

Re-establishment of life orientations in five infaunal bivalve species in soft substrata

SUGURU UJINO¹ & AKIHIKO MATSUKUMA²

¹Department of Biological Sciences, Graduate School of Science, The University of Tokyo, Hongo 7-3-1, Tokyo, 113-0033 Japan. Email: ujino@kahaku.go.jp

²Kyushu University Museum, Hakozaki 6-10-1, Higashi-ku, Fukuoka, 812-8581, Japan

Abstract

In this study, we investigated the response of five infaunal bivalve species to changes in their life positions (life orientations) by tilting the aquariums in which they were placed. The results show that the bivalves returned their orientations to normal when they were inclined ventrally or dorsally, but not when they were inclined to the left or right side. The conditions were not changed in any other respect except for tilting the aquarium. The only difference in conditions of all the aquaria was the degree of inclination. That the animals readjusted to their normal position in such circumstances indicates that they control their orientation, presumably in response to gravity. The different responses to dorsal-ventral right-left tilting may be due to their style of movement which is in turn related to their shell, musculature and external body form. This and previous studies indicate that antero-posterior life orientations of bivalves have functional or ecological significance. It is proposed that bivalve antero-posterior orientation can be interpreted to be intermediate between the burrowing orientation and the orientation with the siphons extended upright most efficiently.

Introduction

Bivalves in many groups live infaunally to avoid predators. These infaunal bivalves are known to adopt a position in the substratum called 'life position' or 'life orientation' that is species-specific. This has been described in many studies including Stanley (1970), Fürsich (1980) and Kondo (1990). Stanley (1970) described the life positions of many species using X-radiography, and inferred relationships between life positions and shell morphology. Kondo (1990) described preserved life orientations in a Quaternary fossil bed in Chiba prefecture, Japan. These studies showed that common infaunal bivalve groups such as Veneridae and Mactridae orient their commissure plane (the plane that the two valves unite on) vertically with the posterior end up, and that many bivalves incline their long axis to a greater or lesser degree. Ujino and Matsukuma (2009) measured and statistically analysed the life orientations of many individuals of nine species as determined by the inclinations of their long axis and commissure plane (Fig. 1). Their study concluded that in many species the angles fell within a narrow range and showed distributions statistically close to a normal distribution.

Despite the numerous descriptions of life orientations (e.g. Holme 1961; Stanley 1970; Kondo 1987, 1989, 1990; Ujino and Matsukuma 2009, 2010), the meanings, reasons and mechanisms behind the adoption by infaunal bivalves of defined life orientations have received little attention. For instance, although the antero-posterior inclinations are different for each species (Stanley 1970; Ujino and Matsukuma 2009), no one has attempted to determine the meaning or reason for the inclination. Furthermore, the influence of factors such as gravity and sediment conditions on life positions has not been explored.

Conditions affecting bivalve life orientations include inclination of substrate, conditions of sediment surface, and light, but the most influential is thought to be gravity because

its directionality can be detected by the statocysts (Charles 1966). The function of molluscan statocysts has been studied by many investigators (e.g. Wood and Baumgarten 1972; Janse *et al.* 1988; Wiederhold *et al.* 1990). The perception of gravity and the function of statocysts have been examined in a series of studies on *Pecten* by Buddenbrock (e.g. Buddenbrock 1911, 1915, 1952). In particular, Buddenbrock (1952) observed the behaviour of *Pecten* when hung by a thread, and showed that, regardless of the starting position, they always attempt to swim on their right side and achieve the same position indicating that their position control is based on a response to gravity. However the significance of gravity sensing to controlling life orientations in infaunal bivalves, as opposed to epifaunal *Pecten* species, has so far not been determined.

In this study we focus on the response behaviour when the inclination of the specimens in the substrate (and thus the direction of gravity relative to the specimens) is changed. In this study, this behaviour was examined by tilting the aquarium in which the individuals were placed. This changes the inclination of the specimens relative to gravity but leaves other conditions unchanged; the sediment is almost undisturbed until the angle becomes too great. If infaunal bivalves return to their original preferred angles relative to gravity when they are tilted, it can then be assumed they are controlling their orientation in response to gravity. Such behaviour is also important in deducing whether life orientations are largely fortuitous or innate, because we assume that returning behaviour suggests the need for each species of burrowing bivalve to maintain a certain orientation.

We also examine the difference between the two types of response behaviours—whether inclined dorso-ventrally or in a right-left direction. Usually bivalves move or rotate in the substratum using foot and retractor muscle contractions, first of the anterior and then of the posterior pedal retractors, which produce forward and backward motion respectively (Stanley 1970). These movements allow rotation in the

antero-posterior direction to be achieved with minimal resistance. Conversely, left-right rotation is more difficult and requires much more energy (Stanley 1970).

