the caging experiments, in which only *R. variegatus* survived less often under high predation pressure (i.e. no-net

cage) than under low predation pressure (i.e. netted cage). Higher predation pressure in the no-net cages is reinforced by the observations that predators and pieces of shell from dead *R. variegatus*, probably broken by crabs and/or fishes, occurred only around the no-net cages. The vulnerability of *R. variegatus* to predation is also suggested by the predation experiments, in which *R. variegatus* were eaten by the single crab more often than *G. tumidum* were. Although only the medium-body-sized crab showed such prey selectivity in the predation experiments, *R. variegatus* is still considered to be more vulnerable to predation. The result may mean that medium-body-sized crabs can crush *R. variegatus* more easily than *G. tumidum*, while large crabs can readily crush both clam species, and small crabs cannot crush either. This is supported by the result that the largest crab ate the same number of both clam species and the third largest to the smallest crabs ate none. Such size-specific predation by crabs on clams has been observed previously (Hughes and Elner 1979; Arnold 1984; Boulding 1984).

The resistance of *G. tumidum* to predation is attributable to three morphological characteristics. First, its shells are globose (i.e. large in width and height), which may be more difficult for crusher-type predators to handle and crush with chela and jaw. This is suggested by the experiments of Blundon and Kennedy (1982a), in which a globose-shelled clam species was more immune to predation by blue crab than a flat-shelled species was. The second advantageous characteristic of *G. tumidum* is the thickness of its shells, which may make crushing and drilling more difficult for predators. This is in part suggested by the experiments of Boulding (1984), in which thicker-shelled clam species resisted a greater number of crushing behaviors of crabs. The third favorable characteristic of *G. tumidum* is the relatively limited amount of flesh in the shell. This increases the cost/benefit ratio (i.e. ratio of energy consumed/gained) for predators and possibly lowers the probability of predation (Charnov 1976).

In addition to predation, *G. tumidum* is likely to be more immune to desiccation than *R. variegatus* is, as indicated by the caging and desiccation experiments. The caging experiments showed that only *R. variegatus* died in significantly larger numbers in the no-net cages than in the netted cages. In the no-net cages desiccation may be more severe due to the stronger irradiance and higher temperature inside. In the desiccation experiments *R. variegatus* showed heat coma significantly more frequently than *G. tumidum* did.

It is unclear whether such resistance of *G. tumidum* to desiccation is due to morphology. The globosity and thickness of *G. tumidum* shell may be simultaneously advantageous and disadvantageous. The globosity decreases the ratio of shell surface area to body volume. On the one hand, this characteristic lowers the amount of gain of heat per unit volume of *G. tumidum* body (Porter and Gates 1969), which prevents a sharp rise in body temperature. On the other hand, shell globosity

lowers the amount of heat loss, which hinders rapid cooling. The thickness of *G. tumidum* shells may also add to the uncertainty of whether the shell is desiccation resistant, because the thick shell may slow heat conduction between the inside and outside. Therefore, characteristics of *G. tumidum* other than morphology, such as possible physiological mechanisms, should be examined to explain why *G. tumidum* is more immune to desiccation than *R. variegatus* is.

Avoidance of *R. variegatus* from predation and desiccation

R. variegatus is more likely than *G. tumidum* to remain in the sediment. This is indicated from the observations that, although *R. variegatus* were more abundant than *G. tumidum* under the sediment surface (see "Materials and methods"), only *G. tumidum* lay on the sediment surface. The ability of *R. variegatus* to remain in the sediment is attributable to its quick digging behavior. This is suggested by the laboratory experiments of Sakurai and Seto (1999), in which a congeneric clam *R. philippinarum* was able to dig into sandy sediment quickly enough to stabilize its position when the sediment was artificially deposited and eroded. In the present study, although *R. variegatus* did not dig quickly in one observation at high tide, this exceptional result appears to be due to the strong wave action and low salinity during this observation. The interferences with digging behavior by these physical factors have been previously reported for *R. philippinarum* (Sakurai et al. 1996; Sakurai and Seto 1999).

By remaining in the sediment, *R. variegatus* may be able to shelter from desiccation and predation. Desiccation is milder in the sediments than on the sediment surface (see "Study site"). Predators are less abundant and diverse in the sediment (polychaete) than on and above the surface at the study site (e.g. crabs, fishes, gastropods and octopi) (Kurihara et al. 2000; Kurihara, personal observation). Predation pressure has been reported to be lower in the sediment than near the surface in many regions of the world (Blundon and Kennedy 1982b; Haddon et al. 1987; Zwarts and Wanink 1989). Staying in the sediment under cobbled shores, such as the present study site, may be particularly effective to avoid predation, since obstacles such as cobbles can protect clams from predatory attacks (Arnold 1984; Sponaugle and Lawton 1990). Overall, the ability of *R. variegatus* to remain in the sediment may offset its weaknesses against desiccation and predation.

The ability of *R. variegatus* to move quickly is attributable to the shell morphology. Its shell is less dense, which allows good mobility. Its shell is relatively flat, which facilitates movement into narrow interstices between cobbles. Further, even when dislodged from sediment by abiotic disturbances (e.g. Matthiessen 1960; Commito et al. 1995; Turner et al. 1997), the distance

between the shell ventral margin and sediment surface is relatively short because of the flatness of the shell; as such, *R. variegatus* can touch the sediment surface effortlessly with its foot and dig quickly into the sediment.

Similarity in growth pattern between *G. tumidum* and *R. variegatus*

The weaknesses of *R. variegatus* against predation and desiccation are unlikely to be offset by "escaping in size" (sensu Paine 1976; see also Seed and Brown 1978; Eggleston 1990). This is indicated by the mark–recapture surveys. Small *R. variegatus* did not grow faster than small *G. tumidum* did.

It is, however, possible that *R. variegatus* overcomes its weaknesses by fast sexual maturity. That is, *R. variegatus* might increase the chances of producing offspring before death due to predation or desiccation, as reported for the bivalve *Macoma balthica* (Commito 1982). According to Ota and Tokeshi (2000), the oldest cohort of *R. variegatus* has a shell length mode of 20 mm, which suggests that *R. variegatus* can sexually mature before attaining this size. In contrast, Baron (1992) reported that *G. tumidum* can sexually mature after attained this shell length. Thus, it is possible that *R. variegatus* sexually matures faster than *G. tumidum* does, even if their growth rates are similar.

Conclusions

G. tumidum may overcome predation and desiccation through greater endurance, while *R. variegatus* may avoid stress through greater mobility. This interspecific difference is attributable in part to species-specific morphology. Yet, the difference may also arise from physiological mechanisms, which should be further investigated. In addition, characteristics other than endurance and mobility (e.g. the age at which they sexually mature) should also be compared between the species in the future.

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