Adaptive evolution in spatangoid echinoids living in the shallow sublittoral zone

Masaya Saitoh

Graduate School of Science
Course of Biological Sciences
Kanagawa University
Student no. 201170261

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Abstract

In spatangoids new types of test morphology related to new modes of life suddenly appeared in the Eocene. This morphological change was probably induced by predation of cassid gastropods which appeared in the same regions in the same epoch with the new type spatangoids. Flat tests with long, stout spines on the dorsal and ventral sides, as in *Lovenia*, probably burrowed near the sediment surface and enabled the urchins to escape from gastropod attack by emerging onto sediment surface. Oval tests with the specific ventral morphology for efficient burrowing, as in *Brissus*, allowed the spatangoids to burrow deeply in sand to avoid the gastropod predation. From Eocene to Miocene, these spatangoids apparently struggled along with the co-existing gastropods. However, when the predators with the shell size about 4 times larger than their prey spatangoids appeared, many of the spatangoids have left their habitats and evolved into deep water environment, the very shallow sublittoral zone and the temperate zone where the predatory cassid gastropods did not live. In the very shallow sublittoral zone, the morphologies for anti-predation probably facilitated the sea urchins to inhabit the unstable environments. The spatangoids with the ability for burrowing deep in sand can avoid being washed out to death in storm disturbance. The spatangoids with the ability for rapid and powerful movement can burrow deeper than usual before it is washed out by currents. In contrast to these spatangoids, there is other type of spatangoids that live in the unstable environment without specific morphology against either predation or storm disturbance, indicating that their ancestors would not have suffered cassid predation. They adapt there with a specific trade-off between test growth and sexual maturity in their life history; it reduces the cost of test construction with very thin plates and allocates more energy to the development of the gonads, resulting in certain alternation of generations. Thus, spatangoids adapt to the shallow sublittoral zone in different ways depending on their respective evolutionary histories.

I. General introduction

Spatangoid echinoids appeared in the Early Cretaceous and made a conspicuous dramatic diversification during the Eocene. Today, they live in a variety of substrates from intertidal to abyssal zones down to 5000 meters in all oceans. Because of their calcareous skeletons and the infaunal mode of life, there are a lot of fossil records. Spatangoid echinoids, therefore, are good materials suitable for studying long-term, continuous evolution. Actually, many taxonomic and phylogenetic studies have been made on the basis of their skeletons mainly by paleontologists (e.g. Rowe 1899; Kermack 1954; Fischer 1966; Ernst 1972; Stokes 1977; Smith & Stockley 2005; Kroh & Smith 2010). Also, their morphologies with respect to function, ontogeny, evolution, etc. have been studied in detail (e.g. Nichols 1959; Smith 1980; McNamara 1987; Kanazawa 1992; Nérauderau *et al.* 1998; Eble 2000; Villier *et al.* 2004; Saucède *et al.* 2006). In contrast to the extensive knowledge from these fields, surprisingly little is known about their ecology. This is probably attributable to the difficulty *in situ* observation of spatangoids; diving observation should be made for it. Only some species have been intensively studied: Brattström (1946) for *Brissopsis lyrifera* (Forbes); Moore & Lopez (1966) for *Moira atropos* (Lamarck); Chesher (1969) for *Meoma ventricos* (Lamarck); Ferber & Lawrence (1976) for *Lovenia elongata* (Gray); Moore (1936), Buchanan (1966), Beukema (1985), De Ridder & Jangoux (1987, 1993), Nakamura (2001), Nunes & Jangoux (2004, 2007) for *Echinocardium cordatum* (Pennant); Schinner (1993) for *Schizaster canaliferus* (Lamarck); Thompson & Riddle (2005) for *Abatus ingens* (Koehler). These studies have shown that each spatangoid species is well adapted to its habitat with a specific ecology in relation to the environmental condition, such as substratum and water depth. Only from the results of these studies, however, it is not easy to identify the factors that control the distribution of the spatangoids. Each study dealt with one species, and the ecological data were taken only from the area in which the target echinoid lived and not from the surrounding area. Astonishingly, there has been no comprehensive ecological study on several spatangoids, which live in an area, and thus it is still difficult to consider the factors that allow the spatangoids to live in aparticular area.

Spatangoid echinoids are highly diversified in the shallow sublittoral zone, where various kinds of spatangoids are adapted to their respective habitats (Mortensen 1951). Fortunately, in the shallow water environment it is relatively easy to obtain their ecological data directly from their habitats on the sea floor by diving. If the ecological investigation into several spatangoid species in an area is possible, a great deal can be learned about the factors controlling the spatangoid distribution by comparative analysis of the ecological data on each species (§ II). The ecological knowledge of the Recent spatangoids eventually makes it possible to study the adaptive evolution in spatangoid echinoids.

Fossil echinoids, including burrowing irregular echinoids, are known to have suffered high levels of predation from the cassid gastropods because there are many fossil echinoid tests with predatory holes (Fig.1) presumably produced by gastropods (e.g. Beu 1972; McNamara 1994). McNamara (1994) demonstrated that from late Oligocene to Early Miocene in Australia many spatangoids suffered quite high levels of predation from the cassid gastropods, and thereby the successive species migrated into the regions of lower predation pressure. Kanazawa (2004) indicated that the morphological diversification which occurred in spatanogids in the Eocene was presumably brought about by cassid predation because the new types of morphology apparently enable the spatangoids to escape from the predators. These studies imply that cassid predation was an important factor which presumably controlled the adaptation of spatangoids. There is, however, no other previous study that showed the impact of gastropod predation on evolution of spatangoids. To be able to assess the significance of cassid predation, it is necessary to know the mode of cassid predation on spatangoids (§ III).

With the information obtained from these different sources a possible adaptive significance can be ascribed to the evolution of spatangoid echinoids in the Cenozoic (§ IV).

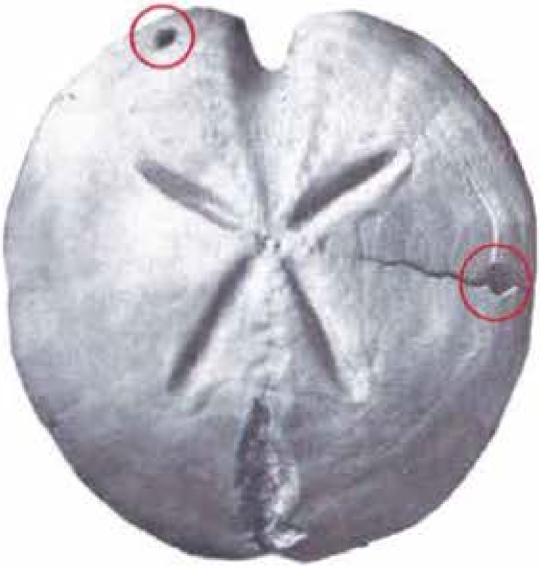


Fig.1. A fossil spatangoid test with predatory hole. Two holes are indicated by red circles. *Pericosmus crawfordi* (Beu et al 1972).

II. Adaptation for living in the shallow sublittoral zone in spatangoid echinoids

1. Introduction

For a comprehensive ecological study on spatangoids, the Oki-Islands in Japan Sea are excellent. Six spatangoid species live in an area about 1 km^2 at water depths of 5-18 m, where there are different kinds of environments that apparently enable the six different spatangoids to inhabit such a small area. In these spatangoids, their special modes of burrowing, feeding, respiration and locomotion are closely correlated with the particle size of the substratum in which they live, and this adaptation is expressed in many features of their tests, in particular the position and degree of development of the fascioles (special bands of heavily ciliated spines), and the division of labor in the tube-feet and spines, which show a marked specialization in different parts of the test (e.g. Nichols 1959; Smith 1980a, 1980b; Kanazawa 1992 etc.). Here, based on field investigations and aquarium experiments, the factors that control the spatangoid distribution in the shallow sublittoral zone are examined from the viewpoint of adaptive morphology and life history strategy.

2. Material & Methods

Field work

Field investigations were carried out around Takugi village of the Oki-Islands in Japan Sea (Fig.2). Observations and specimen collection were made by scuba diving at five stations at depths from 5 to 18 m (Fig.3). In each station, the investigation area about 80 m^2 was defined by locating posts on the seafloor. Six spatangoid species, *Lovenia elongata* (Gray), *Nacosptangus alta* (A. Agassiz), *Metalia spatagus* (Linnaeus), *Brissus agassizii* Döderlein, *Echinocardium* *cordatum* (Pennant) and *Moira lachesinella* Mortensen were found in all the stations. Echinoids were collected by digging in sand manually. The water turbulence conditions of sediment surfaces at the stations were examined through ripple marks made by water disturbance on the sea floor and through the substratum particle size distribution tested afterwards by sieving the surface sediment. The field investigations were carried out 21 times between November 2007 and July 2013 (November 2007; April and October 2008; January, May, August and November 2009; February, May, July and November 2010; April, June, July, September and October 2011; April, July and November 2012; May and July 2013). Diving operations were conducted in daytime, except station E, where they were done at night as well in April and October 2008.

Fig.2. Map of Japan and adjacent regions. The study area (Oki-Islands) is located in the Japan Sea.

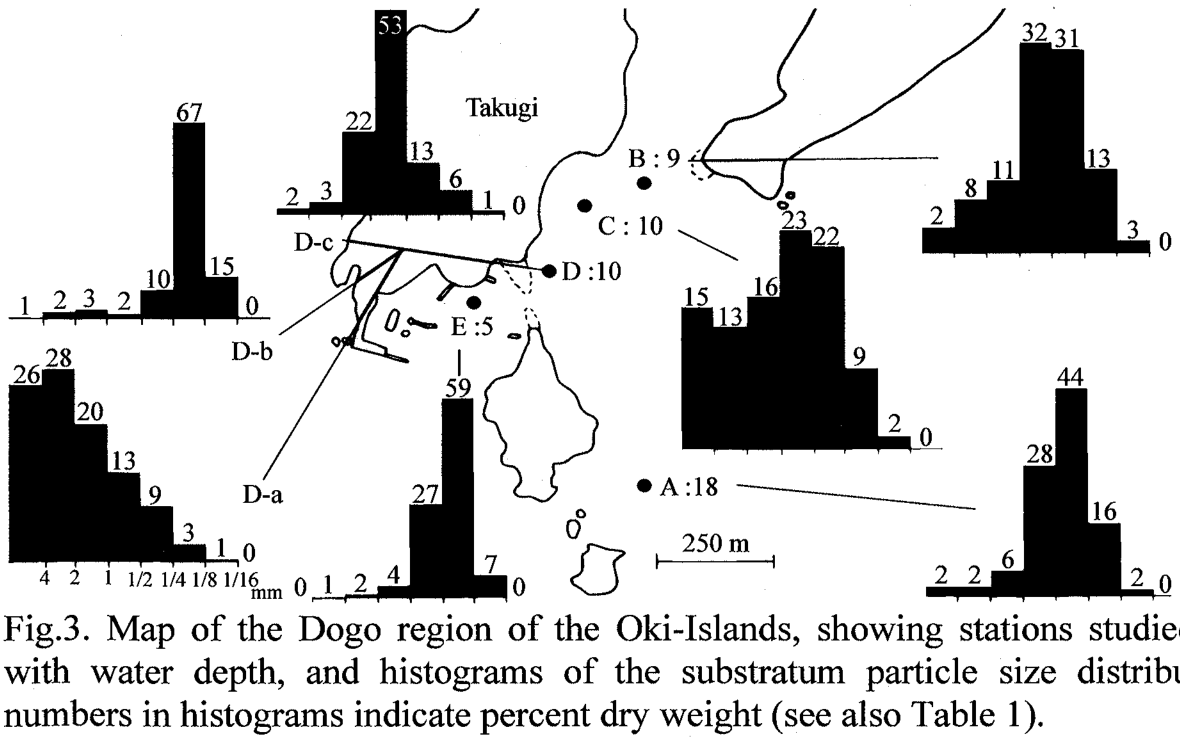


Fig.3. Map of the Dogo region of the Oki-Islands, showing stations studied (●) with water depth, and histograms of the substratum particle size distribution; numbers in histograms indicate percent dry weight (see also Table 1).

Laboratory work

The animals used for the following experiments were transported from the Oki-Islands to the laboratory of Kanagawa University. To avoid overheating and damage to the specimens, they were carried with a cooler-box and the spatangoids were kept in sediment, taking approximately 7 hours to the laboratory. Subsequently, they were immediately placed in a marine aquarium with circulating sea water maintained at 18 ° C. Terminology of the morphology used in this study is given in Fig.4.

Morphology and behavior in relation to respiration

The placement of fascioles on the test and the current produced around a echinoid in the sediment were examined. Red food dye was used for tracing the course of currents. Also, apical tuft spines which form an apical funnel to draw fresh sea water from sediment surface, were observed. In order to check the effectiveness of an apical funnel, a spatangoid whose apical tuft spines were cut off was allowed to burrow in fine-grained sand in an aquarium and its behavior was observed.

Morphology and behavior in relation to burrowing

Focusing on the test morphology and related function of spines, burrowing behavior of the spatangoids was examined in aquaria. The activity in the sediment was observed when the urchin appeared at a sidewall of an aquarium. The different kinds of sediments taken from their habitats were used for the experiments, and each echinoid was allowed to burrow not only in the native sediment but also in non-native sediment in different grain size.

Behaviors under water disturbance

The behaviors of the spatangoids under water disturbance were examined in an aquarium. After a sea urchin had completely burrowed into the native sediment, the currents were produced manually by waving a hand in the aquarium, and the sediment overlying a burrowing echinoid was washed away at a rate of 6-10 cm per minute. The behavior of the urchin was recorded by a video camera.

Righting and re-burrowing on the sediment

In an aquarium, each animal was placed in an upside-down position on the native sediment surface and its speed of righting and re-burrowing was measured. In this experiment, 3 individuals (40, 38 and 30mm in test length) for *Lovenia elongata*, 6 (30, 30, 33, 35, 38 and 40) for *Nacospatangus alta*, 2 (35, and 45mm) for *Metalia spatagus*, and 4 (35, 40, 41 and 52) for *Brissus agassizii* were used.

Population dynamics

For every specimen collected in each investigation, the length, width and height of the test were measured, and the number of specimens was counted. The size frequency distributions of each species were made in each investigation for analysis of the population dynamics.

Sexual maturity of gonads

From April 2011 to November 2012 (April, June, July, October 2011 and April, July, November 2012) the gonads of the collected specimens were extracted from the tests and examined. The gonads were fixed for 24 h in Bouin's fluid. In order to determine the gonadal stage of the gonads, they were dehydrated, embedded in paraffin, cut into 5-µm thick sections, stained with Mayer's Hematoxylin & Eosin, and observed under a digital microscope (Keyence VHX-D510). From July 2010 to April 2011 (July, November 2010 and April 2011), for the observation of spawning the collected specimens were injected a 1M KCl through the mouth to test inside.

Nutrients contained in the sediment

The sediments of the spatangoid habitats were collected by coring sediments by pipes (about 30 cm) so as to obtain them as columns with the original layers in the sediments. The columns of the collected sediments were sectioned into three parts; from sediment surface to 5 cm deep, from 5 to 10 cm deep, and from 10 to 15 cm deep. The sediments were dried at 30 ^{o}C. The protein contained in 10 g of the dried sediment of each part was extracted using NaOH 1 N for 10 minutes and the lipid contained in 10 g of the dried sediment of each part was extracted using a 2/1 dichloromethane-methanol mixture for 10 minutes, as performed by C. De Ridder *et al.* (1985). In accordance with Jangoux *et al.* (1977), cristalline bovine serum albumin was used as a standard and the optical density was determined using the standard cells at ranging from 700 to 800 nm in a Spectrophotometer (Shimadzu MultiSpec).

Morphology and behavior in relation to feeding

The morphology of the phyllode tube feet, which are arranged around the mouth and used for feeding, in the four spatangoid species was observed under a digital microscope (Keyence VHX-D510). The pores connected to the tube feet were counted and their arrangements were observed. In an aquarium, the behavior of the tube feet in three spatangoids (*L. elongata*, *N. alta* and *B. agassizii*) burrowing in transparent medium (superabsorbent polymer) were observed from the bottom of the aquarium (Fig. 5).

Allometric growth in ventral plates

On the ventral side of spatangoids there are two types of spines that play important roles for burrowing and locomotion. One is plastron spines on interambulacrum 5, which provide the principal thrust for forward locomotion and another is latero-ventral spines on interambulacra 1 & 4, which transport excavated sediment posteriorly though in an exceptional species, *L. elongata*, the latero-ventral spines provide the principal thrust. In order to examine whether the functional significance of these spines would change during the time of growth, two areas on which different types of spines occur respectively, namely, plates 2ab of interamb. 1 and those of interamb. 5 were measured in comparison to the area of plates 2ab of ambulacrum I, on which there is no spine, and the total area of the ventral side, using a digital microscope (Keyence VHX-600). The measured plates were showed in Fig. 6.

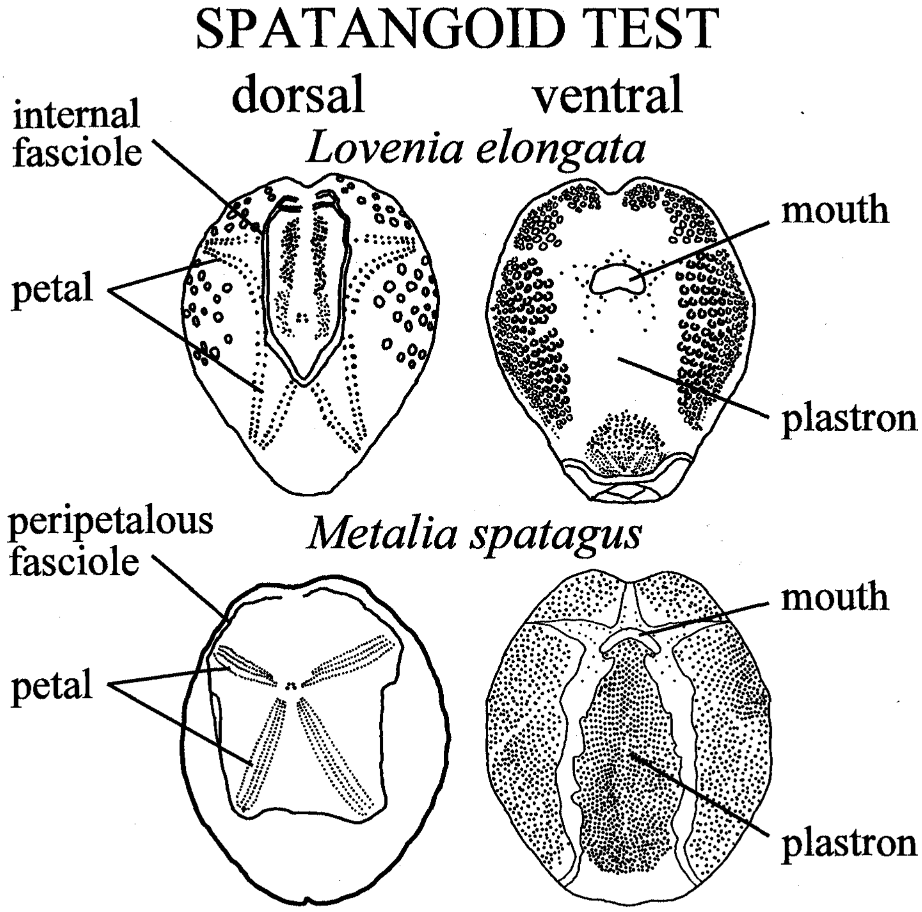


Fig.4. Main features of the test of a spatangoid echinoid.

Fig.5. *L. elongata* burrowing in transparent medium.

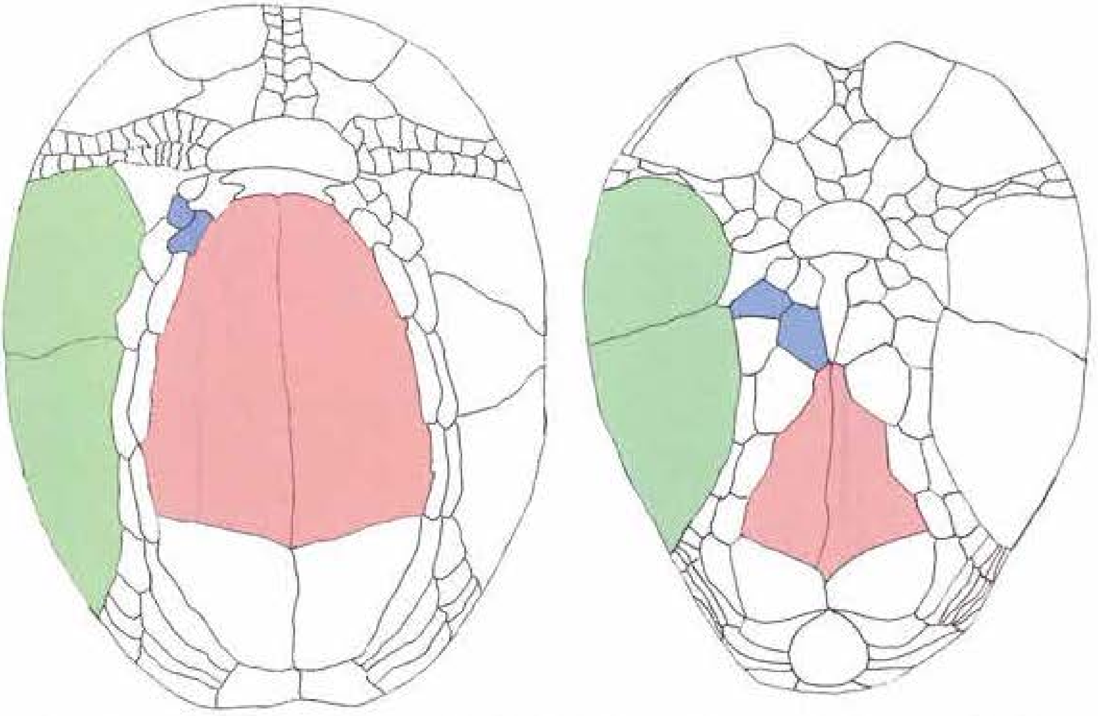


Fig.6. The plates measured for analysis of allometric growth in ventral plates. Each area of the colored paired plate is measured. red, plastron with the spines providing the principal thrust for forward locomotion; green, latero-ventral plates with the spines transporting excavated sediment to the posterior; blue, amb. I plates without functional spines for burrowing. left, *B. agassizii*; right, *L. elongata*

3. Results

Habitat condition in the Oki-Islands

The investigated area is located in a protected bay surrounded by capes and islands and is usually calm except at times of storm. In the Oki-Islands as well as other coastal regions of the Japan Sea, strong storms come in winter: ripple marks about 5 cm high and 20-30 cm wave length formed by storm disturbance were frequently observed on the sea floors at depths shallower than 10 m and sometimes at depths from 10 to 18 m during winter and early spring (Fig.7). Dead tests of *N. alta* were often found on sediment surfaces at depths shallower than 10 m in spring (Fig.8) and numerous dead tests of *M. spatagus* were observed once at the station B at a depth of 9 m in April 2008 (Fig.9). In other seasons ripple marks were rarely observed on the bottoms at depths deeper than 5 m except after a typhoon. The substratum particle size distribution in each station is shown in Fig.3.

Fig.7. In the investigation after winter (April 2008), dead test of spatangoids and ripple marks were observed on the sea floor.

Fig.8. Dead test of *N. alta*. The dead tests were often observed at water depth shallower than 10m.

Fig.9. Numerous dead tests of *M. spatagus*. They were once observed at a depth of 9 m in April 2008.

Spatangoid in their habitats

Only *Lovenia elongata* was observed in a variety of habitats in different conditions, while the other five species were found in distinct habitats, depending on substratum and water depth (Table 1).