The antero-posterior rotating movement of bivalves influences various behaviours. Most infaunal bivalves adopt a rocking motion in burrowing (Trueman *et al.* 1966; Stanley 1970), characterized by alternate forward and backward shell rotation. Most bivalves do not rotate in right-left directions although some species of Tellinidae seem to change their inclination of the commissure plane in the substratum (Holme 1961; Stanley 1970; Ujino and Matsukuma 2010). Forward and backward rotation is also detected when rapid mass burrowing, called anastrophic burial, occurs (Kranz 1974). In that situation, some bivalves reverse their positions and point their anterior end up to escape from the substratum (Kranz 1974). Such differences resulting from the bivalve movement-style may also influence the response to inclining orientation.

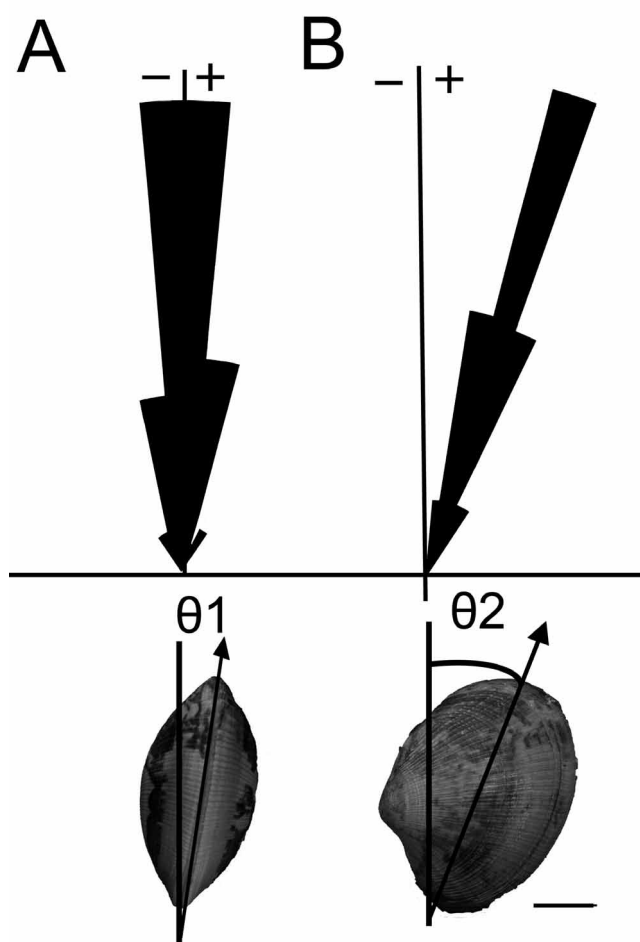


FIGURE 1. Life orientation measurement and rose diagram (from Ujino and Matsukuma 2009 with permission). $\theta 1$ =Inclinations of commissure plane. $\theta 2$ = Inclinations of long axis.

Materials and Methods

Three venerids, *Ruditapes philippinarum* (Adams & Reeve, 1850), *Meretrix lusoria* (Röding, 1798), *Meretrix petechialis* (Lamarck, 1818), a mactrid, *Macra veneriformis* Deshayes in Reeve, 1854, and an arcid, *Scapharca kagoshimensis*

(Tokunaga, 1906), were tested for this study (Table 1). These species were selected because the life orientation of all had been determined quantitatively and all species had been found to adopt fixed life orientations (Ujino and Matsukuma 2009). Therefore it was expected that they would display sensitivity to the inclination of their living positions.

The individuals used in this study were collected at Tsuyazaki in northern Kyushu, Japan or purchased at a market in Fukuoka, Japan (Table 1).

TABLE 1. List of the species examined in this study, with the collection locality. The number of individuals used is given in Table 2.

Family	Species name	Collection locality
Arcidae	<i>Scapharca kagoshimensis</i> (Tokunaga, 1906)	Ariake sea (central Kyushu, Japan) (purchased)
Veneridae	<i>Ruditapes philippinarum</i> (Adams & Reeve, 1850)	Tsuyazaki (N33°47'44' E130°27'34'') (Northern Kyushu)
Veneridae	<i>Meretrix lusoria</i> (Linnaeus, 1758)	Ariake sea (central Kyushu, Japan) (purchased)
Veneridae	<i>Meretrix petechialis</i> (Lamarck, 1818)	Korea (purchased)
Mactridae	<i>Macra veneriformis</i> Deshayes in Reeve, 1854	Tsuyazaki (Northern Kyushu)

Bivalves in substrata cannot be observed directly. They have been observed by X-radiography (Stanley 1970; Kranz 1974) or in transparent sediment made from cryolite (Josephson and Flessa 1972). However, X-radiography equipment is expensive and cumbersome, natural cryolite is now difficult to obtain and artificial cryolite is too fine to be used as sediments because all species tested in this study live in muddy sand substrata. We used muddy sand sediments from Tsuyazaki tidal flat in the experiments.

In this study, we examined the response indirectly by measuring life orientations after the aquaria had been tilted and left for sufficient time (see below) to determine whether or not they return to their position. At first, the bivalves were placed in an aquarium filled with sediment and after all of them had burrowed (usually within 2–12 hours), the aquarium was tilted and left for 1, 2 or 3 days. The depth of sediment in the aquarium was about 15 cm, which is deep enough for the studied bivalves to burrow properly because all five species usually burrow within three cm (Ujino and Matsukuma 2009). The depth of the aerated sea water was about 5 cm prior to tilting. Approximately identical numbers of individuals were placed on their left and right sides. All aquaria were tilted to 20°, which is approximately the limit before the sediment shifts. We then measured the orientation of each individual. We examined whether they had returned to their normal life position or not by comparing the individuals measured in this study with the life orientation data for the same taxa in Ujino and Matsukuma (2009). If the final positions were near the usual life orientations [*i.e.*,

within the average \pm standard deviation (SD) of normal orientation], it was assumed that they had returned to their normal life position.

The method of measuring bivalve orientations is the same as that used by Ujino and Matsukuma (2009). The bivalves were carefully excavated, excluding sediments, by using a hand, brush or dripping water. The individuals in substrata were exposed, and the inclinations of their commissure plane and long axis from vertical were measured (Fig. 1) by use of a clinometer and protractor with a water level, with these measurements carried out with the aquarium tilted. Life orientations of individuals were not checked prior to tilting because it is impossible to observe them without exposing individuals and this will disturb the sediment condition relating to each individual. Research by Ujino and Matsukuma (2009) indicated that, in the five species which were studied, more than 90% of individuals set normal positions in soft substrate, even if they reburrowed after excavation. Because of the large sample size (see Table 2) in this experiment, we assumed that most individuals were at their normal position prior to the aquarium being tilted.

In assessing responses to tilting we recognised two types of response behaviour; when they were inclined dorsally or ventrally (Figs 2A, 5A) and when they were inclined to the left or right (Figs. 2B, 5B). These orientations were interpreted by the direction of the buried individuals relative to the direction of inclination of aquarium (Fig. 2). We measured the angles (θ in Fig. 2) between the two directions after carefully exposing the bivalve. If this angle was 0° – 20° or 160° – 180° (i.e., the directions of the buried individuals and

inclination of the aquarium were close to parallel), the individuals were regarded as having been inclined ventrally or dorsally (Fig. 2A). If this angle was 70° – 110° , namely that is, one direction was almost at right angles to the other, the individual was regarded as having been inclined to the right or left (Fig. 2B). The intermediate individuals whose angles were 20° – 70° or 110° – 160° were not included in the results because these individuals could not be classified in either type, making it difficult to categorise their behaviour in the context of this experiment.

Individuals that emerged from the substrata and reburrowed after the aquarium was tilted were also not included in the results. To avoid measuring those individuals, we recorded the direction of individuals and burrow location when they were initially burrowing. These directions and locations were compared with those of the exposed bivalves when we measured their orientation after the aquarium had been inclined to confirm that they had not emerged and reburrowed. If the directions and locations were almost the same, the individuals were regarded as not having reburrowed. The measured values of life orientations (θ_1 and θ_2 in Fig. 1) are divided into negative and positive values using the methods of Ujino and Matsukuma (2009). The inclinations of the commissure plane (θ_1) were treated as negative values when tilted to the left, and as positive when tilted to the right (Fig. 1A). The inclinations of the long axis (θ_2) were treated as positive when the axis tilted ventrally from vertical, and negative when the axis tilted dorsally from vertical (Fig. 1B).