Lovenia elongata (Fig.10A)

L. elongata was found at water depths of 5 to 18 m (stations A, B, C, D-b, E). The animals burrowed in various kinds of sediments from fine- to coarse-grained sand with the apex 2 to 3 cm below the sediment surface. Many individuals were observed in fine-grained sand at the station E where other sea urchins were rarely found. The burrowing depths of small and large individuals were not different.

Nacospatangus alta (Fig.10B)

N. alta was found at water depths of 9 to 18 m (stations A, B, C, D-c). It burrows in medium- to coarse-grained sand with the apex 2 to 3 cm below the sediment surface. The burrowing depth for small and large individuals were not different.

Metalia spatagus (Fig.10C) *and Brissus agassizii* (Fig.10D)

These spatanogids lived in gravely coarse-grained sand at water depths of 9 to 18 m (stations A, B, C, D-a). Large individuals more than 5 cm test length burrowed 10 to 15 cm deep below the sediment surface, while small ones burrowed only about 5 cm deep.

Echinocardium cordatum and Moira lachesinella

These echinoids were rarely found in the investigated area. They were observed only at the station E, burrowing 10 to 15 cm deep in fine-grained sand.

Table 1. Habitats of the spatangoids studied

Station	Depth (m)	Substratum	Sea grass	Species observed					
				L. elongata	*N. alta*	*M. spatagus*	*B. agassizii*	*E. cordatum*	*M. lachesinella*
A	18	m-c sand	scarcely	25(4%)	209(55%)	35(20%)	7(7%)	1	0
B	9	g m-c sand	patchily	140(21%)	33(9%)	61(34%)	37(36%)	7	0
C	10	g m-c sand	all around	105(16%)	109(29%)	44(24%)	15(14%)	0	0
D-a	10	g c sand	scarcely	0(0%)	0(0%)	38(21%)	44(32%)	0	0
D-b	10	f sand	patchily	129(20%)	0(0%)	0(0%)	0(0%)	2	0
D-c	10	m sand	patchily	0(0%)	19(5%)	0(0%)	0(0%)	0	0
E	5	f sand	patchily	259(39%)	7(2%)	1(1%)	1(1%)	5	4

m-c, medium- to coarse-grained; g, gravelly; c, coarse-grained; m, medium-grained; f, fine-grained

In each species the number and percentage of individuals show the cumulative figure for three-year investigation.

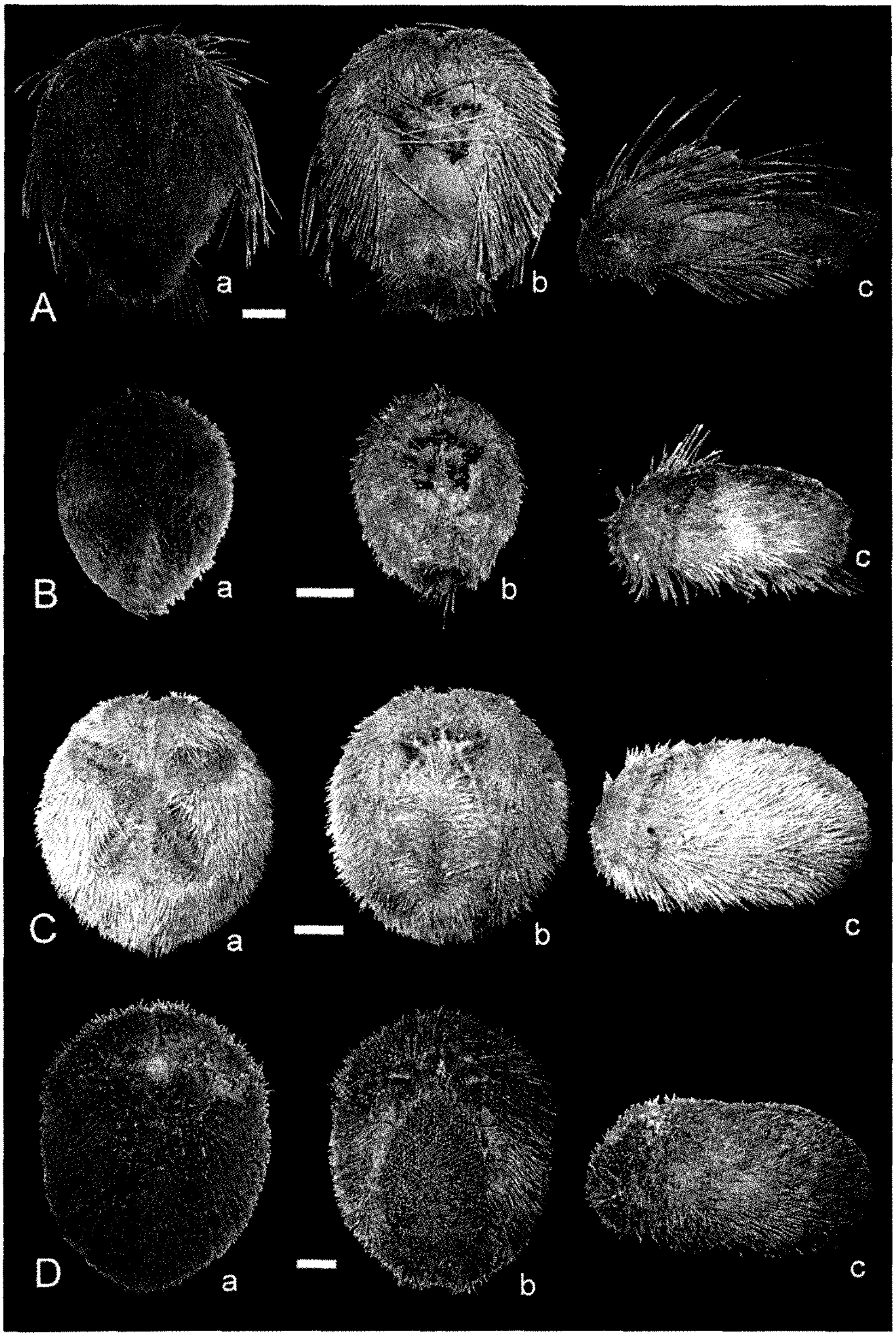


Fig.10. Spatangoids examined in this study. A, *Lovenia elongata* (64 mm long); B, *Nacospatangus alta* (44 mm long); C, *Metalia spatagus* (70 mm long); D, *Brissus agassizii* (76 mm long): a, dorsal side; b, ventral side; c, lateral side. Scale bar is 10 mm.

Morphology and behavior in relation to respiration

L. elongata has an internal fasciole and an apical tuft on the dorsal side. In an aquarium, the sea urchin burrowed in fine-grained sand with the apex 1 to 2 cm below the sediment surface, constructing an apical funnel to the sediment surface. There was a water current drawn from the sediment surface into the apical funnel induced by movement of spines. No other current into the burrow was observed. When the apical tuft spines were cut off, the animal was not completely buried with the apex exposed on the sediment surface. *N. alta* has neither fasciole nor apical tuft on the dorsal side. In an aquarium, the sea urchin was entirely buried in medium- to coarse-grained sand with the apex 1 to 2 cm below the surface. On the sediment surface above the animal no water current filtering through the sediment onto the dorsal area was observed. In fine-grained sand it burrowed exposing the apex on the sediment surface. *M. spatagus* and *B. agassizii* have peripetalous fasciole and no apical tuft on the dorsal sides. In an aquarium, *M. spatagus* and *B. agassizii* burrowed about 10 to 15 cm deep below the sediment surface in coarse-grained sand. In fine-grained sand, the sea urchins burrowed exposing the petalodium on the sediment surface. When the urchins burrowed about 1 to 2 cm deep below the sediment surface, a water current filtering from the sediment surface approximately above the petal region into the burrow was observed.

Morphology and behavior in relation to burrowing

L. elongata has a completely flat oral side, i.e. an entirely flat plastron and no stern-like postero-ventral shape(Fig.10Ab and 14c, d). The flat oral side brings the latero-ventral spines into contact with the bottom of the burrow. Their backward-directed power strokes propel the urchin forwards. The latero-ventral spines also transport the sand excavated in front to the latero-posterior end and push it into the surrounding sand because the flat ventral surface leaves no space below the test for accumulating the transported sand (Fig.11). This burrowing mechanism appears to be useful only in the superficial layer of sediment. In *N. alta* the posterior part of the plastron is slightly projecting, forming a somewhat stern-like shape (Fig.10Bb). In this sea urchin, the plastron spines as well as the latero-ventral spines provide the principal thrust for forward locomotion. The slightly stern-shaped postero-ventral region produces a small space below the latero-ventral area of the test for accumulating the sand excavated in front and transported to the posterior, though the sand is rejected to some extent into the surrounding sediment. *M. spatagus* and *B. agassizii* have inflated plastrons and a remarkable stern-like postero-ventral shape(Fig.10Cb and Db, Fig.14a and b). They also have a much more tuberculated plastron and larger sterna plates in comparison to *L. elongata* and *N. alta*. The elevated plastron brings the plastron spines into contact with the floor of the burrow, whereby the spines support the test. Their backward-directed power strokes provide the principal thrust for forward locomotion. The elevated plastron also provides the latero-ventral spines with a convenient space under the test to transport excavated sediment posteriorly. The stern-shaped latero-ventral region produces a large space adequate to accumulate the posteriorly transported sand below the latero-posterior area of the test without pushing it into the surrounding sediment. This morphology presumably enables the spatangoids to burrow deeply in sediment where the pressure of surrounding sediment is expected to be much greater than near the sediment surface.

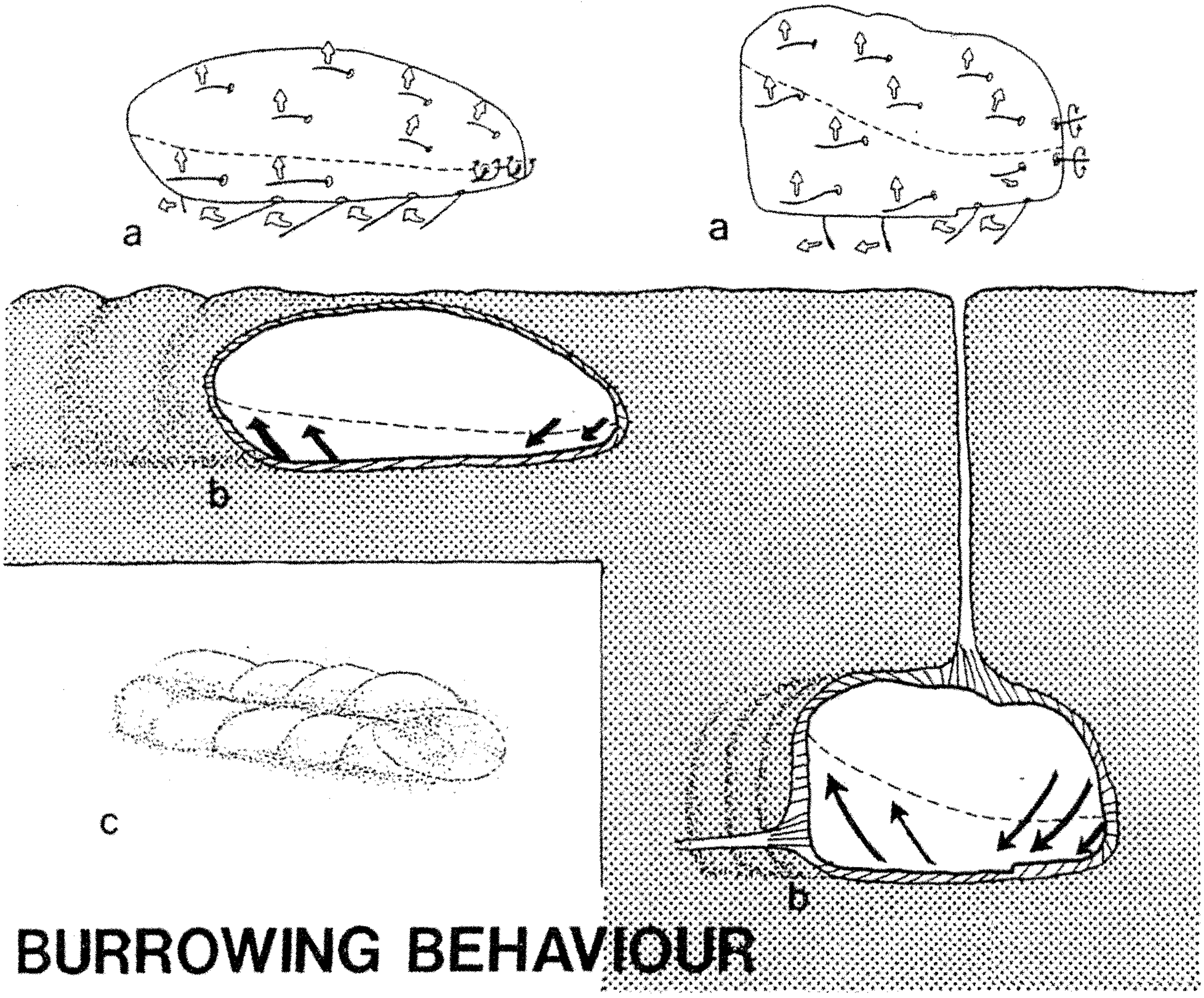


Fig.11. Two types of burrowing mechanism in spatangpids. *Lovenia* type (left) and *Brissus* type. a, posture of spines and the direction of the power strokes (open arrows); b, movement of excavated sediment (solid arrows); c, a set of two mounds formed on the sediment surface behind a burrowing *Lovenia elongata*. (modified from Kanazawa 1992)

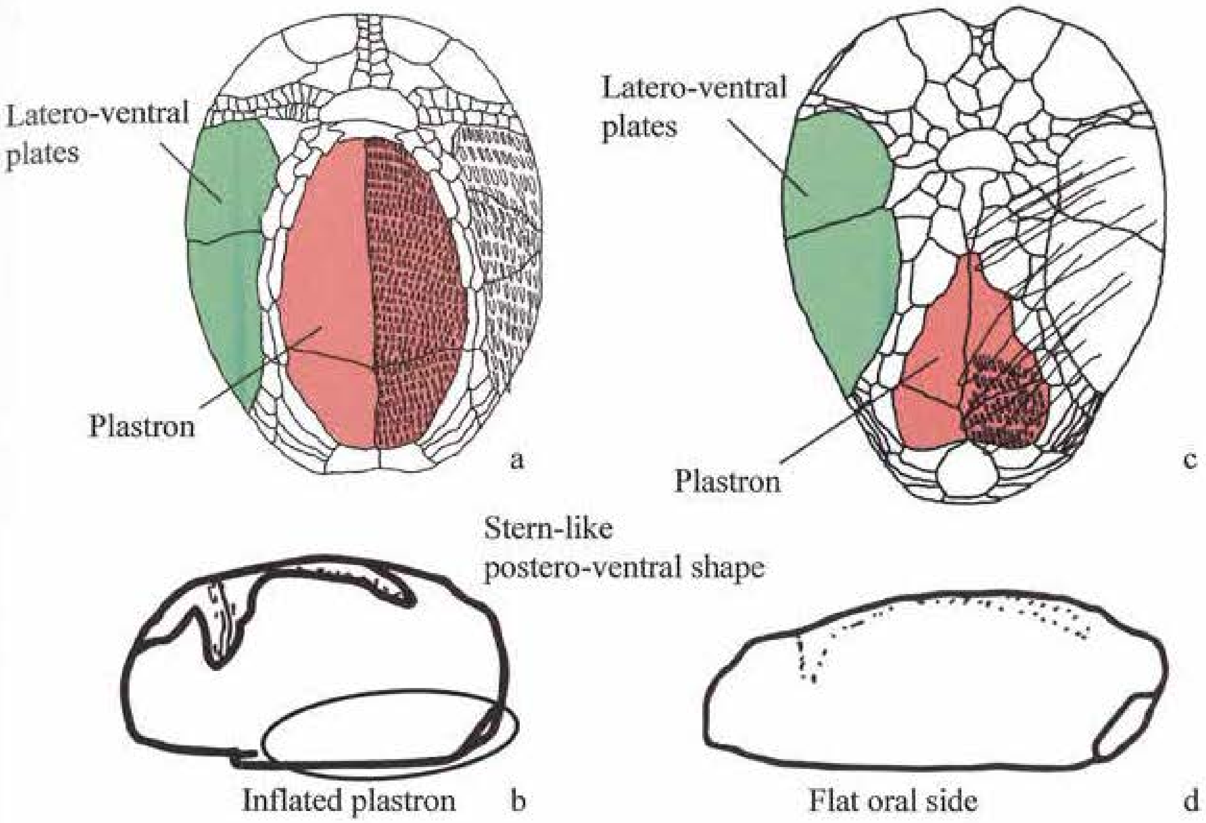


Fig.12. Important morphologies for burrowing and locomotion in spatangoids. *Brissus agassizii* (left) and *Lovenia elongata* (right). The inflated plastron and the stern-like postero-ventral shape produce convenient spaces beneath the lateral and posterior areas of the ventral side of the test, while the flat ventral side produces no such space. a, c, ventral view; b, d, side view.

Behavior under the disturbance

In aquarium experiments with *N. alta*, *M. spatagus* and *B. agassizii*, the urchins were washed out onto the native sediment surface and rolled over when the sediment overlying them was washed away by currents, having no chance to re-burrow (Fig.13). In *L. elongata*, when the dorsal side was partly exposed as overlying sediment was washed away, this urchin started to burrow more deeply and was not washed out. However, after it reached the bottom of aquarium and was no longer able to burrow deeply, the urchin was washed out and overturned. But *L. elongata* soon righted quickly and was not rolled over the sediment surface (Fig.14). The flat test shape with the completely flat ventral side provides the animal with significant stability in currents on the sediment surface.

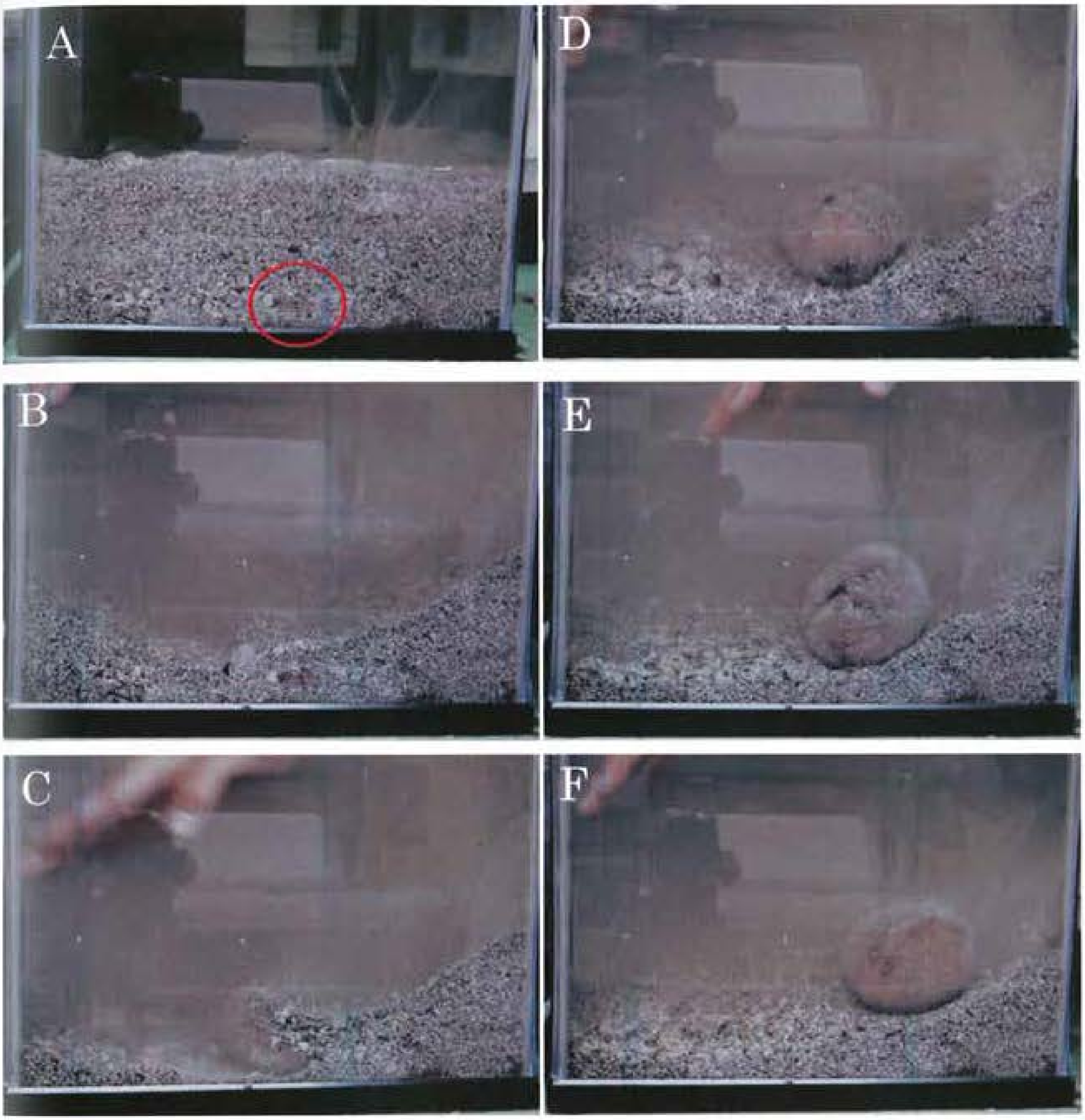


Fig.13. The behavior of *Metalia spatagus* under water disturbance. The sea urchin was burrowing in sediments (indicated by a red circle in A). When the sediment was washed away and the dorsal side was exposed (B and C), *M. spatagus* was washed out onto the sediment surface and rolled over (D-F), having no chance to re-burrow.

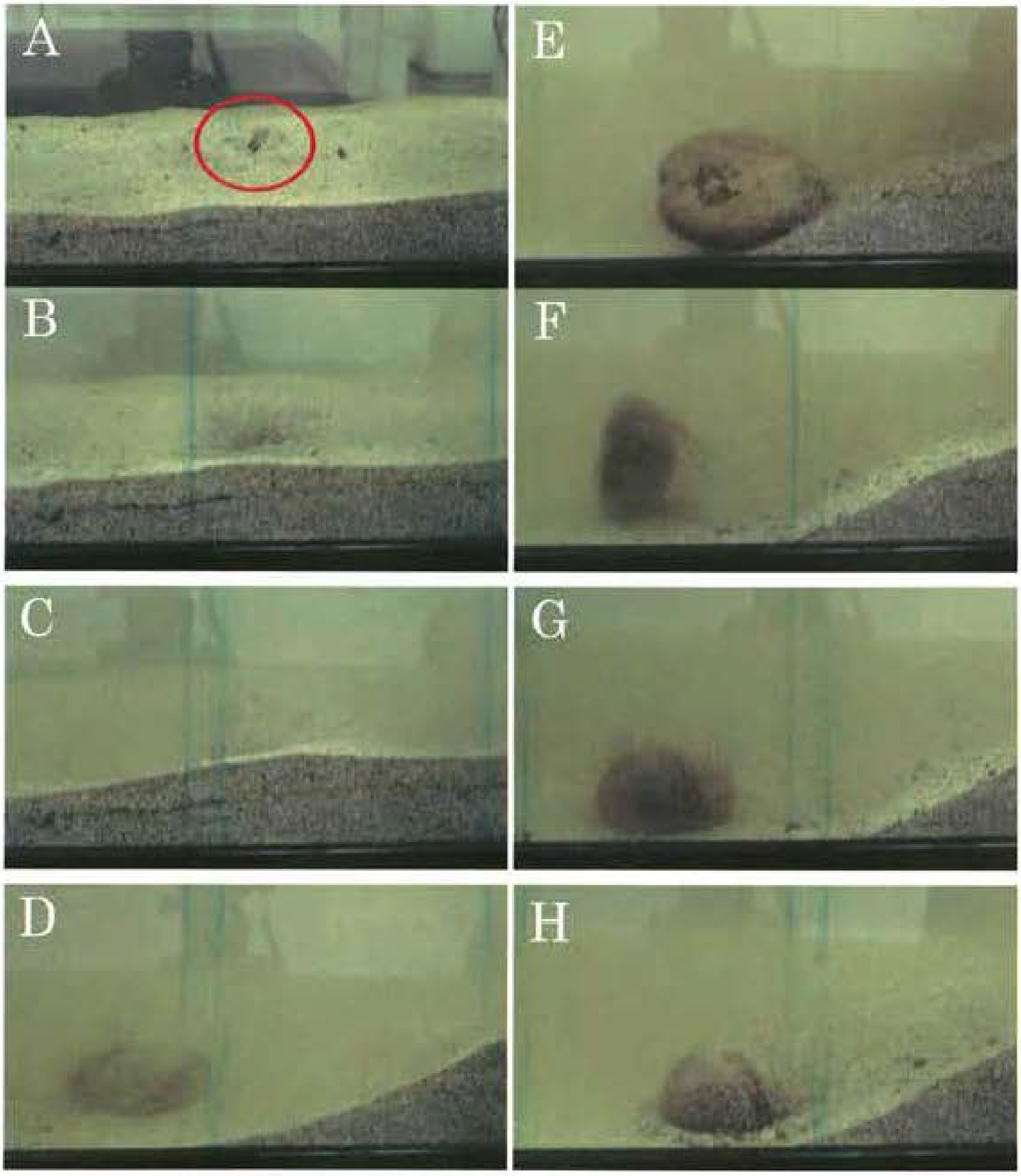


Fig.14. The behavior of *Lovenia elongata* under water disturbance. The sea urchin was burrowing in sediments (indicated by a red circle in A). When the overlying sediment was washed away and the dorsal side of the spatangoid was exposed, *L. elongata* burrowed deeper (B-D). After it reached the bottom of aquarium, the urchin was washed out and overturned (E). However, the sea urchin righted quickly by using the long spines on dorsal side (F and G) and tried to re-burrow into the sediment (H).

Righting and re-burrowing on the sediment

In aquarium experiments, *L. elongata* can right much more quickly than the other spatangoids (Table 2): on average 10 seconds, which was about 35 times faster than the other urchins. On the dorsal side, *L. elongata* has very long and stout spines for righting. The tubercles of the spines possess deeply sunken areoles that form large bulges on the inside of the test (camellate tubercles) and provide support for the extremely long and thick muscles (Fig.15). The other echinoids in this study lack such spines.

In re-burrowing experiments it took on average 1 minute for *L. elongata* to disappear under the sediment, which was about 8 times faster than the others. All the spatangoids use the latero-ventral spines for burrowing into sediment, but only *L. elongata* has particularly long, stout spines with deeply sunken tubercles like its long dorsal spines. In the other echinoids, the latero-ventral spines are much smaller and their tubercles are not sunken, providing no support for long thick muscles. The completely flat ventral side of *L. elongata* also facilitates the movement of the latero-ventral spines to excavate the sediment beneath the test rapidly because all the spines are in contact with the sediment surface. Additionally, the ventro-lateral areas in *L. elongata* are enlarged compared to the other echinoids studied here and also bears more muscular spine attachments.

Table 2. Elapsed time for righting and re-burrowing; the average time is shown: 3 individuals for *L. elongata*, 6 for *N. alta*, 2 for *M. spatagus*, and 4 for *B. agassizii*.

	Righting	Re-burrowing
L. elongata	10 sec	1 min
N. alta	5 min	10 min
M. spatagus	10 min	11 min
B. agassizii	7 min	17 min

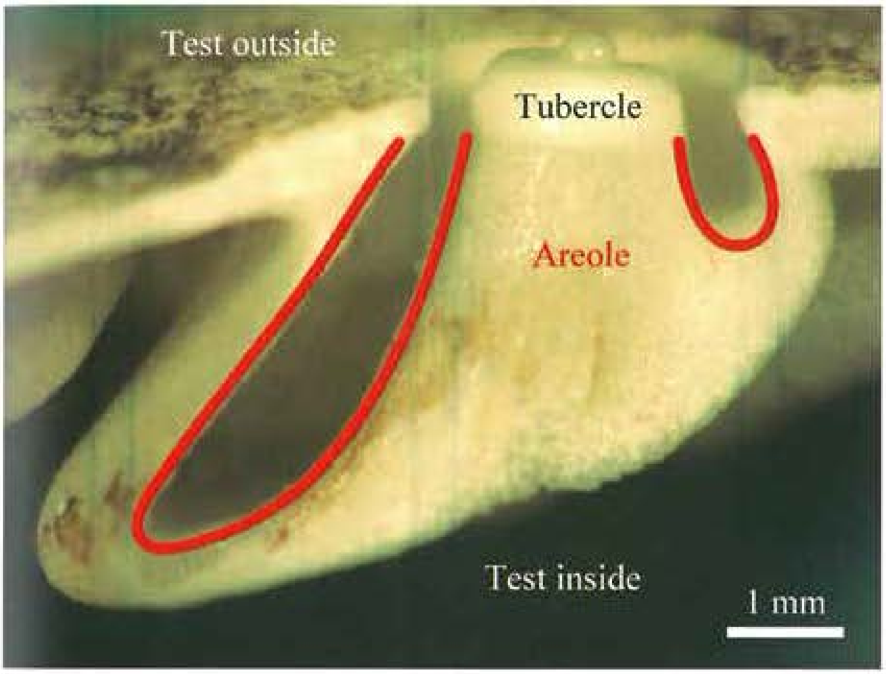


Fig.15. A tubercle with deeply sunken areole. The long stout spines are connected to this type of tubercles in *L. elongata*.

Population dynamics

Nacospatangus alta

During the time of this study, five cohorts of *N. alta* were recognized, and the cohort which appeared in 2009 is a superior example to know the life history of the species, because it can be easily pursued owing to a large number of the collected specimens.

Although in May 2009 no individual of *N. alta* smaller than 2.5 cm in test length was found, in August 2009 individuals around 1 cm in test length and in November 2009 those around 1.5 cm long were collected (Fig.16). The group composed of the new recruits can be regarded as an identical cohort. In this cohort, the sea urchins reached 3.6 cm ± 1.4 cm long in May 2010 and 4.0 cm ± 1.8 cm long in July 2010. The number of individual in this cohort suddenly decreased between May 2010 and July 2010. In November 2010 the individuals of the cohort was scarcely found, and instead, new juveniles around 1 cm in test length, namely, the recruits of the next generation forming a new cohort were collected. Four cohorts recognized in 2008, 2010, 2011 and 2012 showed a similar trend: the recruitment occurs between August and October, and the sea urchins grow 4-5 cm in test length for 7-9 months and mostly exhaust the life-span for 1 year.

In *N. alta* a remarkable decrease in number of individual was often observed in winter seasons (Fig.17).

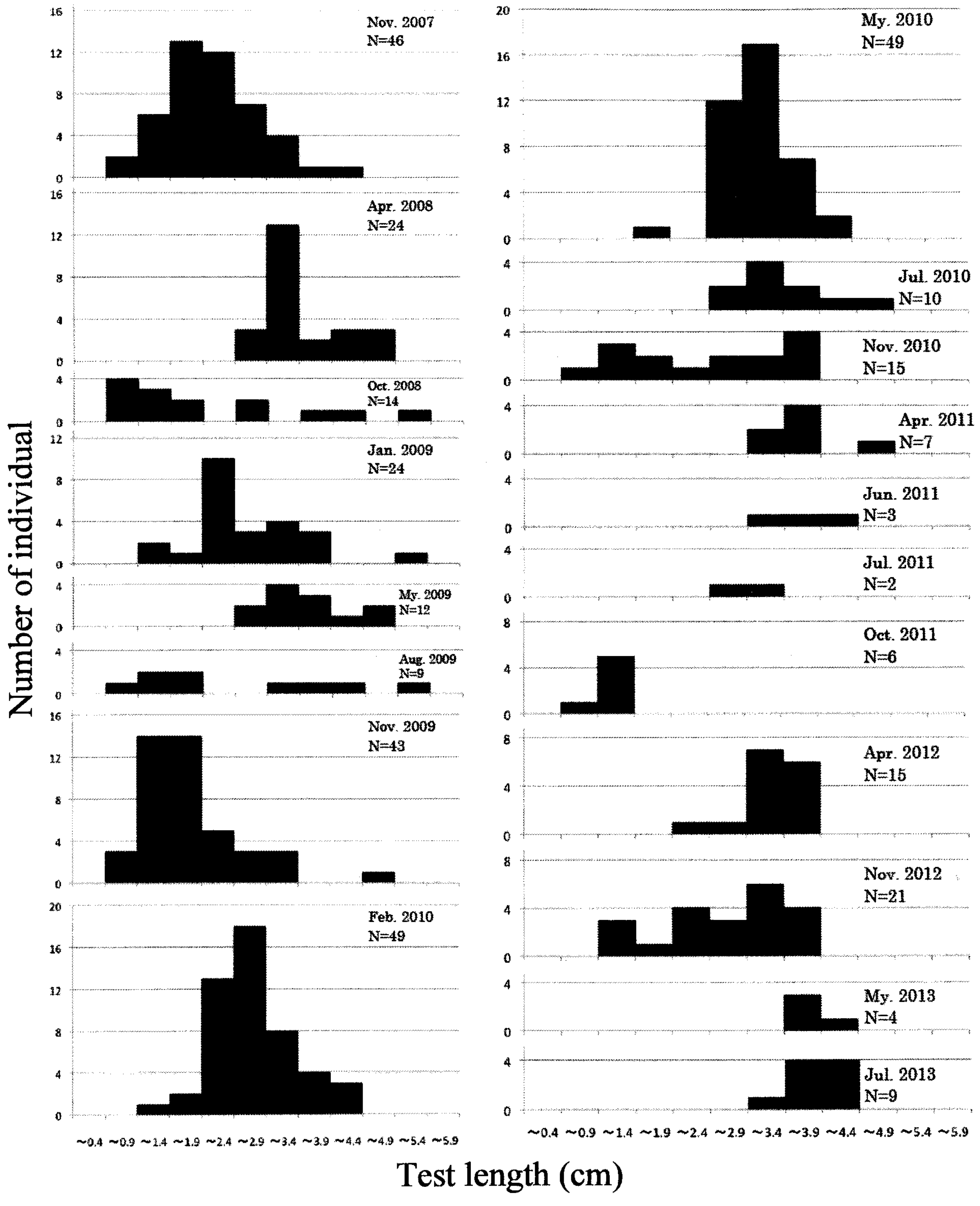


Fig.16. *Nacospatangus alta*. Population size structure in the Oki-Islands from 2007-2013.

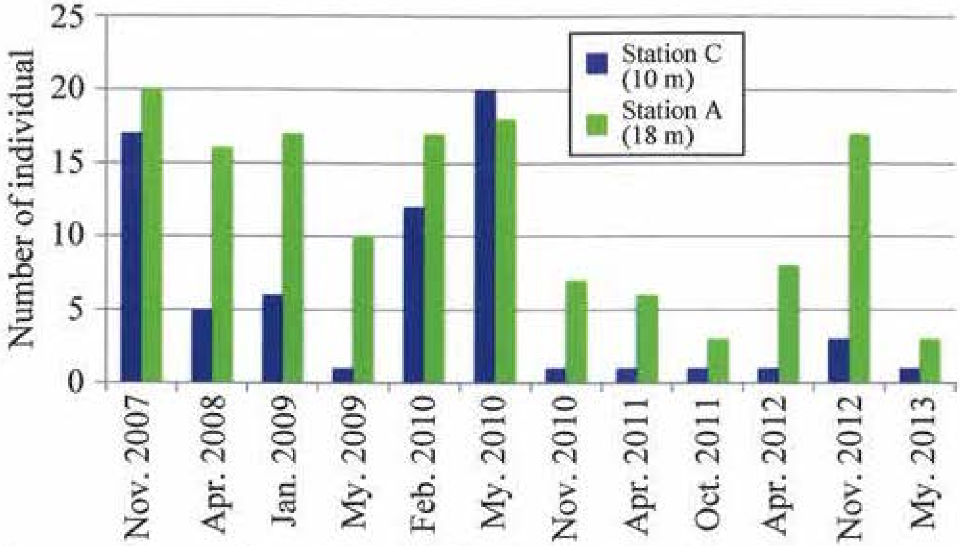


Fig.17. Changes in number of individuals for *N. alta*. The number decreases dramatically in winter storm seasons.

Lovenia elongata

During the time of this study, five cohorts of *L. elongata* were recognized, and the new cohort which appeared in 2008 is a superior example to know the life history of this species, because it can be easily pursued owing to a large number of the collected specimens.

Although no individual of *L. elongata* smaller than 2 cm in test length was found in April 2008, those around 2 cm long were found in the next investigation in October 2008 (Fig.18). The group composed of the new recruits can be regarded as an identical cohort. The sea urchins of this cohort were 1.5 cm ± 0.9 cm in test length in October 2008, and they reached 4.3 cm ± 1.0 cm in November 2009. Afterwards, for about 4 years from November 2009 to July 2013 they grew about 5 cm in test length. In this way, *L. elongata* grows about 4 cm in test length during the first year and later approximately 1 cm a year with a life-span about 5 years. Since in October or November of every year the new recruits of this species of 1-2 cm long were collected, the recruitment probably occurs between September and October.

In *L. elongata* changes in number of individual in winter seasons were not remarkable in contrast to the case in *N. alta* (Fig.19).

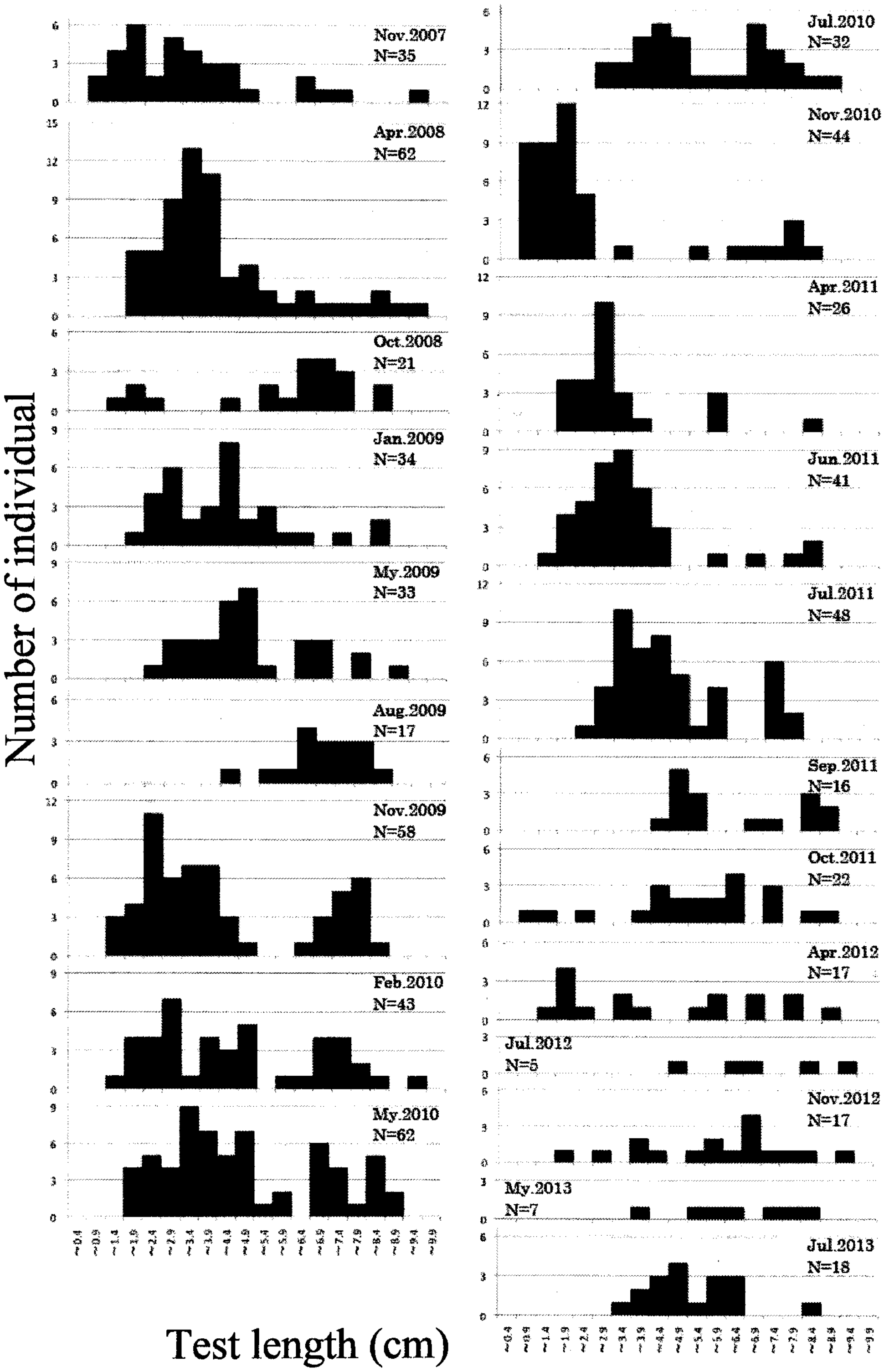


Fig.18. *Lovenia elongata*. Population size structure in the Oki-Islands from 2007-2013.

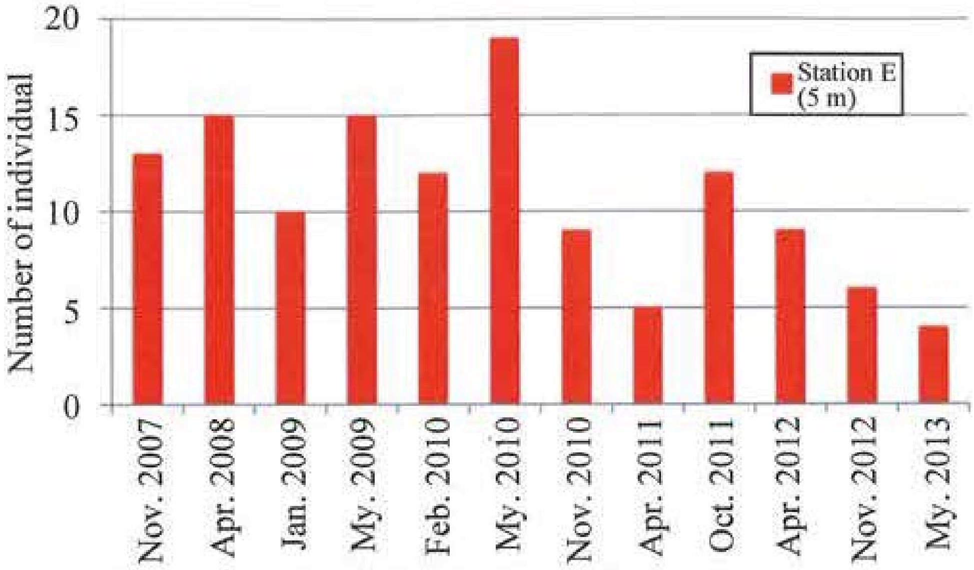


Fig.19. Changes in number of individuals for *L. elongata*.

Brissus agassizii

In this species it is difficult to distinguish and pursue a cohort continuously, except the first year after recruitment. In October 2008, individuals of *B. agassizii*, smaller than 1 cm in test length, were collected (Fig.20). The group composed of the new recruits is regarded as an identical cohort, and the individuals grew 2.4 cm ± 1.0 cm during the first year from October 2008 to August 2009. The cohort, however, cannot be pursued afterwards due to a small number of the collected specimens. The life-span of *B. agassizii* is estimated to be 5-6 years from the maximum test length about 9 cm recorded in the study and the growth rate in the first year. In October of 2008 and 2011 the individuals around 1 cm in test length were also collected, so that the recruitment of this species is assumed to occur around October.

Although there are not many individuals observed, a decrease in number of individual was not found in winter storm seasons.

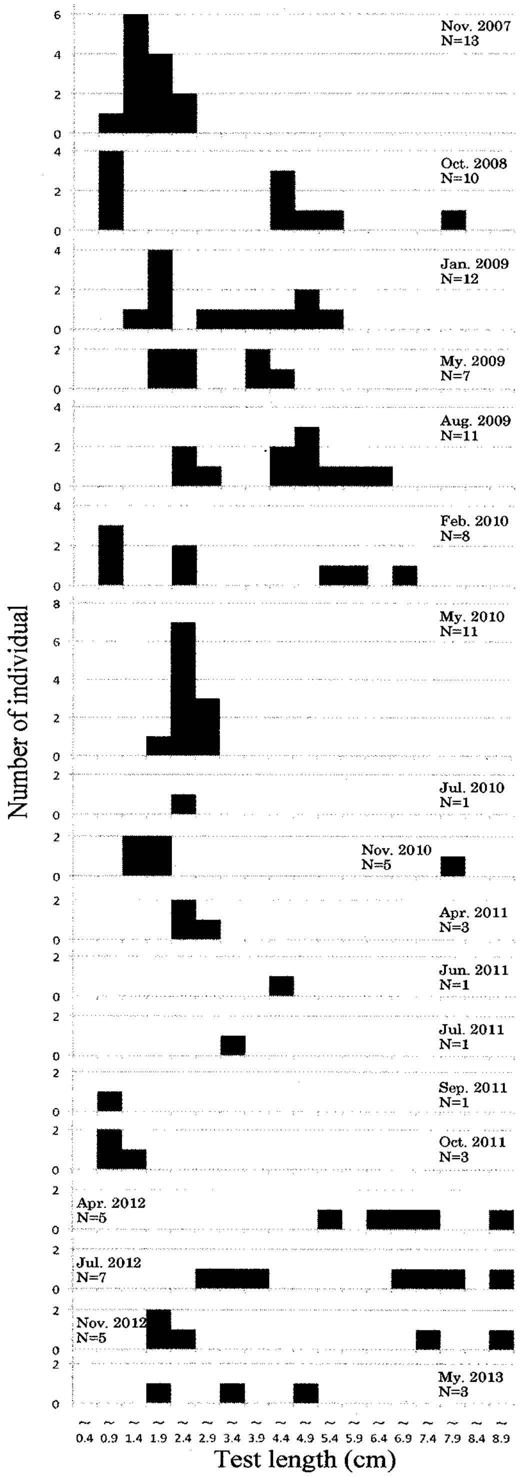


Fig.20. *Brissus agassizii.* Population size structure in the Oki-Islands from 2007-2013.

Metalia spatagus

In this species, like *Brissus agassizii,* it is difficult to distinguish and pursue a cohort continuously, except the first year after recruitment. In October 2008, individuals of this species smaller than 1 cm in test length were collected (Fig.21). The group composed of the new recruits is regarded as an identical cohort, and the individuals grew 2.9 cm ± 0.4 cm in test length during the first year from October 2008 to August 2009. The cohort cannot be pursued afterwards due to a small number of the collected specimens. The life-span of *M. spatagus* is estimated to be 5-6 years from the maximum test length about 9 cm of the specimens found in the study area and the growth rate in the first year. In October of 2008 and 2011 the individuals around 1 cm in test length were also collected, so that the recruitment of this species is assumed to occur around October.

Although there are not many individuals observed, a decrease in number of individual was not found in winter storm.