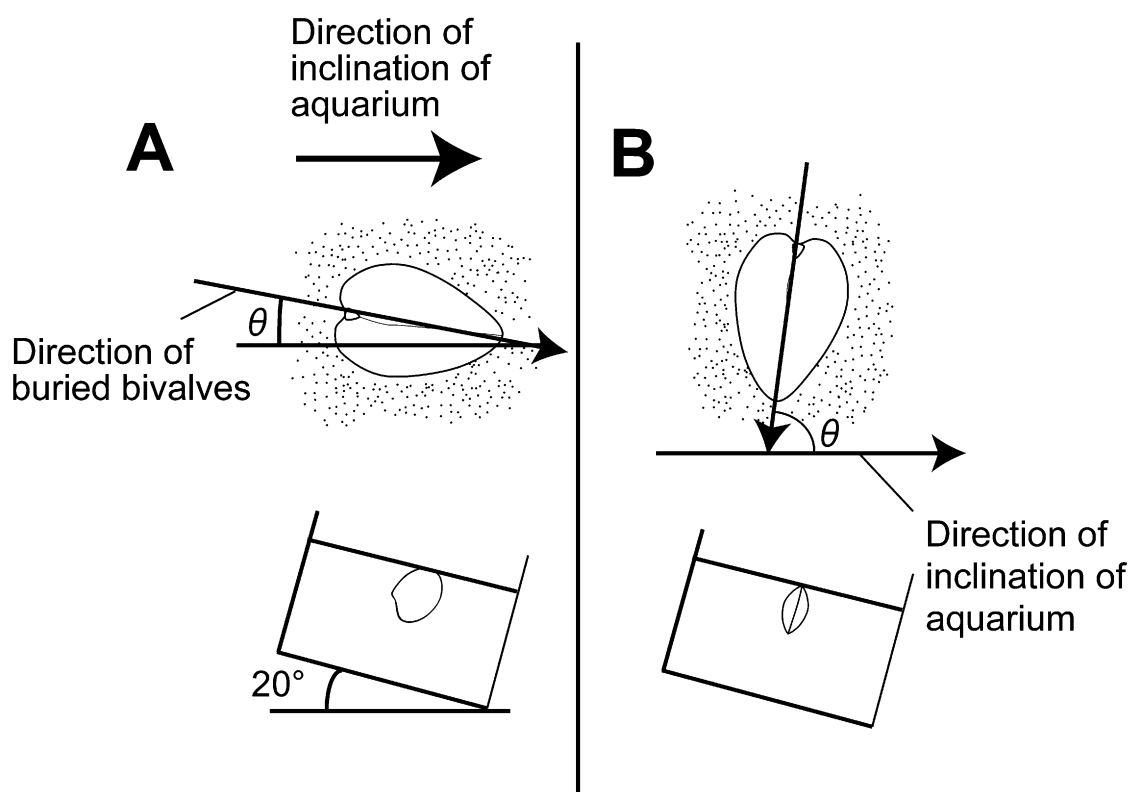


FIGURE 2. :Upper and lateral view of buried bivalves in aquarium with sediment. θ =the angles between direction of buried bivalves and direction of inclination of the aquarium. **A.** Inclined ventrally. **B.** Inclined to the right.

Results

The results for all species are shown in Figs 3 and 4 as scatter plots of inclinations of the commissure plane and the long axis. Points in the scatter plot represent the angle (in degrees) of an individual, including the inclination of the commissure plane and the long axis after the aquarium was tilted and left for one to three days. The numbers of individuals measured are given in Table 2.

When they were inclined dorsally or ventrally, many individuals had values near the average for their usual life orientations as determined by Ujino and Matsukuma (2009). For example, in *Ruditapes philippinarum* the average inclination of the long axis in its usual life orientation was about 19° with a standard deviation (SD) of about 7° (Ujino and Matsukuma 2009), 31 of 37 (83.7%) individuals inclined ventrally or dorsally were within the average \pm SD in the value of inclinations of the long axis (Table 2). Such results

are similar in the other species. In all species, more than 60% of individuals are within average \pm SD and over more than 80% are within average \pm 2 \times SD (Table 2). A few had values that were significantly remote from the average. For example, four individuals of *Ruditapes philippinarum* (Fig. 3IB) inclined their long axis almost 40°, and similar results were observed in other species (Figs 3 and 4).

Individuals inclined to the right or left had values that were clearly different from those inclined ventrally or dorsally. The values of inclinations of the long axis for almost all individuals are within the average \pm 2 \times SD, but the values of inclinations of the commissure plane showed obviously biased distributions (Figs 3IA, 3IIA, 4IA, 4IIA, 4IIIA). When inclined to the right, almost all individuals had highly right inclined values (positive values) and when inclines to the left, they had highly left inclined values (negative values).

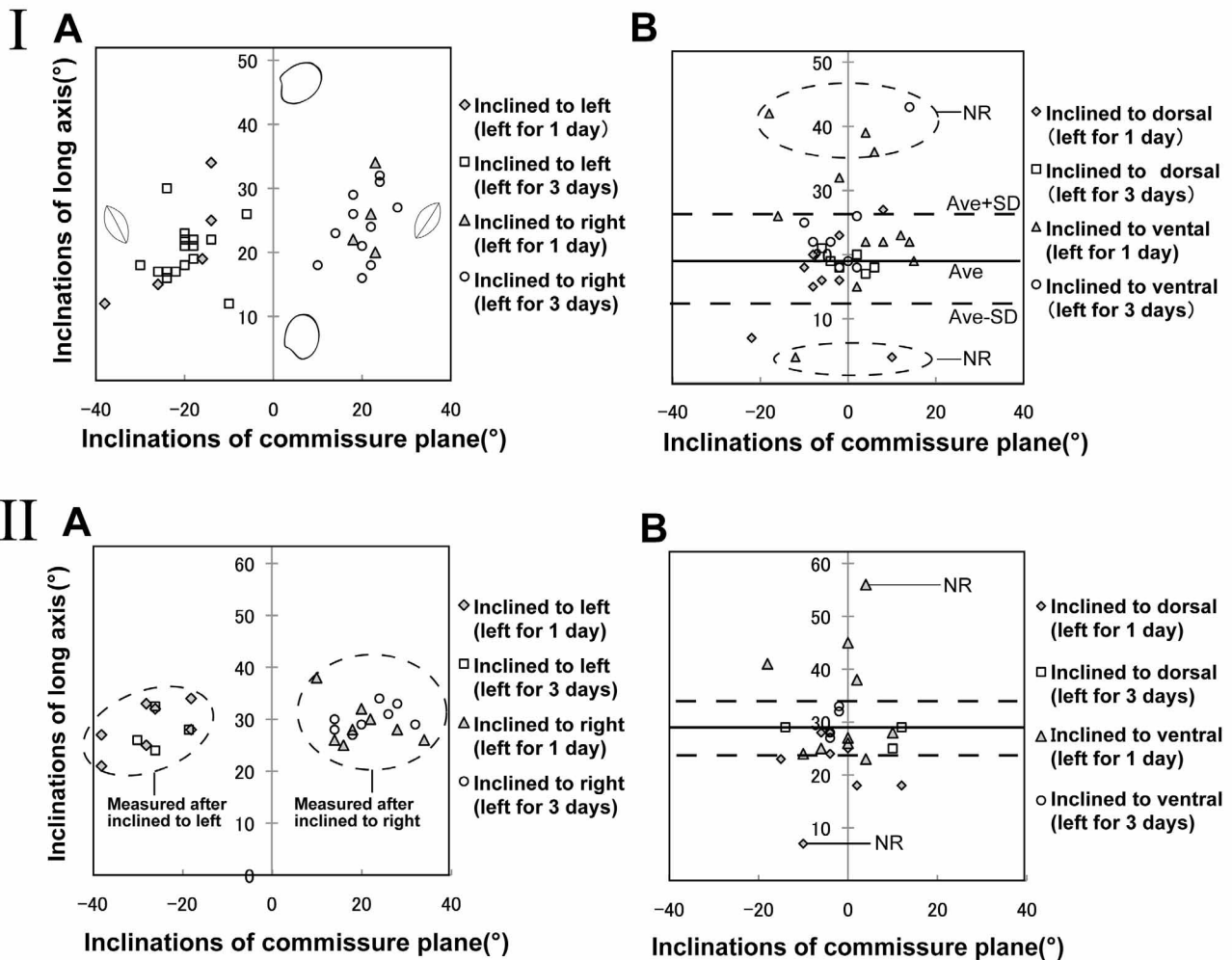


FIGURE 3. Scatter plots of the measurements made on *Ruditapes philippinarum* and *Mactra veneriformis* after tilting their aquaria. One plot expresses the measured orientation datum of an individual including degrees of inclination of the commissure plane and the long axis on the horizontal and vertical axes respectively.

I, *R. philippinarum*; II, *M. veneriformis*. **A.** Inclined ventrally or dorsally. **B.** Inclined to right or left. The average and \pm standard deviation of inclinations of long axis are shown by a solid line and dashed lines respectively. NR = non-returned (see text). Ave = Average of inclinations of long axis in normal position measured in Ujino and Matsukuma (2009). SD = standard deviation. inclinations of long axis in normal position measured in Ujino and Matsukuma (2009)

TABLE 2. Inclinations of long axis of the usual life orientations measured in Ujino and Matsukuma (2009) and in this study.

Species	Average ¹	SD ²	A±SD ³	A±2×SD ⁴	N ⁵
<i>S. kagosimensis</i>	24.1°	3.4°	10/16 (62.5%)	15/16 (93.7%)	32
<i>R. philippinarum</i>	19.0°	7.0°	31/37(83.4%)	33/37(89.1%)	72
<i>M. lusoria</i>	39.4°	4.4°	9/14(64.3%)	12/14(85.7%)	38
<i>M. petechialis</i>	48.9°	4.4°	8/13(61.5%)	12/13(92.3%)	32
<i>M. veneriformis</i>	28.9°	4.8°	16/25(64%)	20/25(80%)	54

¹ Average of usual life orientations from Ujino and Matsukuma (2009)

² Standard deviation of usual life orientations from Ujino and Matsukuma (2009).

³ The number and percentage of the individuals within the average ± standard deviation. The denominator value is the number of all individuals measured.

⁴ Within the average ± 2×standard deviation.

⁵ A Total number of individuals measured in this study.

Mann-Whitney U-tests were carried out on the values of inclinations of the long axis and commissure plane between individuals inclined dorsally or ventrally and those inclined to the right or left. The results were then statistically compared with normal orientation values.

In the tests, individuals inclined dorsally or ventrally can be thought to have normal values in inclinations of the commissure plane, and those inclined to the left or right can be regarded as having normal values in inclinations of the long axis. The results showed there were no significant differences between individuals inclined dorsally or ventrally and those inclined to the right or left, but obvious significant differences were seen in the inclinations of the commissure plane (Table 3).

TABLE 3. Results of Mann-Whitney U-test in the five species examined.

Species	D-RL	V-RL	R-DV	L-DV
<i>S. kagosimensis</i>	N	N	S	S
<i>R. philippinarum</i>	N	N	S	S
<i>M. lusoria</i>	N	N	S	S
<i>M. petechialis</i>	N	N	S	S
<i>M. veneriformis</i>	N	N	S	S

N= no significant difference ($p>0.05$), S= significant difference ($p<0.01$)

D-RL=results of U-test in inclinations of the long axis between the individuals inclined dorsally and inclined to the right or left. V-RL= results of U-test in inclinations of the long axis between the individuals inclined ventrally and inclined to the right or left. R-DV= results of U-test in inclinations of the commissure plane between the individuals inclined to the right and inclined dorsal-ventrally. L-DV= results of U-test in inclinations of the commissure plane between the individuals inclined to the left and inclined dorsal-ventrally.

We also observed individuals of *Mactra veneriformis* which burrowed only half-way and thus left part of their

shell exposed but adopted normal life orientation. Their response following aquarium inclination could be directly observed. When they were inclined ventrally or dorsally, they returned to their original position within about 10 minutes. However this behaviour was not observed when they were inclined to the right or left.