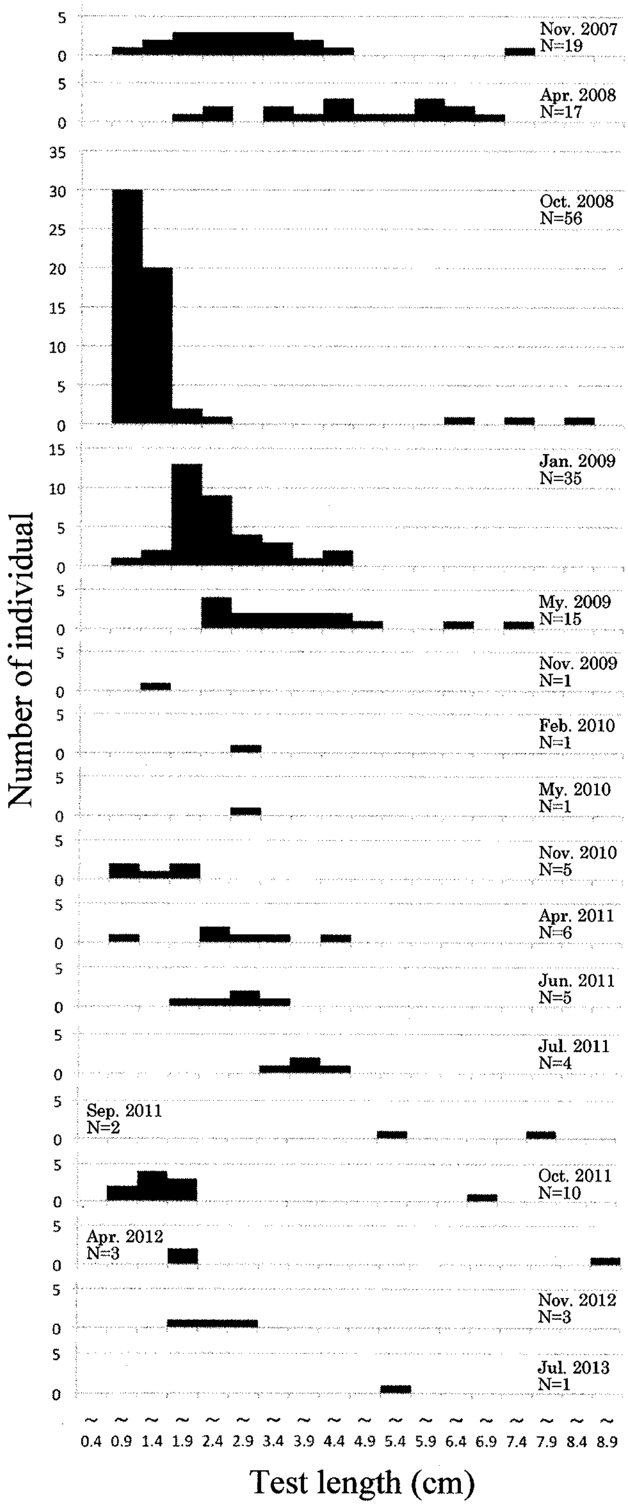


Fig.21. *Metalia spatagus*. Population size structure in the Oki-Islands from 2007-2013.

Sexual maturity of gonads

Nacospatangus alta

The test length of the observed individuals and the condition of the cells in gonads are given in Table 3. In the new recruits collected in October and November, the gonads were not developed and invisible. In the individuals collected in April the gonads had well developed and were almost filled with nutritive phagocytes (Fig.22). In June, the beginning of vitellogenesis was observed in the ovaries, and in the testes spermatocytes start to differentiate. In July, the gonads were fully filled with mature gametes. In October and November the gonads were occupied by large empty spaces, and nutritive phagocytes and mature gametes were scarcely found.

Thus, *N. alta* develops the nutritive phagocytes in the gonad by April during winter, and produces the gametes by July and spawns between July and August. *N. alta* reaches the first sexual maturity within 1 year.

In *N. alta*, the specimen (39mm in test length) that was collected in November 2010 was injected with a KCl, but the sea urchin did not spawn.

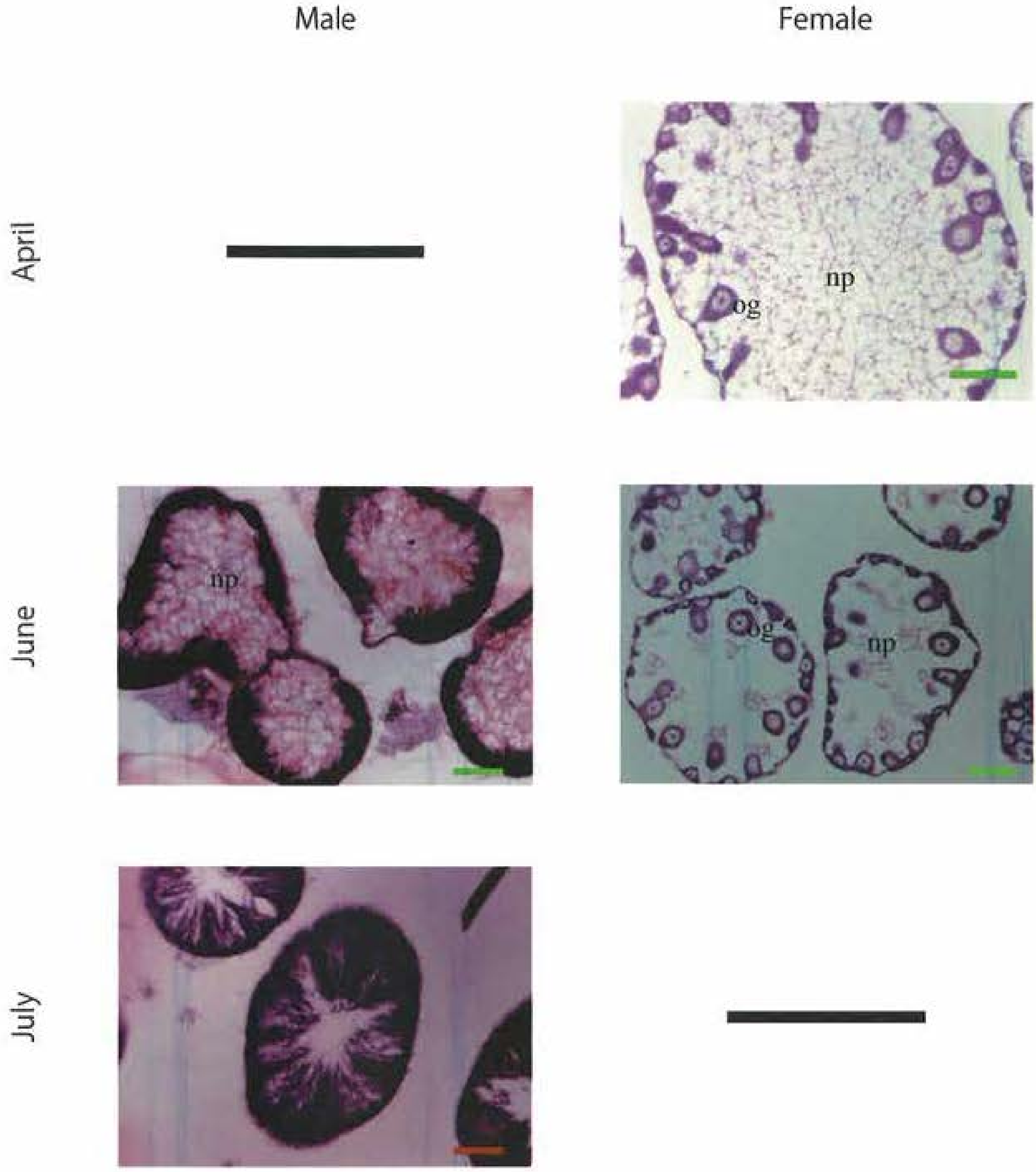


Fig.22. The condition of the cells in gonads of *N. alta*. Scale bar: green = 100μm, red = 10μm. np, nutritive phagocytes; og, ovogonia; s, mature sperm; sg, spermatogonia.

Table 3. Test length of the observed individuals and condition of gonad in *N. alta*

Nacospatangus alta Test length (cm)	Month / Year	Condition of gonad
3.5	April / 2011	spent empty stage
3.9	April / 2011	spent empty stage
3.2	June / 2011	growing stage
4.0	June / 2011	growing stage
2.5	July / 2011	mature stage
3.4	July / 2011	mature stage
1.3	October / 2011	†
1.4	October / 2011	†
2.3	April / 2012	spent empty stage
2.6	April / 2012	spent empty stage
3.0	April / 2012	spent empty stage
3.3	April / 2012	spent empty stage
3.4	April / 2012	spent empty stage
3.5	April / 2012	spent empty stage
3.6	April / 2012	spent empty stage
3.8	April / 2012	spent empty stage
3.9	April / 2012	spent empty stage
3.5	November / 2012	†
3.9	November / 2012	†

The condition of gonad is represented according to the stages defined by C. de A. P. Nunes and M. Jangoux (2004): spent empty stage: almost completely filled with nutritive phagocytes; growing stage: the beginning of gametogenesis; mature stage: almost completely filled with mature gametes; †: not developed and invisible gonads.

Lovenia elongata

The test length of the observed individuals and the condition of the cells in gonads are given in Table 4 and 5. In any individual smaller than 4 cm in test length, the gonad was not developed and invisible. On the other hand, in individuals larger than 4 cm long, the gonads were well developed and almost filled with nutritive phagocytes in April. Afterwards they were fully filled with mature gametes between July and September, and then were filled again with nutritive phagocytes and were not found reproductive cells between October and November (Fig.23).

Thus, *L. elongata* does not develop the gonad until it reaches 4 cm in test length. After it attains to the test size, it develops the nutritive phagocytes in the gonad by April during winter, and starts to produce the gametes by June and presumably spawns between July and September. *L. elongata* reaches the first sexual maturity at second year.

In *L. elongata* the specimen (23, 51 and 75mm in November 2010 and 59mm in April 2011), were injected with a KCl, did not spawn, but, the spatangoid echinoid (71mm in July 2010) spawned, after the specimen was injected it.

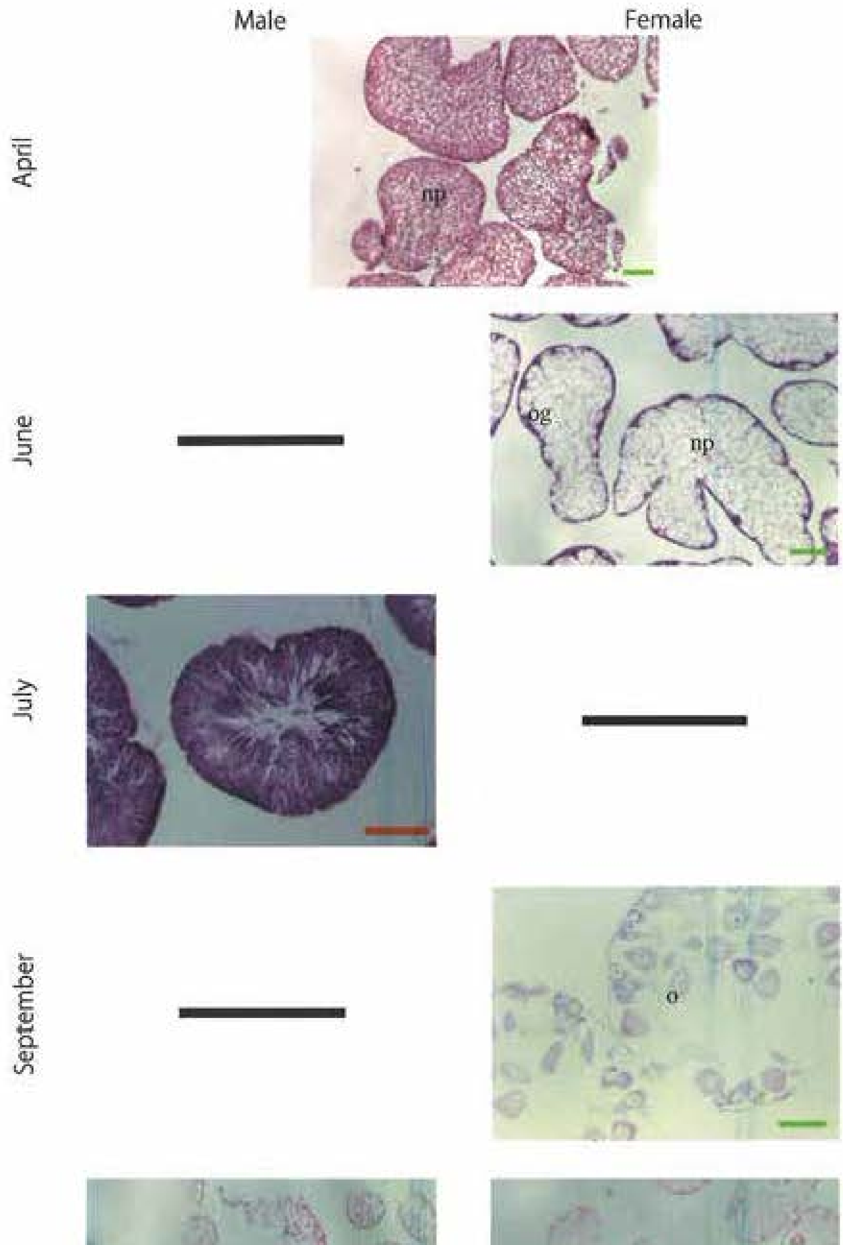


Fig.23. The condition of the cells in gonads of *L. elongata*. Scale bar; green = 100μm, red = 10μm. np, nutritive phagocytes; o, mature ova; og, ovogonia; ro, relict ova; s, mature sperm; sg, spermatogonia.

Table 4. Test length of the observed individuals and condition of gonad in *L. elongate* in 2011

Lovenia elongata Test length (cm)	Month / Year	Condition of gonad
3.3	April / 2011	spent empty stage
5.9	April / 2011	spent empty stage
2.5	June / 2011	spent empty stage
3.7	June / 2011	spent empty stage
4.4	June / 2011	growing stage
7.7	June / 2011	growing stage
3.5	July / 2011	spent empty stage
4.6	October / 2011	mature stage
5.6	July / 2011	mature stage
4.4	September / 2011	mature stage
4.6	September / 2011	mature stage
5.0	September / 2011	mature stage
7.2	September / 2011	spent stage
4.2	October / 2011	spent stage
4.6	October / 2011	spent stage
5.8	October / 2011	spent empty stage
6.3	October / 2011	spent empty stage
8.7	October / 2011	spent stage

The condition of gonad is represented according to the stages defined by C. de A. P. Nunes and M. Jangoux (2004): spent empty stage: almost completely filled with nutritive phagocytes; growing stage: the beginning of gametogenesis; mature stage: almost completely filled with mature gametes; spent stage: relict gametes and somatic cells are found.

Table 5. Test length of the observed individuals and condition of gonad in *L. elongate* in 2012

Lovenia elongata Test length (cm)	Month / Year	Condition of gonad
1.7	April / 2012	†
1.8	April / 2012	†
1.9	April / 2012	†
2.0	April / 2012	†
3.0	April / 2012	spent empty stage
3.5	April / 2012	spent empty stage
5.1	April / 2012	spent empty stage
5.8	April / 2012	spent empty stage
6.7	April / 2012	spent empty stage
7.5	April / 2012	spent empty stage
8.8	April / 2012	spent empty stage
4.5	July / 2012	mature stage
6.2	July / 2012	mature stage
6.5	July / 2012	mature stage
9.0	July / 2012	mature stage
4.0	November / 2012	spent empty stage
6.9	November / 2012	spent empty stage

The condition of gonad is represented according to the stages defined by C. de A. P. Nunes and M. Jangoux (2004): spent empty stage: almost completely filled with nutritive phagocytes; mature stage: almost completely filled with mature gametes; †: not developed and invisible gonads.

Brissus agassizii

The test length in the observed individuals and the condition of the cells in gonads are given in Table 6. In any individual smaller than 3 cm in test length, the gonad was not developed and invisible. In the individuals larger than 3 cm long, the gonads were well developed and filled with nutritive phagocytes between April and June, and in July mature gametes were observed in the gonads (Fig.24).

Thus, *B. agassizii* does not develop the gonad until it reaches 3 cm in test length. After it attains to the test size, it develops the nutritive phagocytes in the gonad between April and June, and starts to produce the gametes by June and presumably spawns between July and September. *B. agassizii* reaches the first sexual maturity at second year.

In *B. agassizii*, the specimen (76mm in test length) that was collected in November 2010 was injected with a KCl, but the sea urchin did not spawn.

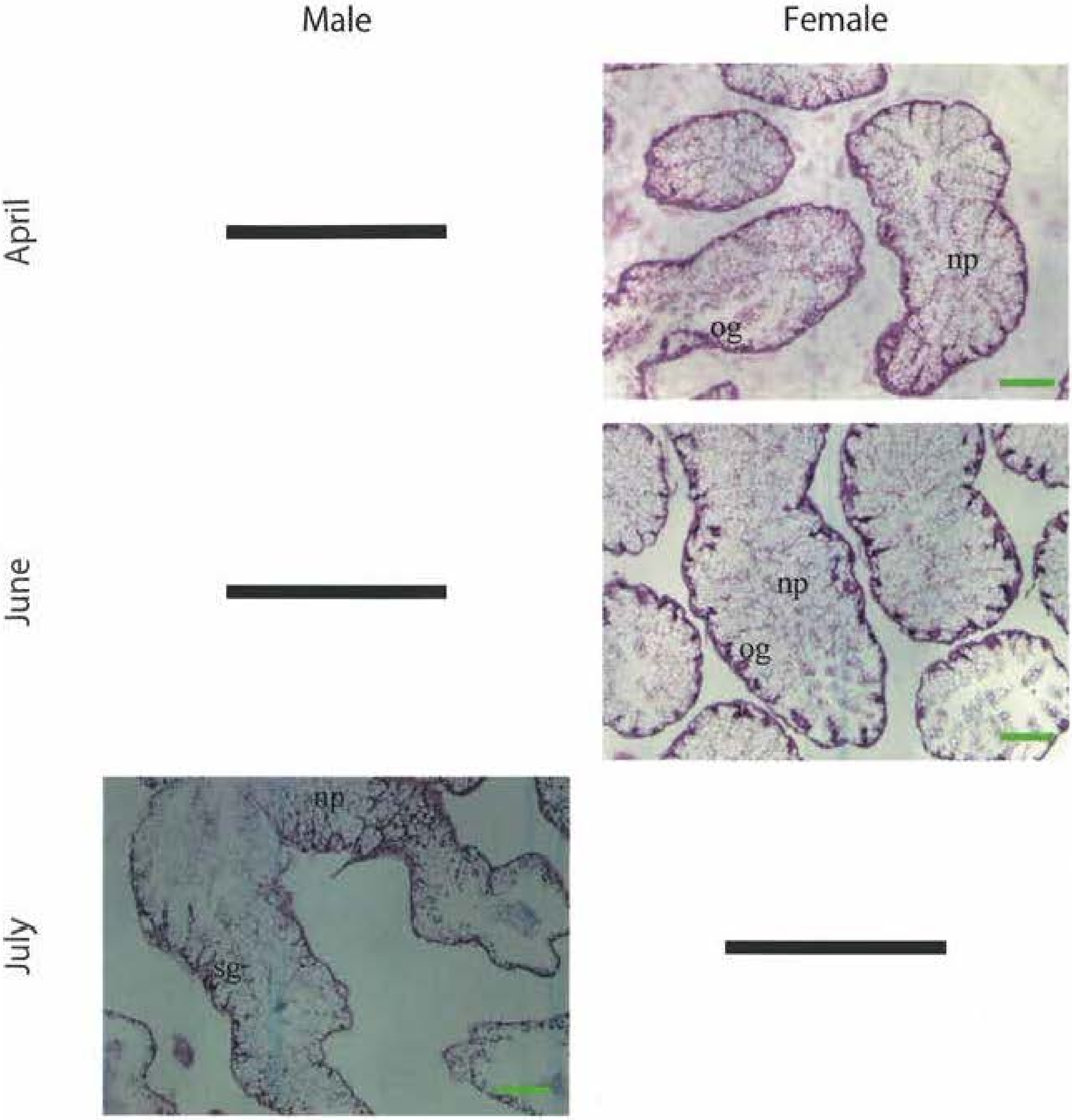


Fig.24. The condition of the cells in gonads of *B. agassizii.* Scale bar; green = 100μm. np, nutritive phagocytes; og, ovogonia; sg, spermatogonia.

Table 6. Test length of the observed individuals and condition of gonad in *B. agassizii*

Brissus agassizii Test length (cm)	Month / Year	Condition of gonad
2.3	April / 2011	spent empty stage
2.4	April / 2011	spent empty stage
2.6	April / 2011	spent empty stage
4.2	June / 2011	growing stage
3.3	July / 2011	growing stage
1.0	October / 2011	†
5.4	April / 2012	spent empty stage
6.5	April / 2012	spent empty stage
3.5	July / 2012	mature stage?
6.8	July / 2012	mature stage
7.0	July / 2012	mature stage
7.5	July / 2012	mature stage
9.0	July / 2012	mature stage

The condition of gonad is represented according to the stages defined by C. de A. P. Nunes and M. Jangoux (2004): spent empty stage: almost completely filled with nutritive phagocytes; growing stage: the beginning of gametogenesis; mature stage: almost completely filled with mature gametes; †: not developed and invisible gonads.

Metalia spatagus

The test length in the observed individuals and the condition of the cells in gonads are given in Table 7. In any individual smaller than 5 cm in test length, the gonad was not developed and invisible. In the individuals larger than 5 cm long, the gonads were well developed and almost filled with nutritive phagocytes in April, and in September mature gametes were observed (Fig.25).

Thus, *M. spatagus* does not develop the gonad until it reaches 3 cm in test length. After it attains to the test size, it develops the nutritive phagocytes in the gonad by April and apparently spawns between August and September. *M. spatagus* reaches first sexual maturity at fourth year.

In *M. spatagus*, there was no specimen that was injected with a KCl.

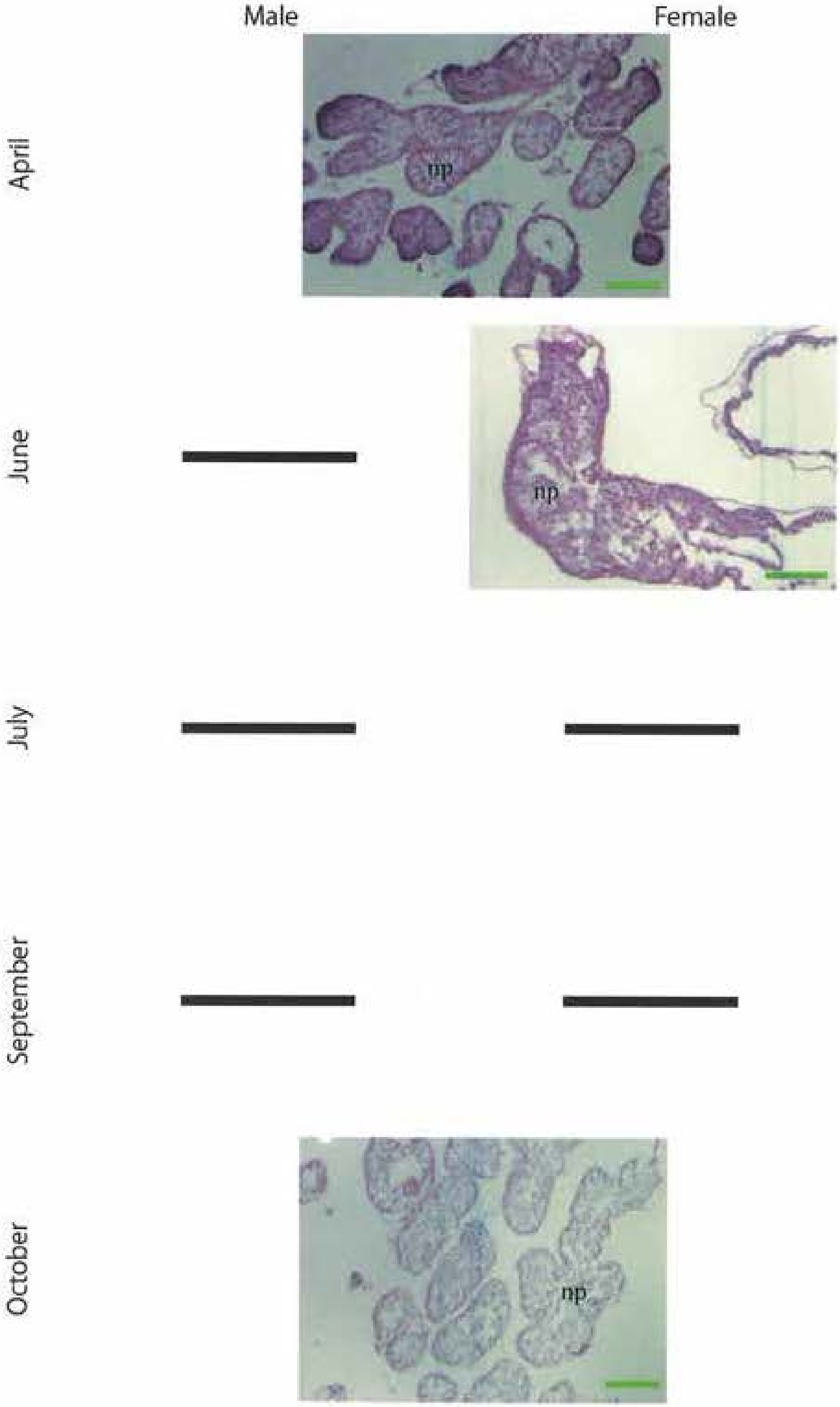


Fig.25. The condition of the cells in gonads of *M. spatagus*. Scale bar: green = 100µm. np, nutritive phagocytes.

Table 7. Test length of the observed individuals and condition of gonad in *M. spatagus*

Metlia spatagus Test length (cm)	Month / Year	Condition of gonad
2.1	April / 2011	†
2.7	April / 2011	†
3.0	April / 2011	†
4.3	April / 2011	spent empty stage?
2.0	June / 2011	†
2.6	June / 2011	†
2.8	June / 2011	†
3.2	June / 2011	†
3.4	July / 2011	†
3.5	July / 2011	†
4.1	July / 2011	†
4.5	July / 2011	†
4.5	July / 2011	growing stage?
5.4	September / 2011	mature stage
1.9	October / 2011	†
6.5	October / 2011	mature stage

The condition of gonad is represented according to the stages defined by C. de A. P. Nunes and M. Jangoux (2004): spent empty stage: almost completely filled with nutritive phagocytes; growing stage: the beginning of gametogenesis; mature stage: almost completely filled with mature gametes; †: not developed and invisible gonads.

Nutrients contained in the sediment

The amount of organic matter (protein and lipid) contained in the sediment of each station is given in Fig.26.

In each station, the protein amount shows a similar trend: largest in the upper part and smaller in the deeper part of the sediment. This indicates that the protein amount of the sediment near the sea floor where *L. elongata* and *N. alta* live is lager than that of the deeper sediment which *B. agassizii* and *M. spatangus* inhabit.

In lipid, a common trend to the station, as seen in Protein, is not recognized, but in each station the lipid amounts of the upper, middle, and deeper parts of the sediment appear to differ little among them, except the station A.

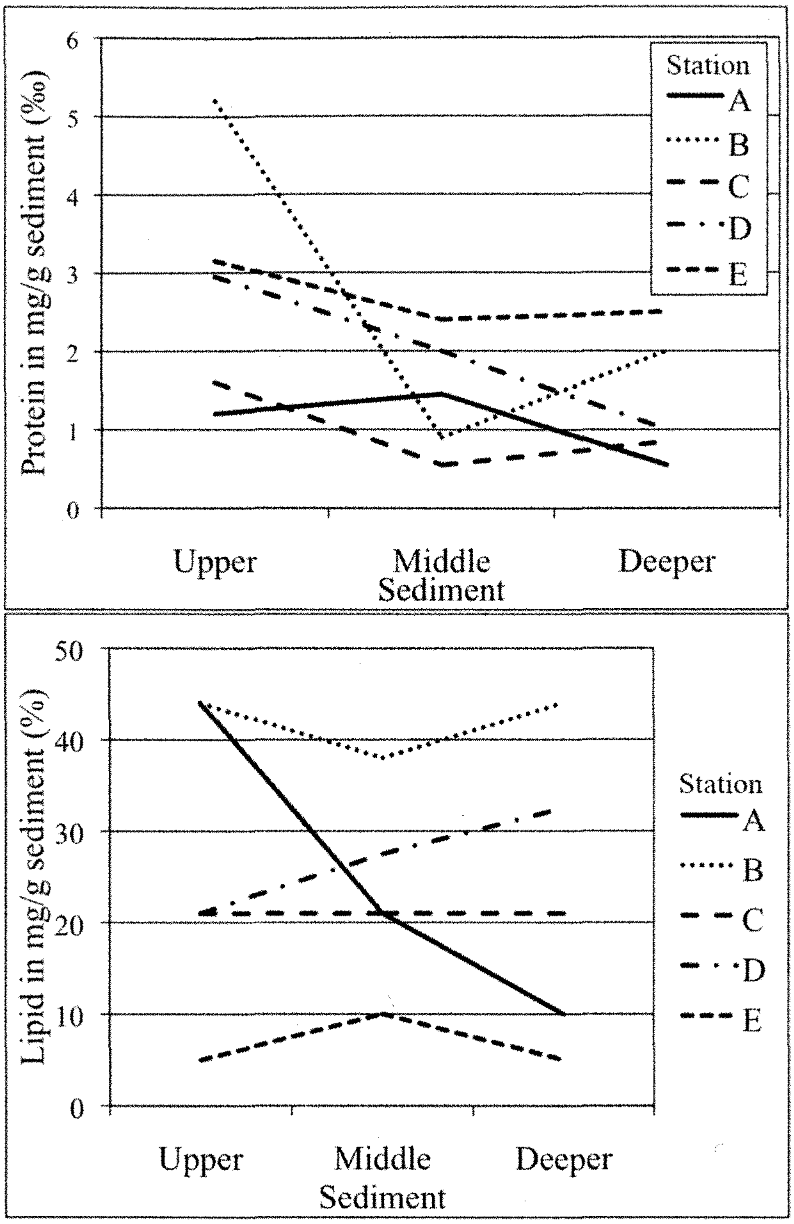


Fig.26. The amounts of organic matter contained in the sediment of spatangoid habitats. The upper graph: Protein, the lower graph: Lipid. *L. elongata* lives in the upper part of the sediment in Sta. B, C and E; *N. alta* lives in the upper part of the sediment in Sta. A, B and C; *B. agassizii* lives in the deeper part of the sediment in Sta. B and D; *M. spatagus* lives in the deeper part of the sediment in Sta. A, C and D. Sta. A: m-c sand at water depth of 18 m; Sta. B: g m-c sand at water depth of 9 m; Sta. C: g m-c sand at water depth of 10 m; Sta. D: g c sand at water depth of 10 m; Sta. E: f sand at water depth of 5 m. m-c, medium- to coarse-grained; g, gravelly; c, coarse-grained; f, fine-grained

Morphology and behavior in relation to feeding

The morphology of the phyllopodia, which are the tuve feet distributed around the mouth and used for feeding, in each spatangoid species is shown in Fig.27. Their phyllopodia have a common structure, ending in chimney-brush-like discs which facilitate to collect sediment particles. The disc area of the phyllopodium of *L. elongata* is about 2 times larger than those of the others.

The number of phyllopodia of each spatangoid echinoid is given in Table 8, and the distribution of them is shown in Fig.28. The deep-burrowing brissid spatangoids, *M. spatagus* and *B. agassizii*, have a larger number of phyllopodia on the amb. II, III and IV, than the shallow-burrowing spatangoids, *N. alta* and *L. elongata.* In contrast, their number of the amb. I and V is not different among 4 species, though in *N. alta* and *L. elongata* they are located farther away from the mouth.

The behavior of phyllopodia of *L. elongata* was observed from the bottom of an aquarium when the sea urchin was staying there (Fig.29). The phyllopodia on amb. II, III and IV, expanding the fringe discs, reached toward the aquarium bottom to seek and grasp particles and drew the fringe tips back into the mouth. On the other hand, though the tube feet on the amb. I and V apparently tried to reach toward the bottom, in many cases their tips did not reach there and were not put into the mouth. This is presumably because the long latero-ventral spines on the interamb. 1 and 4, leaning inside and swaying back and forth, disturbed the movement of the tube feet. In *N. alta* and *B. agassizii,* similarly, they transported sediment to their mouth by the tube feet on amb. II, III and IV.

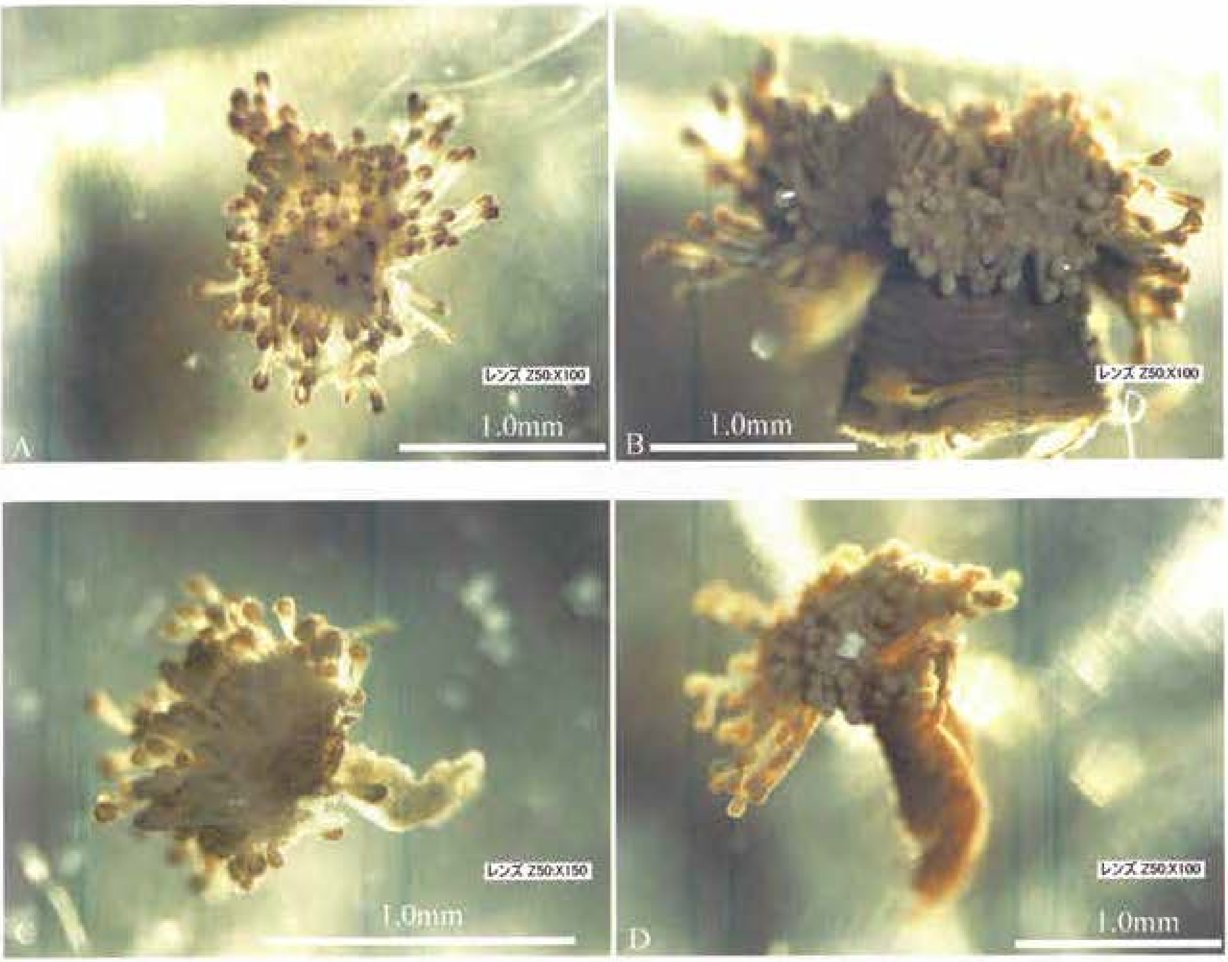
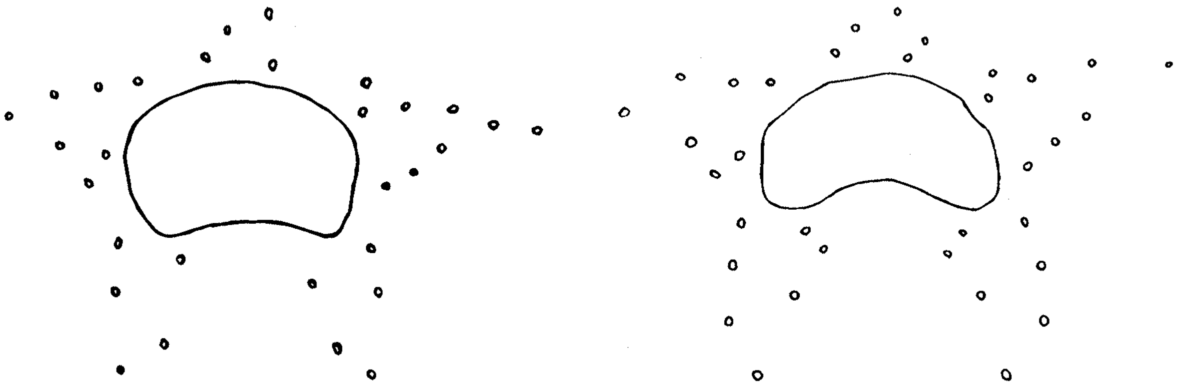
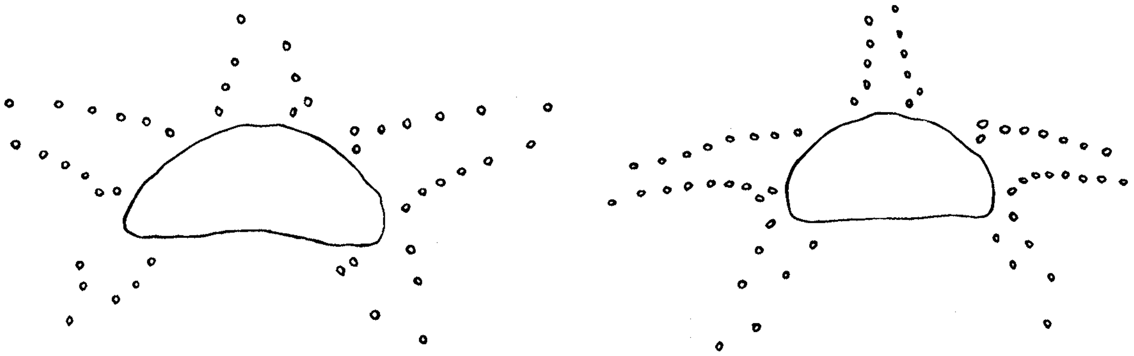


Fig.27. The morphology of the phyllopodia of each spatangoid species. A: *N. alta*, B: *L. elongata*, C: *M. spatagus*, D: *B. agassizii*.



Nacospatangus alta *Lovenia elongata*



Metalia spatagus *Brissus agassizii*

Fig.28. The distribution of the phyllopodia of each spatangoid species.

Table 8. The number of pore on ambulacra each spatangoid

	I	II	III	IV	V
N. alta	5	7	4	9	5
L. elongata	7	7	5	8	7
M. spatagus	6	12	8	13	6
B. agassizii	7	17	11	16	6

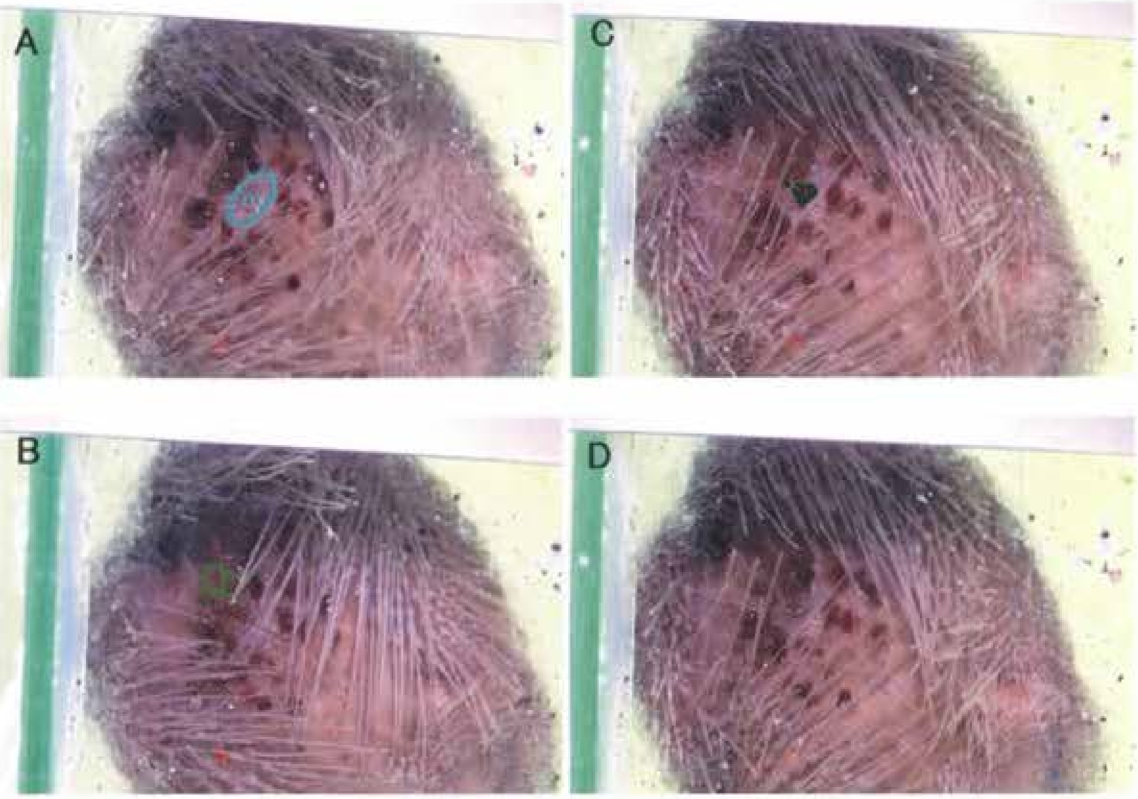


Fig.29. The behavior of phyllopodia of *L. elongata*. The tube feet on amb. II, III and IV, expanding the fringe discs, reached toward the aquarium bottom to seek and grasp particles (B) and drew the fringe tips back into the mouth (C). m; mouth.

Allometric growth of the test plates

The growth rates of three area of the ventral side, namely, plates 2ab of ambulacrum I, those of interambulacra 1 and 5, were examined in comparison to the total ventral area (Fig.30-35). In all of the spatangoids, the plates of ambulacrum I show negative allometory, indicating that the non-spine area becomes relatively smaller through the growth of ventral area. In *N. alta* (Fig.30) and *L. elongata* (Fig.31), the plates of interamb. 1 show a positive allometry and those of interamb. 5 do a negative allometory. This allometric growth means that in the shallow-burrowing spatangoids, the area for latero-ventral spines becomes relatively much larger than that for plastron spines, and this is remarkable in *L. elongata*. In *B. agassizii* (Fig.32), both areas of the interambulacura 1 and 5 exhibit similar positive allometories, implying that the plastron and latero-ventral areas maintain a fixed allometric relationship between them and become relatively larger in the ventral area during the time of test growth. In *M. spatagus* (Fig.33) both areas of the interambulacura 1 and 5 exhibit similar isometry, suggesting that the plastron and latero-ventral areas maintain a fixed allometric relationship in proportion to the ventral area during the time of test growth.

The growth rates in thickness of the aboral plates were examined in comparison to the test length (Fig.34). Only the plates of *N. alta* show negative allometry are thinnest in the 4 spatangoid echinoids, resulting from the lowest growth rate about a half of those of *L. elongata* and *B. agassizii*.

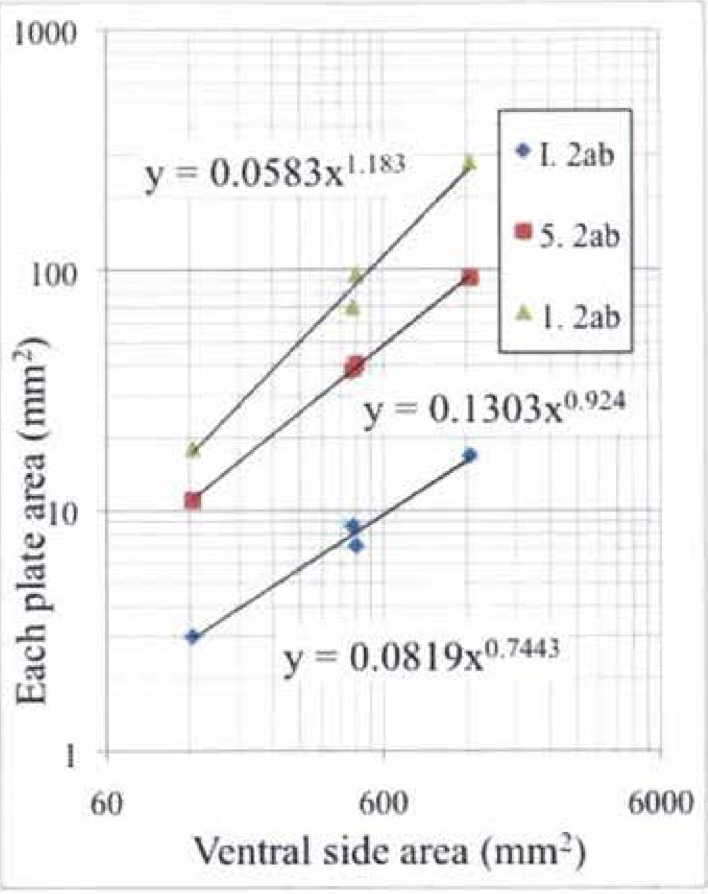


Fig.30. Allometric relationship between the area of the plates and the total ventral area in *N. alta*.

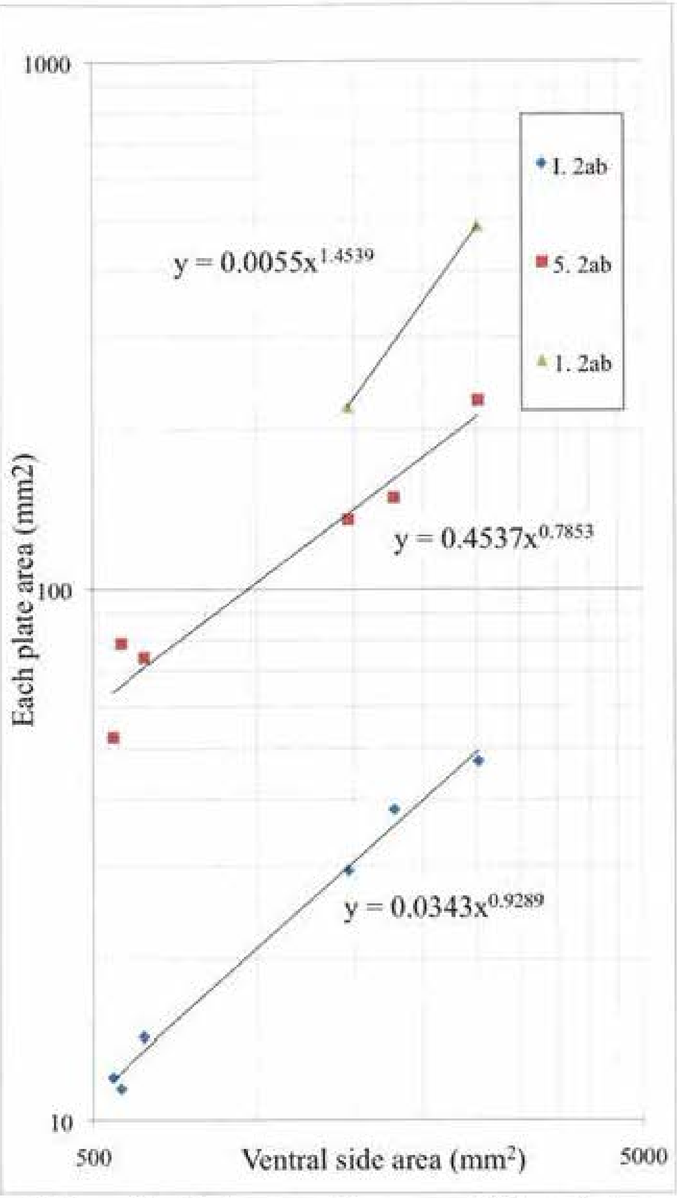


Fig.31. Allometric relationship between the area of the plates and the total ventral area in *L. elongata*.