Discussion

Response behaviour when inclined dorsally or ventrally.

Most individuals that were inclined dorsally or ventrally showed normal life orientation values, and this was also statistically indicated by the U-test (Table 3). Of those individuals of the five species tested which did not return to life orientation, the measured orientation values were far from the average, because their values had been added to or reduced by about 20° by as a result of being inclined. Therefore, it is expected that individuals whose original values were near the average will return to their normal life orientation (Fig. 5A).

A few individuals of five species tested inclined dorsally or ventrally have values remote from their usual orientation. Most of these values become nearly close to average by reducing or adding 20°. Therefore, it is thought that these individuals did not return to their life orientations probably due to their poor condition. We marked the plots of these individuals as non-returned (NR) in Figs 3 and 4.

These response behaviours indicate that the specimens orient themselves based at least in part on the angle of their body to gravity. We assume this because the other conditions are altered only minimally and there is no reason for them to restore their positions if they were orienting themselves based on other conditions such as inclination of substrate, conditions of sediment surface, and light direction, Although the angle of the light entering the tank changed slightly by tilting the aquarium. It also changed during the day, so if the bivalves oriented based on light direction, they would change their orientation as the sunlight direction changed. We saw no evidence of this occurring.

It is remarkable that individuals of the arcid *Scapharca kagosimensis* restored their position. Infaunal species of the Arcidae orient themselves with their posterior shell surface nearly parallel to the sediment surface (Stanley, 1970), which implied that these arcid species orientate themselves relative to the sediment surface. However this species in the present study was observed orienting regardless of the relation to the sediment surface. For example, they sometimes exposed part of the posterior section of the shell when inclined ventrally. Such behaviour indicates that their control of life orientation strongly depends on the relationship of their body angle to gravity.

Response behaviour when inclined to the right or left.

The distributions of the orientation angles when the shell is inclined to the right or left are obviously biased as indicated statistically by the U-test of the values of the commissure plane when compared with the individuals

inclined to the right or left and dorso-ventrally (Table 3). This result indicates that specimens did not resume their original position (Fig. 5B). These distributions often include individuals that inclined their commissure planes strongly. These probably inclined somewhat before being tilted, and

were made to incline more strongly by tilting the aquarium. This evidence implies that infaunal bivalves do not usually resume their position when they are strongly inclined to the right or left.

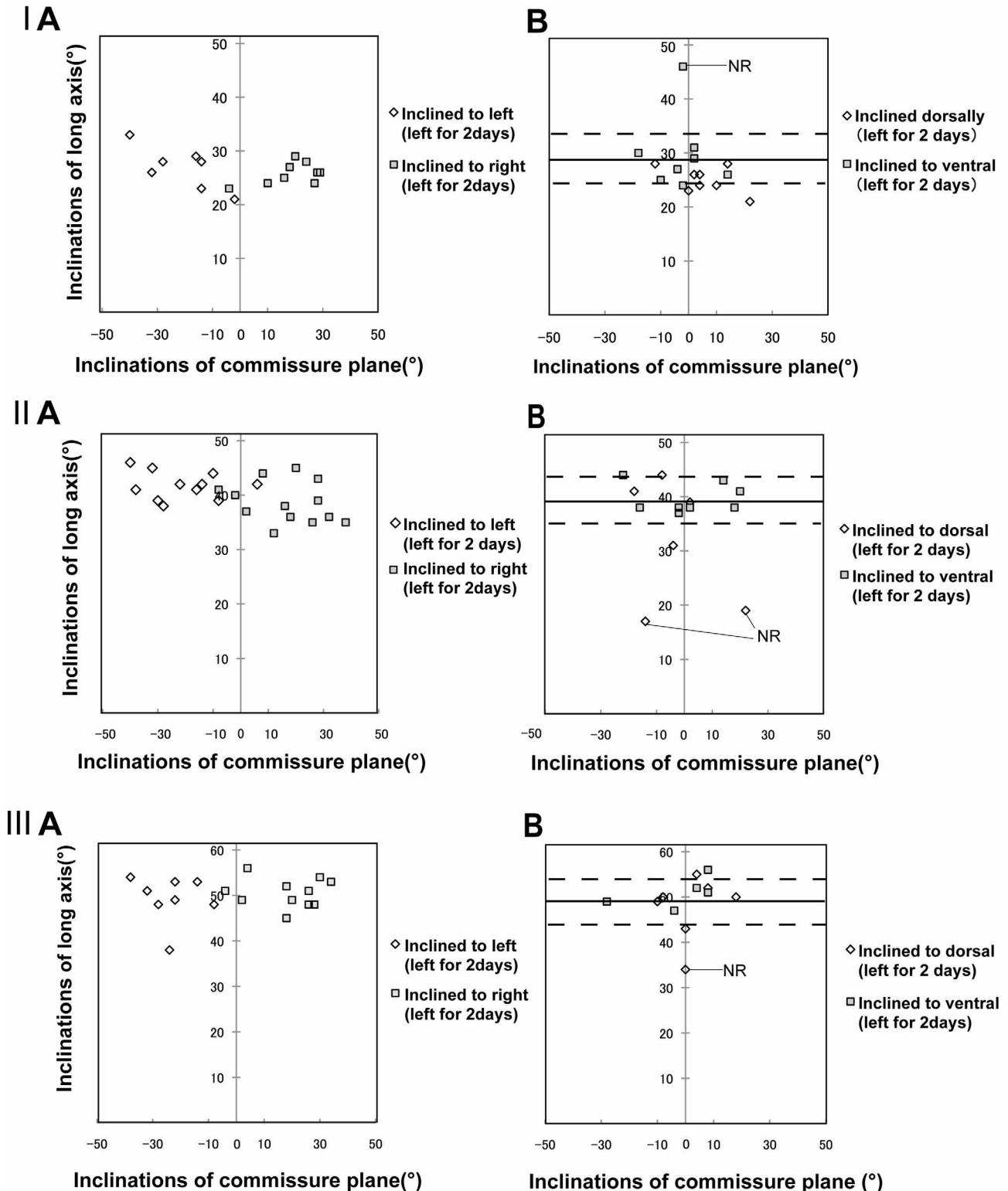


FIGURE 4. Scatter plot showing the measurement of the angle of inclination in *Meretrix lusoria*, *Meretrix petechialis* and *Scapharca kagoshimensis*. **I**, *M. lusoria* **II**, *M. petechialis* **III**, *S. kagoshimensis*. **A**. Inclined ventrally or dorsally. **B**. Inclined to right or left. The average and \pm standard deviation of inclinations of long axis are shown by a solid line and dashed lines respectively. NR- non-returned (see text).

The difference in response between the inclination directions is likely to be caused by their type of movement in the substratum (see Introduction). Antero-posterior rotation is more easily achieved than right-left rotation in most infaunal bivalves. Therefore bivalves in the present study probably did not resume their position when tilted in the left-right plane because this change in orientation is difficult and consumes considerable energy. This suggests that the antero-posteriorly rotating movement of infaunal bivalves also influences their behaviours when controlling life orientations.

These observations provide an explanation regarding life orientations that could not be explained by Ujino and

Matsukuma (2009). At that time the authors detected a trend for small sized individuals to show great diversity in inclination angle of the commissure plane in some species, but this trend is not detected in the inclination of the long axis. Ujino and Matsukuma (2009) thought that this trend reflected differences in the stability of the substratum, with small individuals being shifted more easily by the water current or other factors. This study shows that this trend was detected only in the inclination of the commissure plane because the specimens regain their antero-posterior orientation themselves if they are shifted.