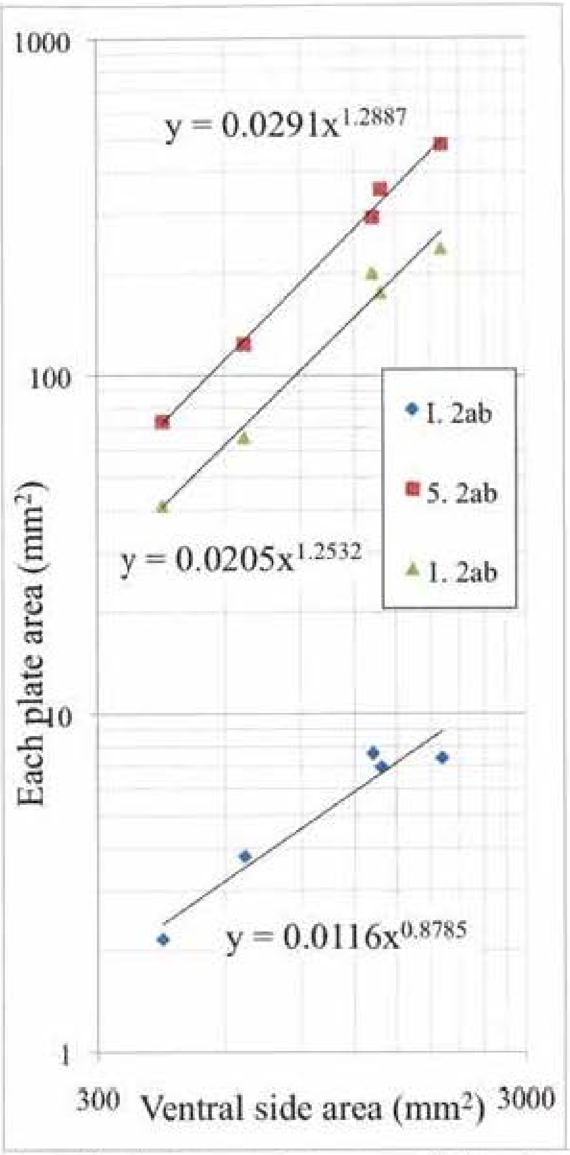


Fig.32. Allometric relationship between the area of the plates and the total ventral area in *B. agassizii*.

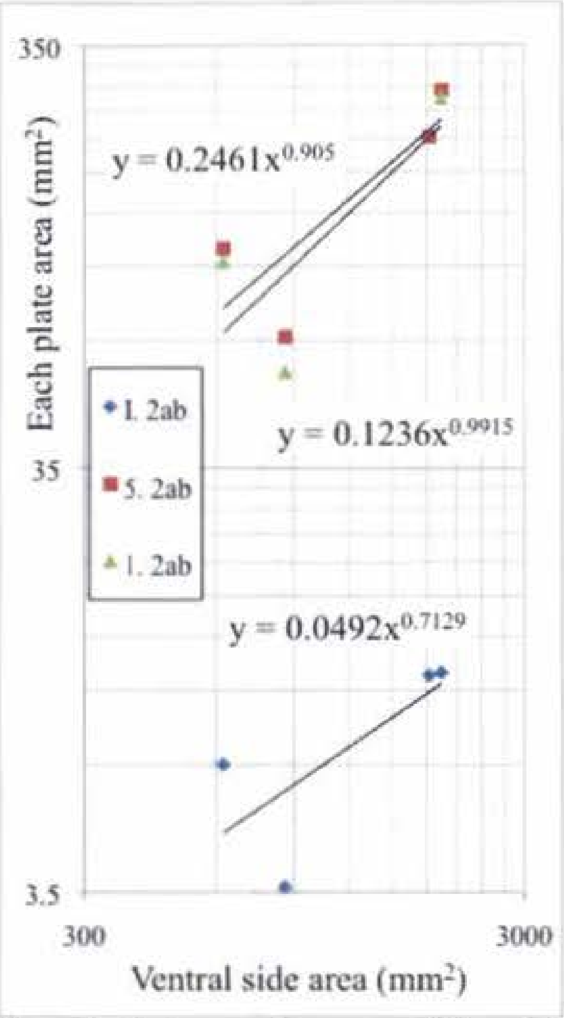


Fig.33. Allometric relationship between the area of the plates and the total ventral area in *M. spatagus*.

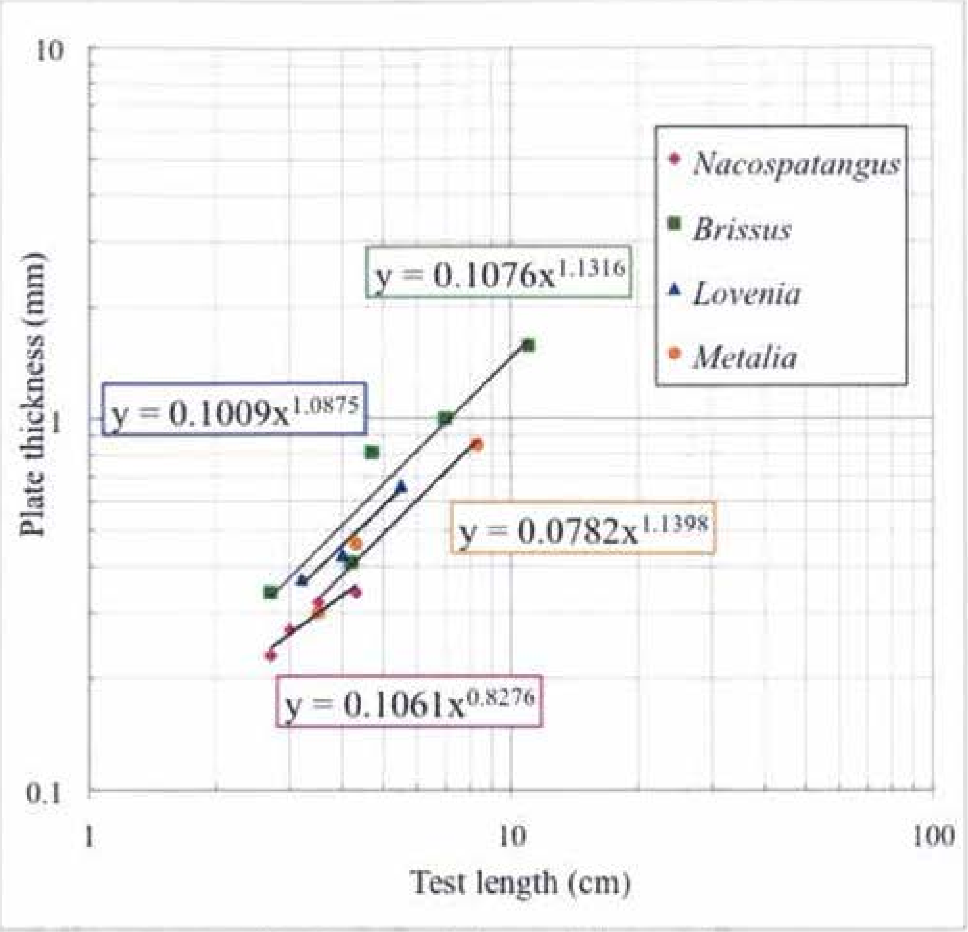


Fig.34. The growth rates of thickness of plate of aboral side.

4. Discussion

Adaptive morphologies to fine-grained sand bottom in shallow sublittoral zone

In field investigations, *L. elongata* exclusively inhabits fine-grained sand in the study area. In the aquarium observation, only *L. elongata* was completely buried in fine-grained sand, constructing a respiratory funnel formed by the apical tuft spines. However, if the apical tuft spines were cut off, the animal was no longer able to burrow completely, under the sediment. Considering that in fine-grained sand *N. alta*, *B. agassizii* and *M. spatagus* that have no apical tuft spine burrowed exposing the petal areas on the sediment surface, the respiratory funnel must be essential for spatangoids to be buried under fine-grained sand, which has already repeatedly noted by many authors (e.g. Nichols 1959; Chesher 1963; Smith 1984). However, unlike *Echinocardium cordatum* and *Moira atropos* observed by those authors, *L. elongata* has no funnel-building tube feet, and it constructs only a short respiratory funnel about 1 to 2 cm that is slightly longer than the apical tuft spines. It is probable that this constraint allows the animal only to burrow just below the surface of fine-grained sediment.

In the field observations, the fine-grained sand bottom at a depth of 5 m where *L. elongata* lives was often disturbed by water currents. *L. elongata* has specific morphologies for quick burrowing and rapid righting. In a disturbance, this urchin presumably burrows deeper than usual before it is washed-out by currents. Even if washed out, it could rapidly right and re-burrow. *L. elongata*, thus, would survive, though it burrows just below the unstable sand surface in very shallow water environment. No decrease in the number of individual was actually observed for *L. elongata* in storm seasons. It is noteworthy that in *L. elongata* during the time of test growth the latero-ventral area exhibits an extremely positive allometry to the ventral area, resulting in increase in the number and size of the latero-ventral spines that bring the specific behavior against water disturbance.

Other spatangoids (*E. cordatum* and *Moira lachesinella*) found together with *L. elongata* in fine-grained sand burrow 10-15 cm deep below the sediment surface, constructing long respiratory funnels by the funnel-building tube feet. Owing to their deep-burrowing mode of life, these spatangoids would survive in storm disturbance.

Although in aquaria *N. alta*, *B. agassizii* and *M. spatagus* apparently have no problem of living in fine-grained sand by exposing their apices on the sediment surface, in the natural environment these spatangoids would be undoubtedly washed out by water disturbance and die. Also, the spatangoids exposed on the sediment surface would easily become prey of many predators like fishes living in shallow waters.

Adaptive morphologies to coarse-grained sand bottom in shallow sublittoral zone

In the field investigations, four spatangoids, *L. elongata*, *N. alta*, *M. spatagus* and *B.agassizii* were found from coarse-grained sand, but their respective distributions are strongly controlled by water depth except *L. elongata*. *N. alta* has no specific morphology to draw water from the sediment surface and the ventral morphology is not appropriate for deep burrowing. These morphological constraints probably confine this sea urchin to live just below the surface of coarse-grained sand, as observed in the habitat and the aquarium. *N. alta* was found at depths from 9-18 m, but in winter storm seasons a remarkable decrease in the number of individual was observed at depths shallower than 10 m, where dead tests of *N. alta* were frequently found in spring. No such decrease in number occurred at a depth of 18 m. *N. alta* living just below the sediment surface in unstable environment without specific morphology for righting and re-burrowing could be subject to death by storm disturbance. In the other regions in Japan, *N. alta* was usually found in habitats deeper than 20 m (Shigei 1986; Kanazawa 1992). *M. spatagus* and *B. agassizii* have morphologies appropriate to burrow deeply in sand: an inflated plastron and a stern-like postero-ventral shape for transport and accumulating sand in great pressure of surrounding sand. They, however, have neither apical tuft spines nor funnel-building tube feet to construct a respiratory funnel, though they possess peripetalous fasciole to draw water through the sediment above. Owing to these functional morphologies, *M. spatagus* and *B. agassizii* burrow deeply only in coarse-grained sand. In their habitats, large individuals were found in gravelly coarse-grained sand 10-15 cm deep below the sediment surface, where they can usually avoid being washed out to death in storm disturbance. However, numerous dead tests of *M. spatagus* were once observed during the five-year investigation, which indicates that it seems still difficult for *M. spatagus* to survive in severe disturbance caused by a very strong storm.

Contrastingly, in *B. agassizii* such mass mortality has been never observed during the investigation time. This can be ascribed to the superior ability for burrowing; allometric growth of the ventral plates suggests that the plastron and latero-ventral areas, on which the spines for burrowing occur, become relatively larger in the ventral area through the growth of test, resulting in marked increase in number of the spines for burrowing. In *M. spatagus*, the area for burrowing spines isometrically increases in propotion to the whole ventral area. *B. agassizii*, therefore, may be capable of burrowing more deeply than *M. spatagus*. It should be noted that in Toyama Bay *B. agassizii* was found burrowing 20 cm deep in gravelly coarse-grained sand in high-energy environment near the tidal zone (Kanazawa 1992), indicating that *B. agassizii* could inhabit more unstable environment.

Although *L. elongata* is found more frequently in fine-grained sand, it seems easy for it to inhabit coarse-grained sand because of facility for respiration. In addition, the main habitat of fine-grained sand is obviously more unstable than other habitats of coarse-grained sand. It seems impossible to explain this inhabitation from the viewpoint of adaptive morphology. This, however, will be explained later in view of the nutrients contained in the sediment.

Life history corresponding to habitat-stability

In the investigated area, the surface layer of sediment about 5 cm thick is frequently disturbed by storms occurred most severely in winter and dead tests of *N. alta* are often found after the season (Saitoh and Kanazawa 2012). In such environment the spatangoid echinoids apparently have different kinds of life histories corresponding to the condition of the respective habitats. In *N. alta* that lives in unstable surface sediment, it grows rapidly and reaches sexual maturity early, but the life span is short (Fig.35). In contrast, *M. spatagus* and *B. agassizii* that live deep in the sediment in relatively stable condition grow slowly and reach sexual maturity late, and the life span is long. Accordingly, the spatangoids living in unstable environments have rapid alternation of generations, and those living in stable environments have slow alternation of generations. This principle, however, is not applicable to *L. elongata*. In unstable environment, the animal grows rapidly, but its sexual maturity is not early and the life span is long. The contradiction is explainable from its surprising ability of survive in water disturbance by virtue of the specific morphologies for quick burrowing and rapid righting.

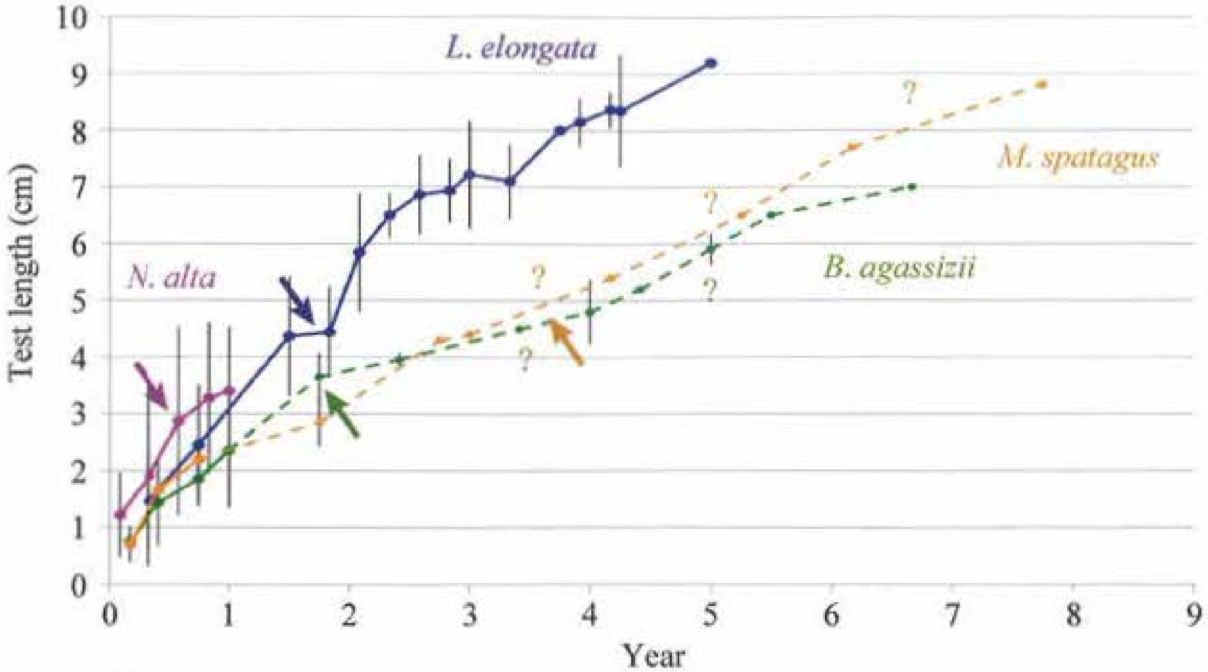


Fig.35. Growth rate, sexual maturity and life span of four spatangoid species. A solid line shows the growth curves based on an identical cohort, a dotted line shows the growth curves based on some mixed cohorts and an arrow indicates the timing of first sexual maturity.

Food-collecting ability

Spatangoid echinoids are deposit feeders and in feeding they use phyllopodia around the mouth to collect sediment. In all four spatangoids, the tube feet have a common structure, ending in chimney-brush-like discs, which facilitate to collect sediment. However, the number of phyllopodia in *M. spatagus* and *B. agassizii* is about twice as many as that of *N. alta* and *L. elongata*. *M. spatagus* and *B. agassizii* can probably collect sediment more efficiently. The amount of protein contained in the surface sediment where *N. alta* and *L. elongata* live is 3-5 times larger than that of the sediment where *M. spatagus* and *B. agassizii* live. It is presumably not coincident that the spatangoids living in nutrient-poor environment have more phyllopodia which facilitate their sediment-collecting.

Although *L. elongata* has a small number of tube feet, the disc area of the tube foot is about 2 times larger than of other spatangoids. The larger chimney-brush-like discs may be effective in collecting fine-grained sand in which only *L. elongata* prefer to live in the four spatangoids.

Trade-off and life history

It is quite interesting that *N. alta* reaches sexual maturity earliest at one year in addition to the fastest growth rate of test length among the four spatangoid echinoids. Its habitat, nutrient-rich surface sediment, probably enables the echinoid to have the life style. It should be, however, noted that *N. alta* construct the test with very thin plates, whereby the echinoid can reduce the cost of test construction and allocates more energy to the development of the gonads. It must be essential for *N. alta* to reach sexual maturity earlier to spawn within 1 year, because it has no specific morphology against storm disturbance. This is understandable by contrast with *L. elongata*, another spatangoid living near the nutrient-rich sediment surface with a similar fast growth rate of test length. *L. elongata* constructs the test with thicker plates on which stout, longer spines supported by thicker muscles occur, and it reaches sexual maturity at two years. In this sea urchin, the energies derived from nutrients should be first allocated to the construction of the rigid test with the stout long spines by which it can survive in storm disturbance. In *L. elongata*, the gonad develops in accordance with a marked decrease in growth rate of the test. It seems, therefore, inevitable that the energies are not allocated to the gonad until the second year when the sea urchin possesses the specific morphology against storm disturbance. Owing to the specific morphology, *L. elongata* is able to live several years, resulting in several times of spawning in a life span.

In *M. spatagus* and *B. agassizii* living in nutrient-poor environment, the growth rates of the test length are low and the gonads need more than 2 years to begin to develop. They, however, possess more phyllodal tube feet which enable them to obtain more nutrients, and they form more rigid tests with thicker plates than *N. alta*. They undoubtedly allocate the energies not to the gonad development but to the test growth first. This is possible because these spatangoids burrow deeply in sediment where they can avoid storm disturbance and have the long life span as a result. In the safe place deep in sediment, on the other hand, the pressure from surrounding sand is relatively high, so that the spatangoids must resist the high pressure under which they excavate and transport sediment to move. Therefore, the deep-burrowing spatangoids should allocate the energies first to forming the rigid tests with the thick plates on which the spines play those roles under high pressure.

III. Predation of *Cassis* on spatangoid echinoids

1. Introduction

Living echinoids, including burrowing irregular echinoids, are known to suffer quite high levels of predation from the family Cassidae (Hughes and Hughes 1981). Not only in the Recent but also in the Cenozoic, especially in the Paleogene, spatangoids seem to have suffered cassid predation because there are many fossils of spatangoid tests with predatory holes presumably produced by cassid gastropods (Beu 1972; Gibson & Watson 1989, 1991; McNamara 1991, 1994; Abdelhamid 1999; Woodcock & Kelley 2001). McNamara (1994) demonstrated that from late Oligocene to Early Miocene in Australia many spatangoids living in shallow water environments suffered quite high levels of predation from cassid gastropods, and this incident resulted in evolution of the successive species into deeper water habitats, which were regions of lower predation pressure. This study indicates that the predation of cassid gastropods was an important factor which controlled the adaptation of spatangoids, though there in no other comparable study that showed the impact of gastropod predation on evolution of spatangoids. Kanazawa (2004) indicated that the morphological diversification of spatanogids in the Eocene was presumably brought about by cassid predation because it occurred at the same time when the first certain cassid appeared and rapidly diversified, and the new types of morphology in spatangoids correlate with new ability to burrow deeply and to move rapidly, whereby they could apparently escape from cassid predation. This interesting hypothesis, however, is not supported by information on predatory behavior of cassid gastropods, and consequently it is uncertain whether the new types of morphology were essential for escaping from cassid predation.

Although living echinoids are well known to be attacked by cassid gastropods, surprisingly little is known about their predatory behavior. Hughes and Hughes (1971 and 1981) is the only study in which the mode of attack of cassid gastropods was observed in aquaria and described in detail. This study, however, dealt with only epibenthic regular sea urchins, and the predatory behavior on irregular echinoids including spatangoids is still unknown. To be able to assess the significance of cassid predation it is necessary at first to know the mode of cassid predation on spatangoids. With the information on the predatory behavior, if the fossil records of spatangoid echinoids and cassid gastropods are re-examined, the impact of cassid predation on the adaptation of spatangoid echinoids can be exactly deduced. In this study, a large cassid gastropod, *Cassis cornuta* which has appeared since the Miocene (Abbott 1968) and seems to have been a key predator on echinoids is used.

2. Habitat of *Cassis cornuta*

The helmet snail, *Cassis cornuta,* was observed by scuba diving in its habitat on sea floor at depths of 3-22 m in Oura Bay, Okinawa, Japan in May 2009 (Fig.36). The habitat is located in a protected bay surrounded by capes. The substratum is mainly composed of fine-grained sand, becoming slightly finer and silty with the increase in water depth, and almost exposed without rocks and sea grass. On the sea floor shallower than 6 m deep, ripple marks were observed, indicating frequent disturbance by currents. Five individuals of *C. cornuta* were found from the area of about 500 x 500 m^2 at depths of 10-22 m.

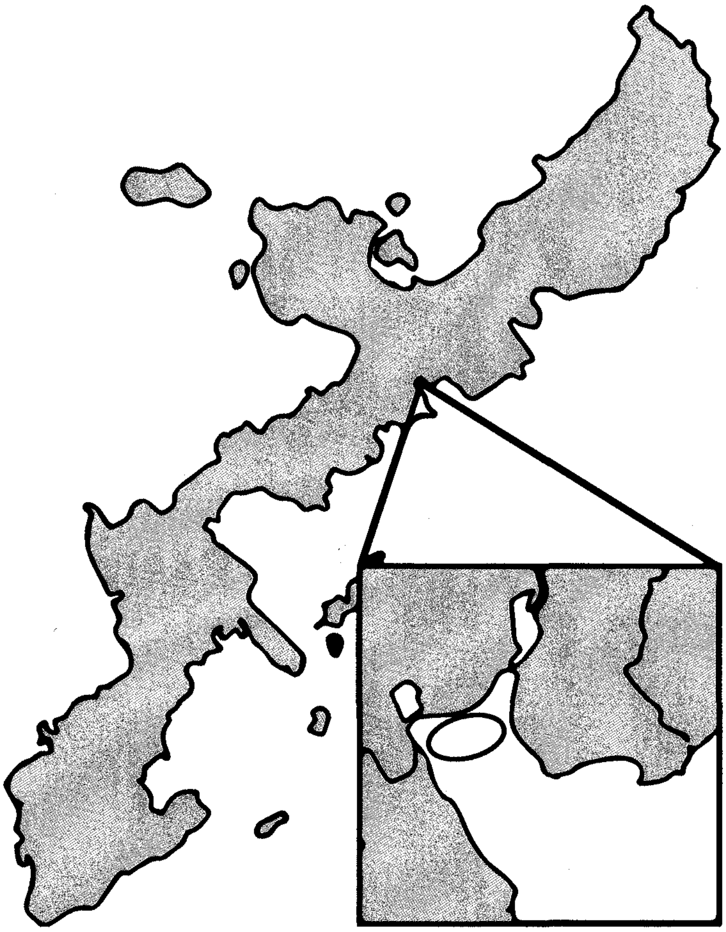


Fig.36. Map of Okinawa and around Oura Bay. The black circle indicates the investigated area in this study.

3. Predatory behavior of *Cassis cornuta*

An individual of *Cassis cornuta* with the test height of 18 cm was used for aquarium experiments. The animal was carried from the Okinawa to the laboratory of Kanagawa University with a cooler-box in a condition of being wrapped with a few sheets of wet news paper, taking approximately 6 hours to arrive at the laboratory. Subsequently, it was immediately placed in a marine aquarium with circulating sea water maintained at 20 °C.

Burrowing depth in search of prey

Cassis cornuta can burrow into sediment to prey on echinoids. Two types of sediments (coarse-grained sand and fine-grained sand) were prepared and epifaunal *Anthocidaris crassispina*, instead of burrowing spatangoid echinoids, was buried as a prey in the sediment at a depth of 8 cm or 15 cm (Fig.37) in an aquarium. *C. cornuta* was put on the sediment surface and its behavior, detecting and preying upon the echinoid, was observed.

In the aquarium *C. cornuta* usually crawled on the sediment surface, seeking its prey. In the cases that a prey, *A. crassispina*, was buried 8 cm or 15 cm deep in coarse-grained sand, *C. cornuta* stopped crawling at the place above the buried echinoid, and started to burrow into the sediment. The helmet snail reached the prey in 30-40 minutes and preyed on it there (Fig.38). In the case that the echinoid was buried 8 cm deep in fine-grained sand, *C. cornuta* preyed on the animal in the same way as in the coarse-grained sand (Fig.39). However, when the echinoid was buried 15 cm deep in the fine-grained sand, *C. cornuta* never stopped crawling at the place above the buried echinoid and could not find the prey (Fig.40).

Predation on Lovenia elongata

Nine individuals of *L. elongata* with 5.3-8.5 cm in test length were used (Table 9). In each experiment, an individual of *L. elongata* was put on fine-grained sand in an aquarium, and after it was buried in the sediment, *Cassis cornuta* was placed on the sediment surface.

Since *L. elongata* burrowed near the sediment surface, *C. cornuta* could easily find out the prey and attacked it. When attacked, the sea urchin immediately struggled to escape onto the sediment surface in every experiment. However, seven individuals were preyed and only two individuals could manage to escape onto the sediment surface and ran away from the predator. In the case of successful escape, the urchin noticed the crisis in the moment at which the predator touched a part of the animal and escaped onto the sediment surface at once (Fig.41). It is noteworthy that the specific morphology of *L. elongata* enables it to make the amazing escape; the long, stout dorsal spines push up the gastropod foot to avoid its clasp and the long, stout latero-ventral spines move the echinoid powerfully and quickly. In other preyed cases, the urchins were entirely covered with the large foot of the predator with the heavy snail when they had just noticed the attack, and they had no chance to escape from the predation (Fig.42). On the test of L. elongata preyed by the cassis a cylindrical hole was left (Fig.43).

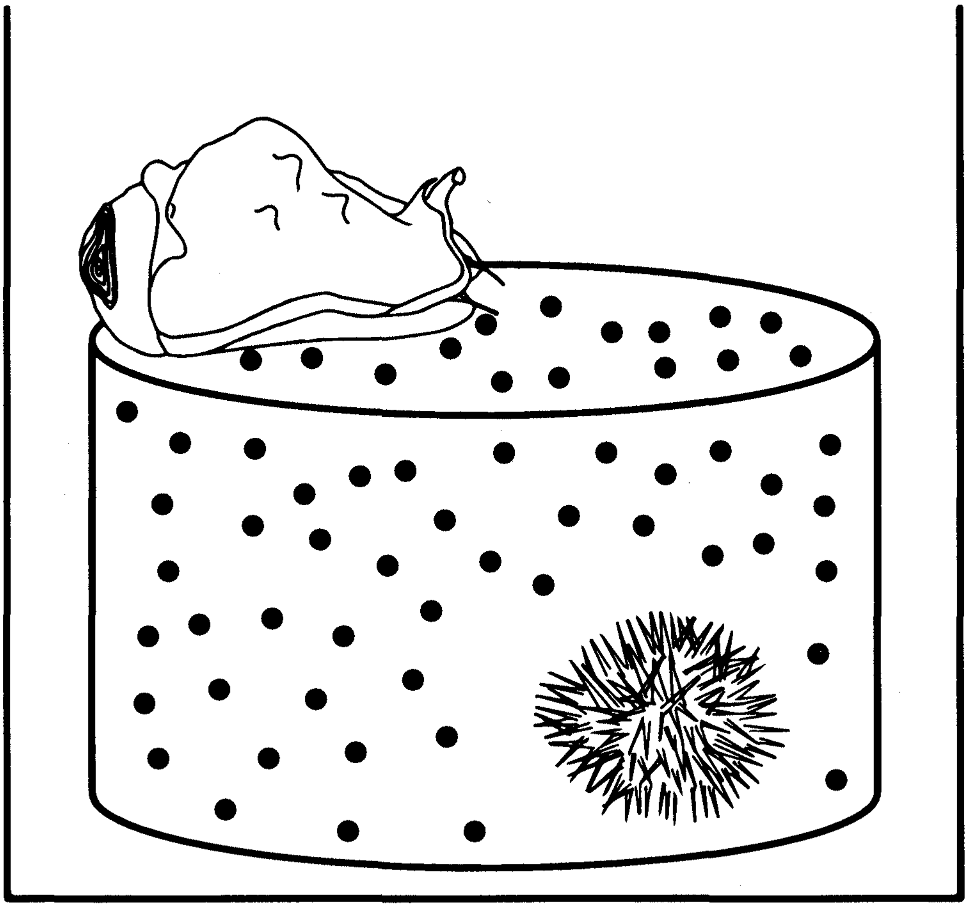


Fig.37. Experiment on burrowing depth in search of praying in *Cassis cornuta*.

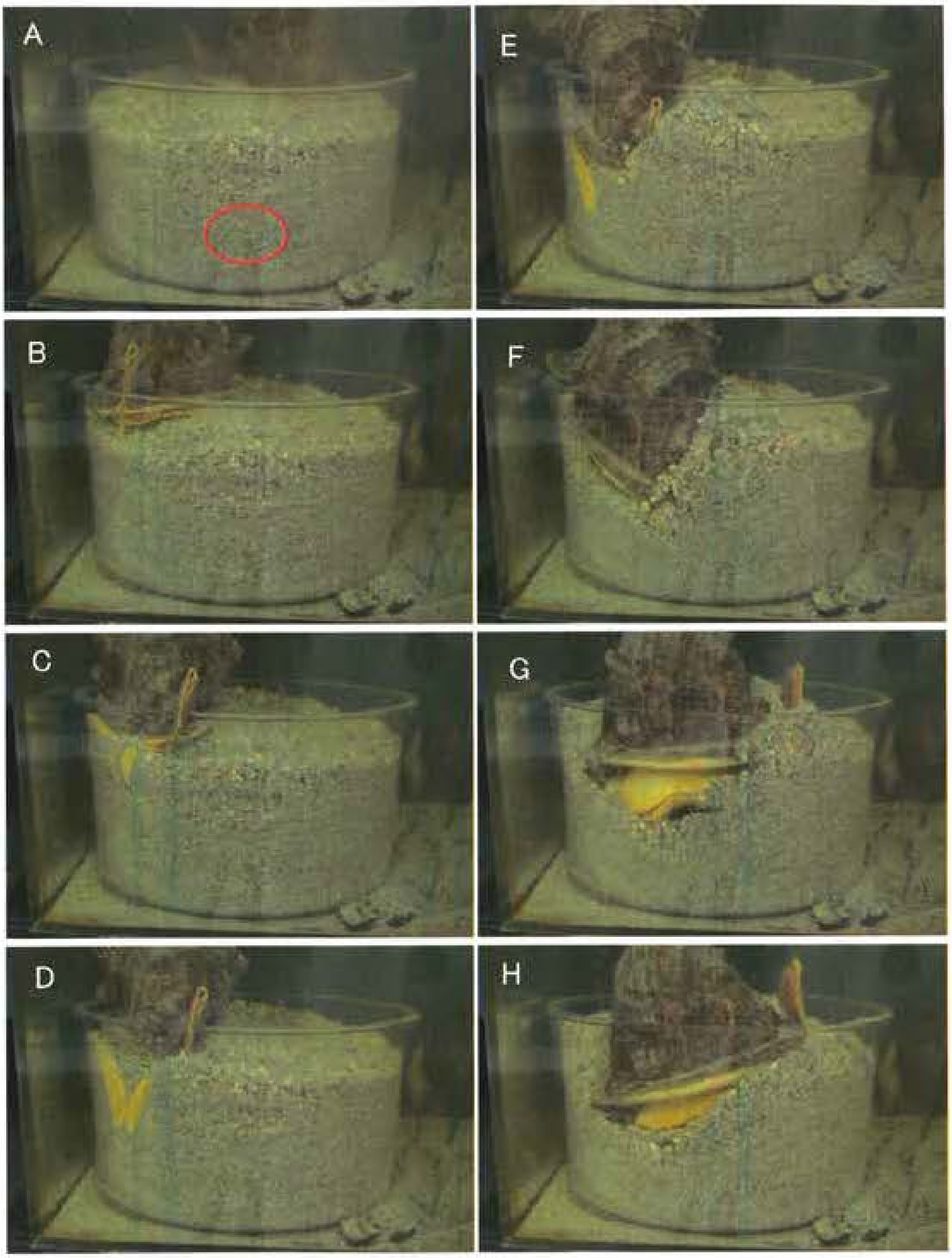


Fig.38. Predatory behavior of *C. cornuta* on a prey *A. crassispina* buried 15 cm deep in coarse-grained sand. The position of the prey is shown with a red circle. *C. cornuta* was put on the sediment surface (A). It stopped crawling at the place above the buried echinoid (B), and started to burrow into the sediment (C). Then, burrowed deeper using the foot (D-F) and finally preyed the sea urchin (G and H).

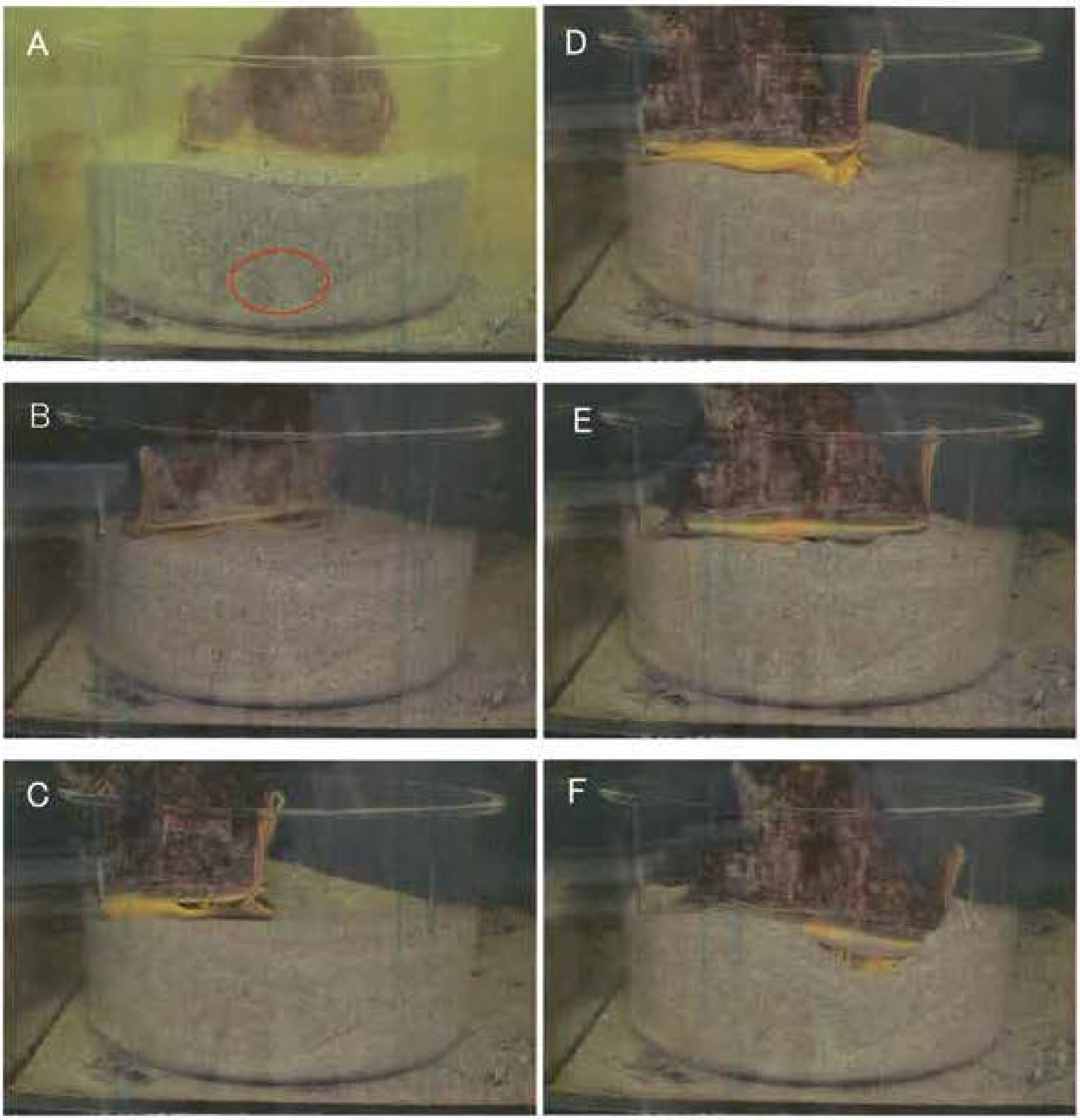


Fig.39. Predatory behavior of *C. cornuta* on a prey *A. crassispina* buried 8 cm deep in fine-grained sand. The position of the prey is shown with a red circle. *C. cornuta* put on the sediment surface (A) crawled about there (B). It stopped crawling at the place above the buried echinoid (C), and burrowed into the sediment (D and E). Then, it reached the echinoid and preyed it (F).

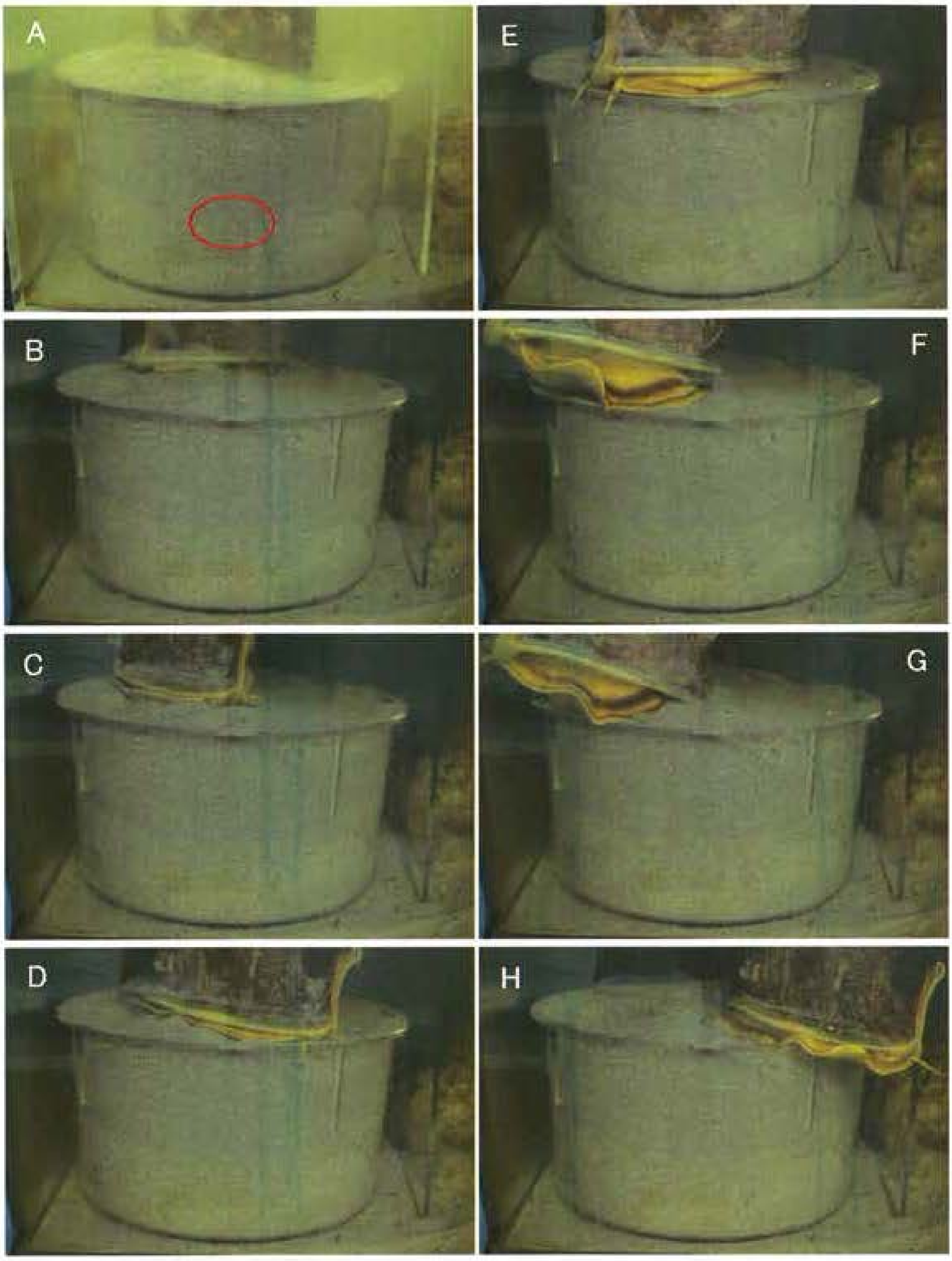


Fig.40. Predatory behavior of *C. cornuta* on a prey *A. crassispina* buried 15 cm deep in fine-grained sand. The position of the prey is represented with a red circle. *C. cornuta* put on the sediment surface (A) crawled about there (B and C). However, it never stopped crawling at the place above the buried echinoid and could not find the prey (D-H).

Table 9. The result of the feeding behavior of *C. cornuta* to *L. elongata*

Individual number (Test length)	Result	Behavior of *C. cornuta*
1. (5.3 cm)	Preyed	Toward the posterior of the prey and covered it completely
2. (5.4 cm)	Preyed	Toward the left side of the prey and covered it completely
3. (5.5 cm)	Preyed	Toward the right side of the prey and covered it completely
4. (5.8 cm)	Preyed	Toward the right side of the prey and covered it completely
5. (6.0 cm)	Preyed	Toward the posterior of the prey and covered it completely
6. (6.5 cm)	Preyed	Toward the right side of the prey and covered it completely
7. (7.1 cm)	Run away by escaping to sediment surface	Toward the right side of the prey and just touched it
8. (7.5 cm)	Preyed	Toward the posterior of the prey and covered it completely
9. (8.5 cm)	Run away by escaping to sediment surface	Toward the posterior of the prey and just touched it

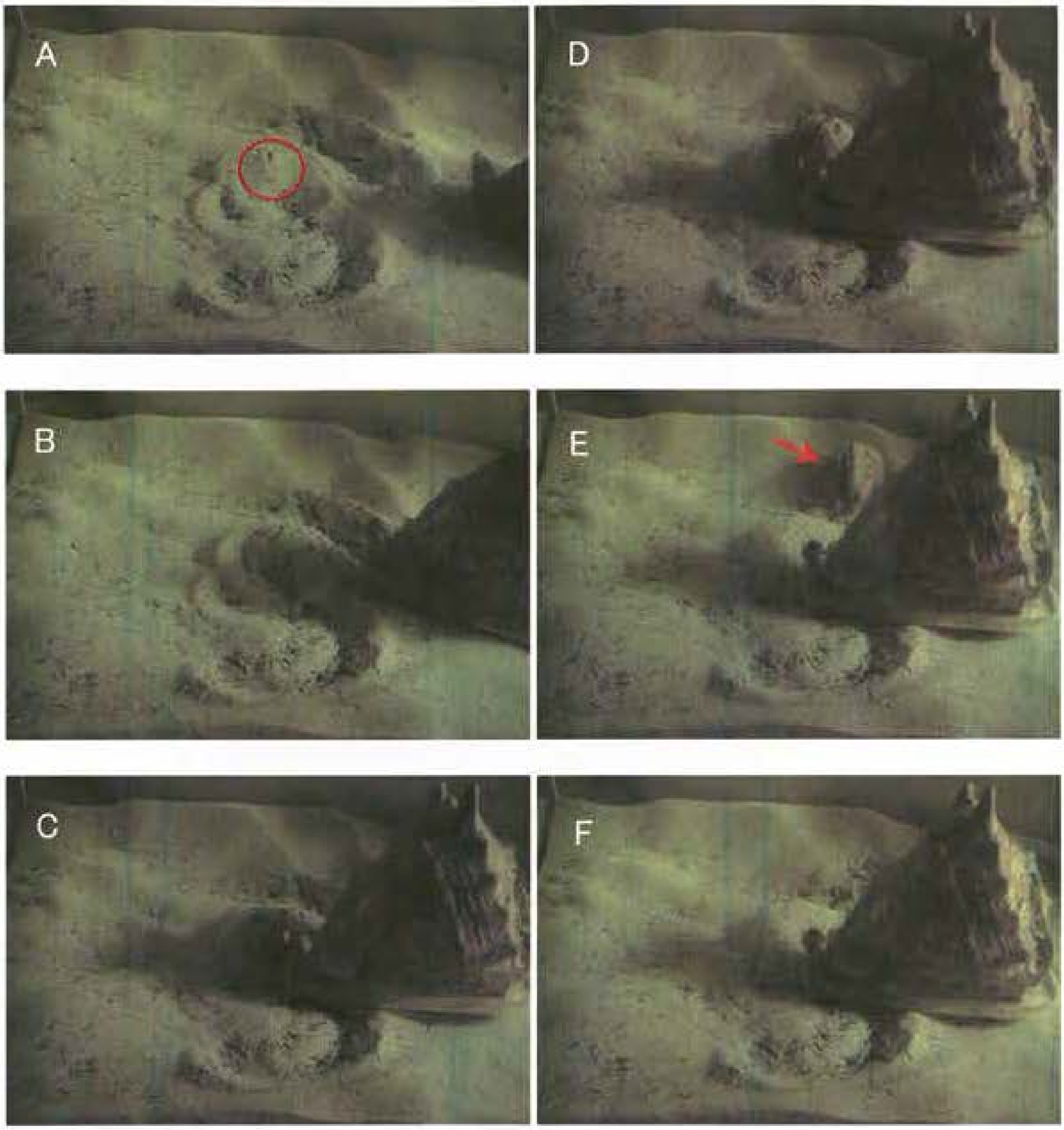


Fig.41. Escape behavior of *L. elongata* from the predation of *C. cornuta*. The spatangoid was burrowing in the sediment (in red circle) and *C. cornuta* was put on the sediment surface (A). *C. cornuta* approached (B) and touched the right side of the spatangoid (C), then *L. elongata* escaped onto the sediment surface quickly (D) and ran away from the gastropod (E). *C. cornuta* was eventually left behind and could not prey the spatangoid (F).