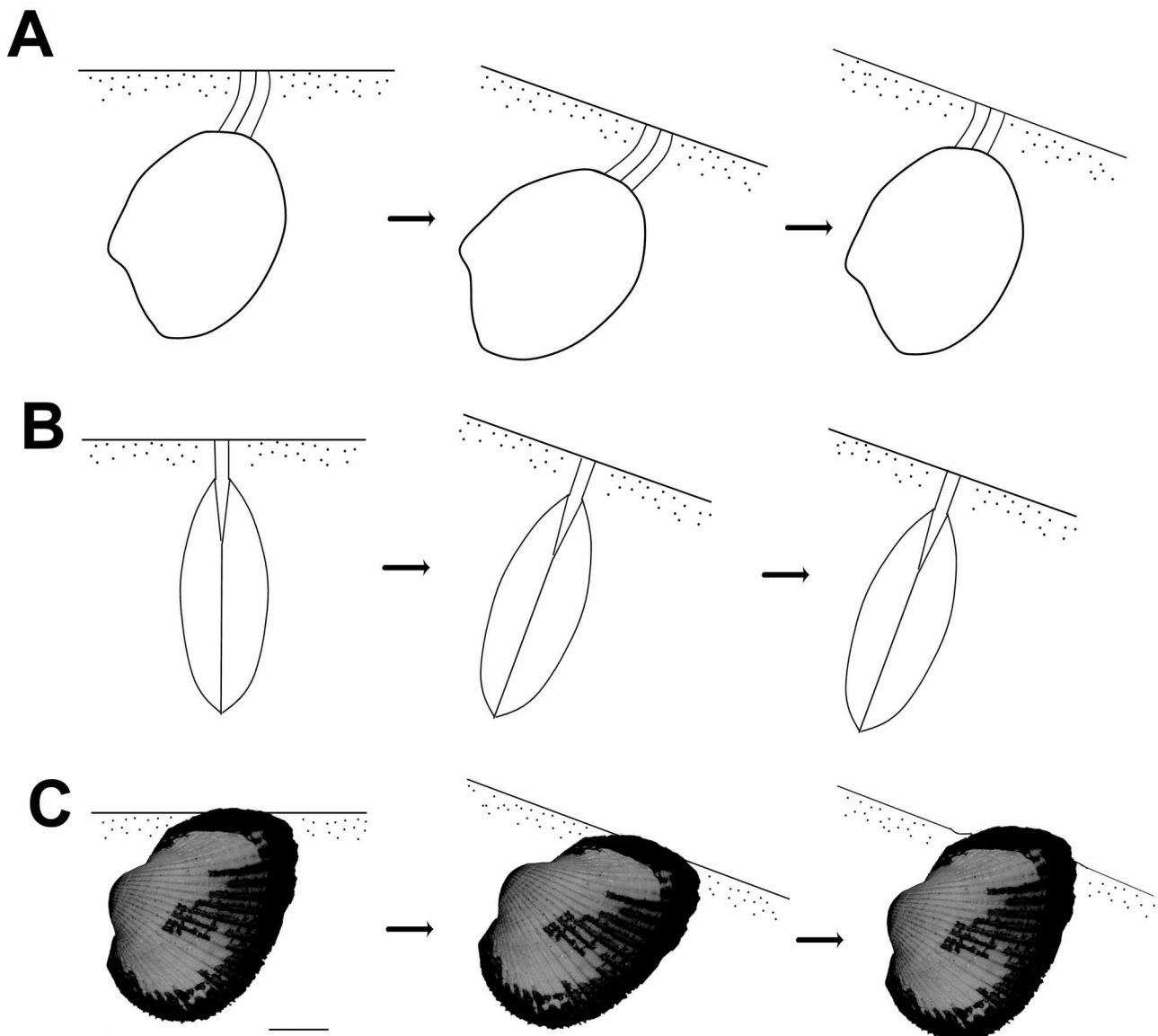


FIGURE 5. Difference of the response behaviour when an individual is inclined ventrally and to the right. **A.** Inclined ventrally—it returns to its life orientation. **B.** Inclined to the right—it does not return to its life orientation. **C.** The response behaviour of *Scapharca kagoshimensis* when inclined ventrally. Sometimes they expose part of their posterior shell. Scale bar = 1 cm.

The significance of life orientation

The results of our series of studies indicate that there is some significance in the specific life orientations seen in

each species. This is especially so in the anteroposterior plane, as shown by quantitative measurement in Ujino and Matsukuma (2009) and we show here in that they recover

their position when they are inclined by up to 20°. Furthermore, the significant differences in life orientation between two closely related species of *Meretrix* Lamarck, 1799 reported by Ujino and Matsukuma (2009) was also detected in the present study even after they resumed their original position. This indicates that different species assume their particular orientation by an innate response and that the life orientation is not taxonomically conservative.

A vertical orientation of the commissure plane would enable the bivalves to burrow deeper more efficiently than if they had adopted an inclined position and they would thus not require a change of orientation in the substratum. On the other hand, the significance of an inclined long axis is harder to explain. We can infer that they need to extend their siphons to the surface of the sediment in the most efficient way, and that stretching their siphon vertically is the best way to achieve this. However many bivalves in our studies do not adopt such orientations but often incline their shells somewhat and their siphons are extended diagonally.

We propose a new interpretation as to the significance of the antero-posterior life orientation of infaunal bivalves with siphons. With respect to initial burrowing into substrata, many bivalves incline their bodies more ventrally than in their final life orientation because their foot position is defined by their body plan. Most infaunal bivalves must extend their foot from the antero-ventral part of their body and inclination of the body is necessary to achieve efficient burrowing. Having a life position that is the same as the burrowing position is useful because they can quickly reburrow again when they are exposed. However, an angled orientation is inefficient in terms of extending their siphons to the sediment surface, because the siphon must be curved (Fig. 6C). On the other hand, a life orientation with the siphon stretched straight and vertically is too far from the burrowing position and makes it difficult to reburrow quickly (Fig. 6A). Therefore, most bivalves probably adopt an intermediate position between these orientations (Fig. 6B). However, these ideas have not been confirmed and testing is required.

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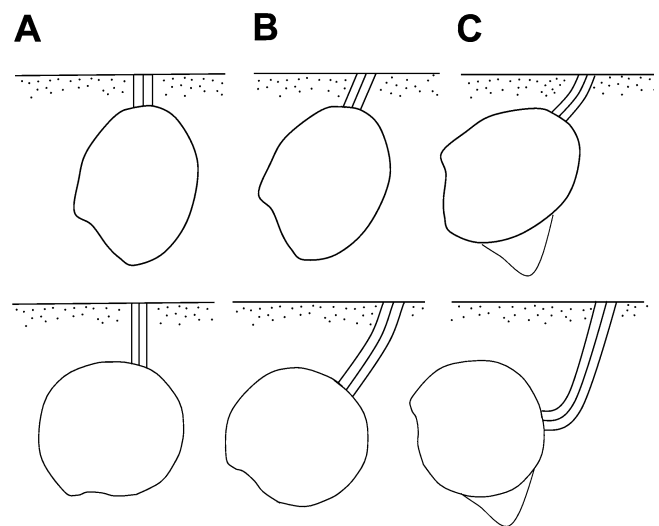


FIGURE 6. Three types of life orientation. **A.** The orientation in which the siphon can reach the surface of sediment most efficiently. **B.** Usual life orientations of infaunal bivalves. These are intermediate positions between A and C. **C.** Life orientation the same as the burrowing position. The siphon must extend further or curve.

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