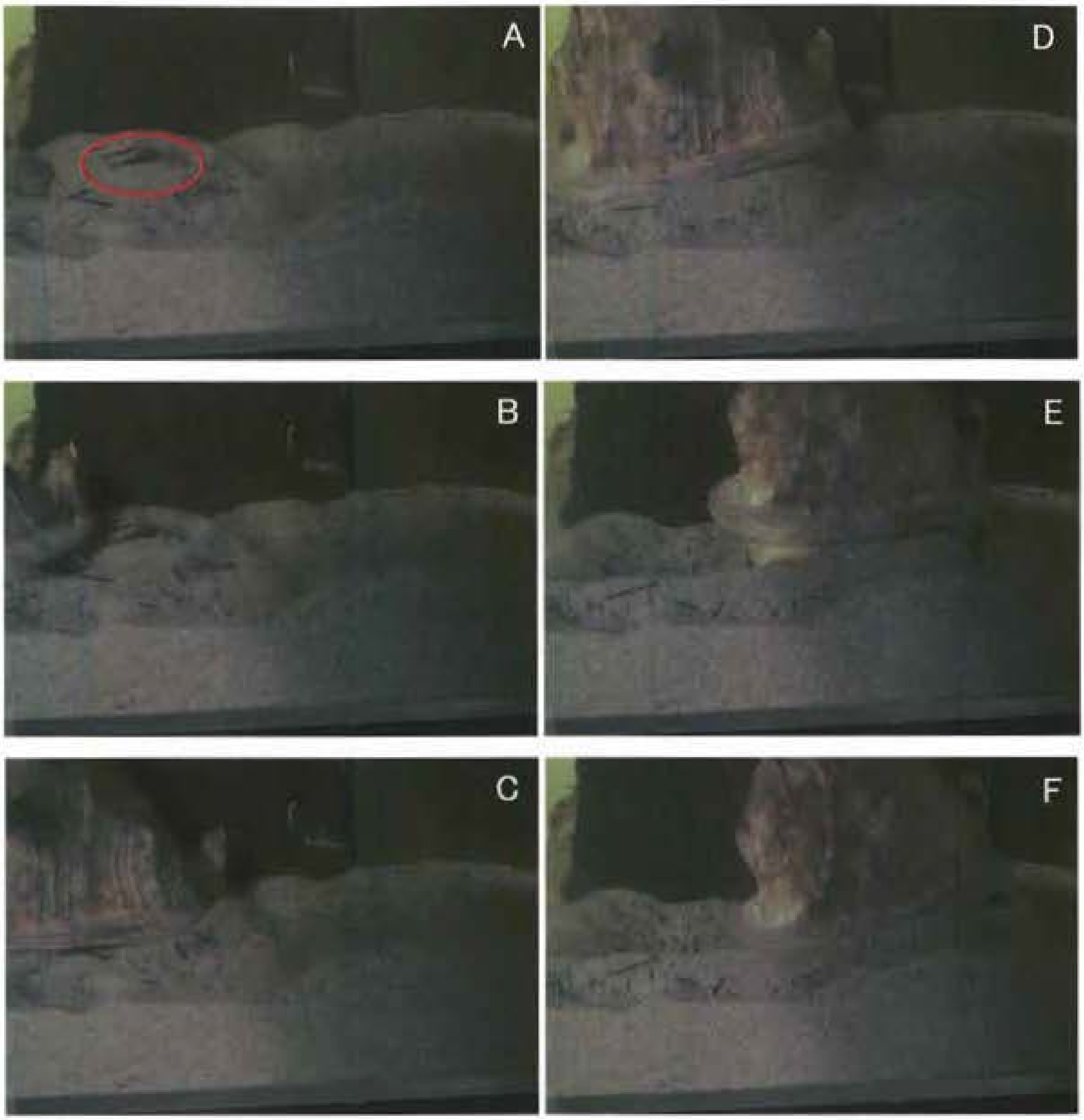


Fig.42. Predation on *L. elongata* by *C. cornuta*. The spatangoid was burrowing in the sediment (in a red circle) and *C. cornuta* was put on the sediment surface (A). *C. cornuta* approached (B) and covered *L. elongata* burrowing in sediment with the large foot at the first attack (C). Then, the spatangoid struggled to escape from the clasp, pushing up the heavy snail and making slow forward progress (D and E). But soon the urchin could not move anymore and was preyed by the predator (F).

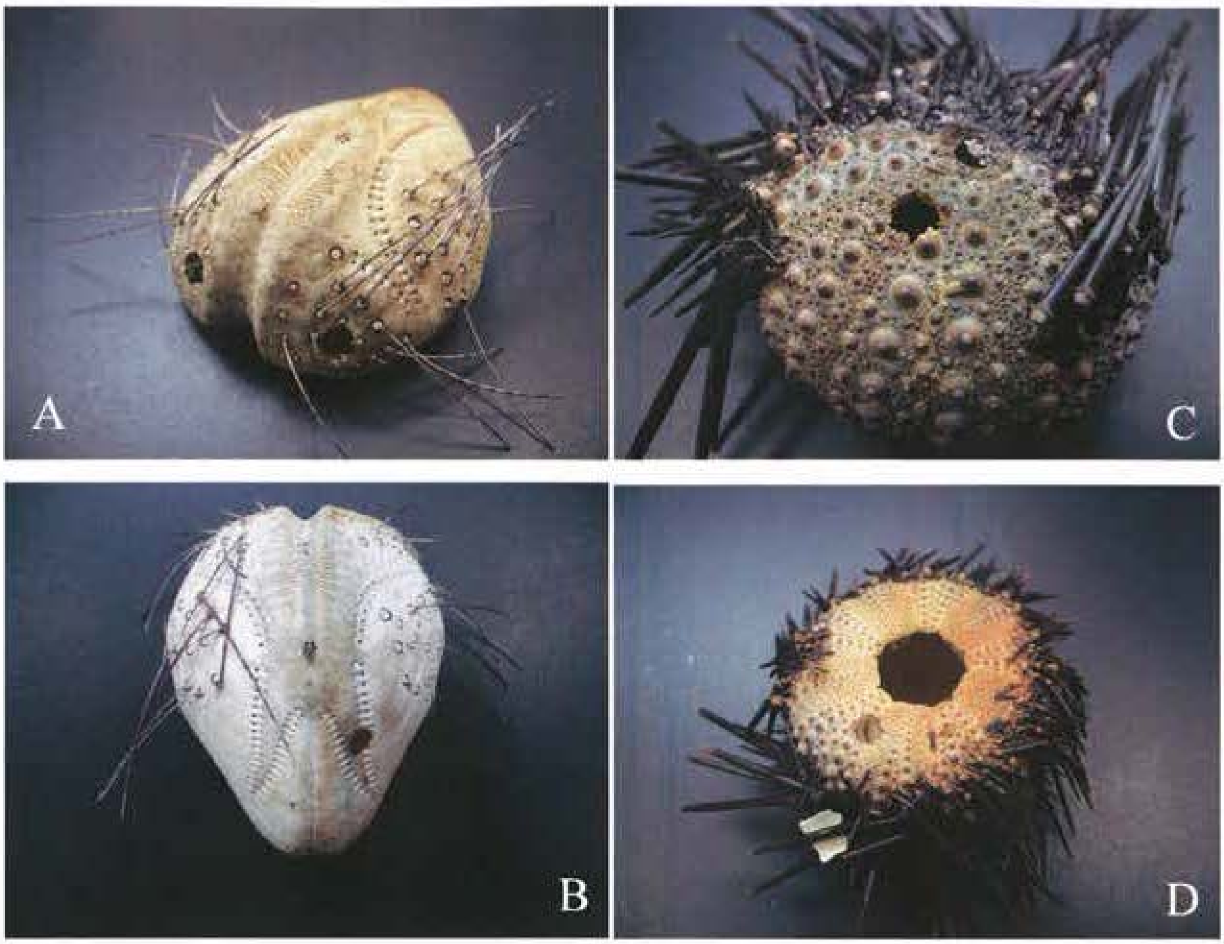


Fig.43. Predatory holes produced by *C. cornuta*. One or two cylindrical holes were left on the test. A; *L. elongata* (65 mm), B; *L. elongata* (75 mm), C; *A. crassispina* (45 mm), D; *A. crassispina* (50 mm).

4. Prey-predator relationship between spatangoids and cassids

The aquarium observation on *Cassis cornuta* suggests that the large helmet snail must be a lethal predator for most spatangoid echinoids, because the predator can seek out the echinoids burrowing in sediment and prey on them. Surprisingly, even *L. elongata* which can probably move most powerfully and rapidly among spatangoids was easily preyed by the predator. It should be noted that the individuals of *L. elongata* preyed by the cassid were all smaller than 7 cm in test length, suggesting that they cannot escape from the predation if the cassid is more than 2.5 times larger than them. The cassid preys on the urchins by mounting and clasping it with the foot, so that the body size, especially the shell weight and the foot size must be important to make a success of the predation.

In the case that *L. elongata* survived the cassid predation, it showed the amazing escape owing to the specific morphologies; while the long, stout dorsal spines pushed up the overlying foot of the gastropod to avoid its clasp, the long, stout latero-ventral spines thrusted the echinoid powerfully and quickly onto the sediment surface. These morphologies are, therefore, undoubtedly essential to escape from the cassid predation.

In the experiments on burrowing depth in search of prey, the cassid could not find out the prey in the case that the prey was buried 18 cm deep in fine-grained sand. Since most spatangoids cannot burrow to such a depth, it seems difficult for them to survive the cassid predation. However, to burrow deeply to escape from the predation might be a possible strategy, if the cassid would be much smaller in size and could not burrow deeply.

According to the fossil records, the first certain cassid gastropod appeard in the tropical region in the Eocene (Abbott 1968), and interestingly, in the same epoch *Lovenia* and *Brissus* also appeared for the first time in the same region (Fischer 1966). It is noteworthy that most of *Lovenia*, *Brissus* and cassids had small size, 3-4 cm in length in the Eocene. With the small difference in body size, *Lovenia* could easily survive the cassid predation because the anti-predatory behavior brought about by the specific morphologies must have been effective enough to escape from the predator, as indicated by the aquarium experiments. This implies that the specific morphologies of *L. elongata* would originally have developed as an anti-predation device. The same could be said for the oval test with specific ventral morphology for efficient burrowing in *Brissus*. It should be paid attention that in the Eocene the specific morphologies convergently appeared in different spatangoid lineages, as in the families Loveniidae, Spatangidae, Brissidae, which fact indicates that a common functional significance can be ascribed to the appearance of the morphologies.

Like many other large species of Genus *Cassis*, the oldest fossil of *Cassis cornuta* is known from the Miocene, and the shell was about 20 cm in length (Abbott 1968). In *Lovenia elongata*, the oldest fossil is also known from the Miocene, and the test was about 5 cm in length (Kier 1972), which was the largest size in *Lovenia* lineage since its appearance in Eocene. *Brissus* also had attained to the largest size in the Miocene since its appearance, but still about 5 cm in length (Kier 1972). The 4 times difference in body size indicates that it was most likely difficult for *Lovenia* and *Brissus* to live together with the cassid. In the Recent *C. cornuta* is the largest helmet snail and attains 36 cm in length. *L. elongata* also reaches the largest size about 12 cm in the Recent. If the urchin would be attacked by the cassid, it probably has no chance to escape. In the Recent sea, therefore, these animals could not live together in the same region.

McNamara (1994) demonstrated that in *Lovenia* linage high levels of predation from cassid gastropods resulted in evolution of the successive species from shallow to deep water habitats. It, therefore, seems possible that the descendant species also evolved into the very shallow sublittoral zone and temperate zone which were region of no predation pressure.

IV. Adaptive evolution in spatangoid echinoids living in the shallow sublittoral zone

According to the fossil records, the first spatangoid echinoid appeared in the Early Cretaceous. During Cretaceous, spatangids had small tests with less diversified morphology (Fischer 1966) and seems to have lived only in stable environments below the extent of water turbulence, burrowing shallowly in the sediment or crawling on the surface. In the Eocene, however, new types of test morphology related to new modes of life suddenly and convergently appeared in the spatangoids which inhabited sandy bottoms in the shallow sublittoral zone in tropical and subtropical regions. This morphological change was probably induced by predation of cassid gastropods which also appeared in the same regions in the same epoch with their prey spatangoids. Flat tests with long, stout spines on the dorsal and ventral sides, as in *Lovenia*, probably enabled the urchins to escape from gastropod attack and emerge onto sediment surface. Oval tests with the specific ventral morphology for efficient burrowing, as in *Brissus*, allowed the spatangoids to burrow deeply in sand to avoid the gastropod predation. From Eocene to Miocene, these spatangoids with the new modes of life apparently struggled along with the co-existing gastropods by virtue of the attainment of large size which resulted from the co-evolution between the predator and the prey. In the Miocene, however, many of the spatangoids appear to have left their habitats so as to avoid the predators which had attained the shell size about 4 times larger than their prey spatangoids. Accordingly, many spatangoids evolved not only into deep water environment, as McNamara (1994) suggested, but probably also into the very shallow sublittoral zone and/or into the temperate zone where the predatory cassid gastropods did not live. The morphologies for anti-predation probably enabled the sea urchins to inhabit the unstable environments of the very shallow sublittoral zone. The spatangoids, like *Brissus* and *Metalia*, with the ability for burrowing deep in sand can avoid being washed out to death in storm disturbance. In the safe habitat they could probably evolve the life history in which they grow slowly and reach sexual maturity late with the long life span and slow alternation of generations. On the other hand, the spatangoid like *Lovenia elongata*, living near the turbulent sediment surface has specific morphologies for quick burrowing and rapid righting. In a disturbance, this urchin can burrow deeper than usual before it is washed out by currents. Even if washed out, it can rapidly right and re-burrow. In the unstable environment, the animal grows rapidly, but its sexual maturity is not early and the life span is long, because in this sea urchin, the energies derived from nutrients should be first allocated to the construction of the rigid test with the stout long spines by which it can survive in storm disturbance. In contrast to these spatangoids, *N. alta* has no specific morphology against either predation or storm disturbance, indicating that its ancestors would not have suffered cassid predation. This spatangoid, instead, adapts to the unstable environments with a specific trade-off between test growth and sexual maturity in its life history; it reduces the cost of test construction with very thin plates and allocates more energy to the development of the gonads. Consequently, *N. alta* can reach sexual maturity earlier at one year in addition to the faster rate of test growth than other spatangoids, resulting in certain alternation of generations in the unstable environment. Thus, spatangoids adapt to the shallow sublittoral zone in different ways depending on their respective evolutionary histories. The outstanding success in adaptation to the unstable environment in the extent of water turbulence would not have been achieved without predation pressure. For deposit-feeding spatangoids that inhabited calm safety environments, like those in the Createceous, it was presumably no use to burrow deep in sediment, where fewer nutrients are contained than near the surface, or to move rapidly, which needs much more energy than to do slowly. This is strongly suggested by the fact that the specific morphologies for these behaviors had never evolved before the Eocene while spatangoids had suffered almost no predation pressure and had stayed in the calm sublittoral zone for about 100 million years.

V. Conclusions

1. The ecology of spatangoid echinoids living in the unstable environment in the shallow sublittral zone was revealed:

- *Lovenia elongata*, living near the turbulent sediment surface has specific morphologies for quick burrowing and rapid righting, whereby in a disturbance, it can burrow deeper to avoid being washed out by currents. The animal grows rapidly, but its sexual maturity is not early (2 years) and the life span is long (5 years). The energies derived from nutrients is presumably allocated first to the construction of the rigid test with the stout long spines by which it can survive in storm disturbance.
- *Metalia spatagus* and *Brissus agassizii* have morphologies appropriate to burrow deeply, whereby they usually burrow deeper below the turbulent sediment surface and can avoid being washed out. In the relatively stable condition, they grow slowly and reach sexual maturity late (2-3 years), and the life span is long (5-6 years).
- *Nacospatangus alta* has no specific morphology against water turbulence, though it lives near the sediment surface. It grows rapidly and reaches sexual maturity early within one year of its life span, reducing the cost of test construction with very thin plates and allocating more energy to the development of the gonad.

2. Prey-predator interaction between *Cassis cornuta* and spatangoids is observed for the first time. *Cassis cornuta* burrows into sediment and preys on spatangoids by mounting and clasping them with the foot. *L. elongata* immediately struggled to escape onto the sediment surface when attacked. The specific morphology, the long, stout spines of the ventral and dorsal sides, enables *L. elongata* to make the amazing escape. The spatangoid, however, cannot escape from the predation if the cassid is more than 2.5 times larger than it, indicating that the body size must be important to make a success of the predation. To burrow deeply to escape from the predation might be a possible strategy.

3. A possible adaptive evolution in saptagnoid echinoids in the Cenozoic was deduced. The morphological changes which dramatically occurred in the Eocene strongly suggest that the spatangoids obtained new modes of life according to the appearance of their predator cassid gastropods; *Lovenia* type with the ability for rapid movement lived near the sediment surface and escaped onto the surface when attacked, and *Brissus* type burrowed much deeper in the substratum, avoiding the predation. In the Miocene, however, when some cassid species about 3 times larger than their prey spatangoids appeared, many of the spatangoids have left their habitats. In the very shallow sublittoral zone, the morphologies for anti-predation probably facilitated the sea urchins to inhabit the unstable environments, enabling them to avoid surface disturbances on sea floor.

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Appendix

1) Masaya Saitoh and Ken'ichi Kanazawa (2012) Adaptative morphology for living in shallow water environments in spatangoid echinoids. Zoosymposia 7 : 2012, 255-265p

2) Masaya Saitoh (2012) Spatangoid echinoids living in the shallow water environments. *Umiushitsushin* No. 74: 8-9. (In Japanese).

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Adaptative morphology for living in shallow water environments in spatangoid echinoids*

MASAYA SAITOH[1] & KEN'ICHI KANAZAWA[1,2]

[1] *Kanagawa University, Hiratsuka, Japan*
[2] *Corresponding author, E-mail: kanazawa@kanagawa-u.ac.jp*

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Abstract

Six spatangoid species living in an area about 1 km^2 at depths of 5–18 m were investigated in the Oki-Islands in the Japan Sea. The spatangoids capable of burrowing deeply principally adapt to unstable environment where the sediment surface is disturbed by storms. They are confined to the respective habitats depending on their functional morphology; apical tuft spines and fascioles for respiration, inflated plastron and stern-like postero-ventral shape for deep-burrowing. An exceptional spatangoid, *Lovenia elongata*, has specific morphologies for quick burrowing and rapid righting against disturbance of superficial sediment, which make it possible for it to live in fine- to coarse-grained sand at various water depths in spite of its burrowing just below the sediment surface.

Key words: Echinoidea, Spatangoida, morphology, distribution, burrowing depth

Introduction

Spatangoid echinoids live in littoral to bathyal zones, burrowing to various depths in different types of sediments. They have a wide variety of test shapes with a complex arrangement of functionally and morphologically distinct spines, and their morphologies with respect to function, ontogeny, phylogeny, *etc.* have been studied in detail (*e.g.*, Nichols 1959; Smith 1980; McNamara 1987; Kanazawa 1992; Nérauderau *et al.* 1998; Eble 2000; Villier *et al.* 2004; Smith & Stockley 2005; Saucède *et al.* 2006; Kroh & Smith 2010). In contrast to extensive morphological knowledge, little is known about ecological aspects of spatangoids, and only some species have been intensively studied: Moore (1936), Nichols (1959), Buchanan (1966), Beukema (1985), De Ridder & Jangoux (1987, 1993), Nakamura (2001), Nunes & Jangoux (2004, 2007) for *Echinocardium cordatum* (Pennant); Brattström (1946), Hollertz & Duchene (2001) for *Brissopsis lyrifera* (Forbes); Chesher (1963), Moore & López (1966) for *Moira atropos* (Lamarck); Kier & Grant (1965), Chesher (1968) for *Meoma ventricosa* (Lamarck), Ferber & Lawrence (1976) for *Lovenia elongata* (Gray); Schinner (1993) for *Schizaster canaliferus* (Lamarck); Thompson & Riddle (2005) for *Abatus ingens* (Koehler). These studies have shown that each spatangoid species has a specific ecology in relation to the environment it is adapted to, such as substratum and water depth. However, a comprehensive ecological study on several spatangoids that live in a region where they are confined to their respective habitats has not been made so far. For such

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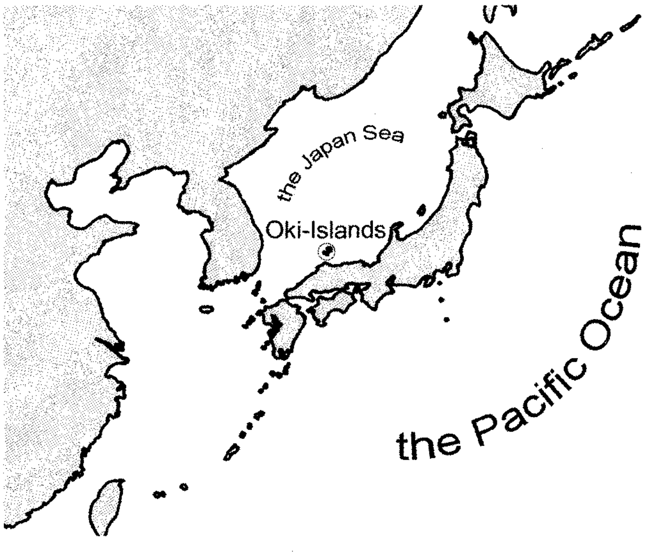

FIGURE 1. Map of Japan and adjacent regions. The study area (Oki-Islands) is located in the Japan Sea.

ecological study the Oki-Islands in the Japan Sea are excellent. Here six spatangoid species live in an area about 1 km^2 at water depths of 5–18 m, where there are different kinds of environments that apparently enable the six different spatangoids to inhabit such a small area. In this paper, based on field investigations and aquarium experiments, the factors that control the spatangoid distribution in shallow water environment are studied from the viewpoint of adaptive morphology.

Materials and Methods

Field work. Field investigations were carried out around Takugi village of the Oki-Islands in the Japan Sea (Fig. 1). Observations and specimen collection were made by scuba diving at five stations at depths from 5 to 18 m (Fig. 2, Table 1). An area of about 80 square meters at each station was investigated. Six spatangoid species; *Lovenia elongata* (Gray), *Pseudomaretia alta* (A. Agassiz), *Metalia spatagus* (Linnaeus), *Brissus agassizii* Döderlein, *Echinocardium cordatum* (Pennant), and *Moira lachesinella* Mortensen were found (Table 1). The echinoids were collected by digging in the sand manually, and their burrowing depths were measured. The number of collected specimens was counted for each species in their respective stations. The conditions of sediment surfaces at the stations were examined through ripple marks made by water disturbance on the sea floor. The field investigations were carried out 11 times (November 2007; April and October 2008; January, May, August and November 2009; February, May, July and November 2010). All the heart urchins collected were transported to the laboratory of Kanagawa University and deposited there for further investigations.

Laboratory work. Taking into account respiration and burrowing, morphology and behavior of the spatangoids were examined because burrowing in sediment to gather food and obtaining fresh water for respiration are essential for infaunal spatangoids.

In spatangoids fascioles that are densely packed bands of small ciliated spines have a specific function to create water currents to draw fresh water (Nichols 1959; Chesher 1968). The placement of fascioles on the test and the current produced around a buried echinoid were examined. Red food dye was used for tracing the course of currents. Also, apical tuft spines that form an apical funnel to

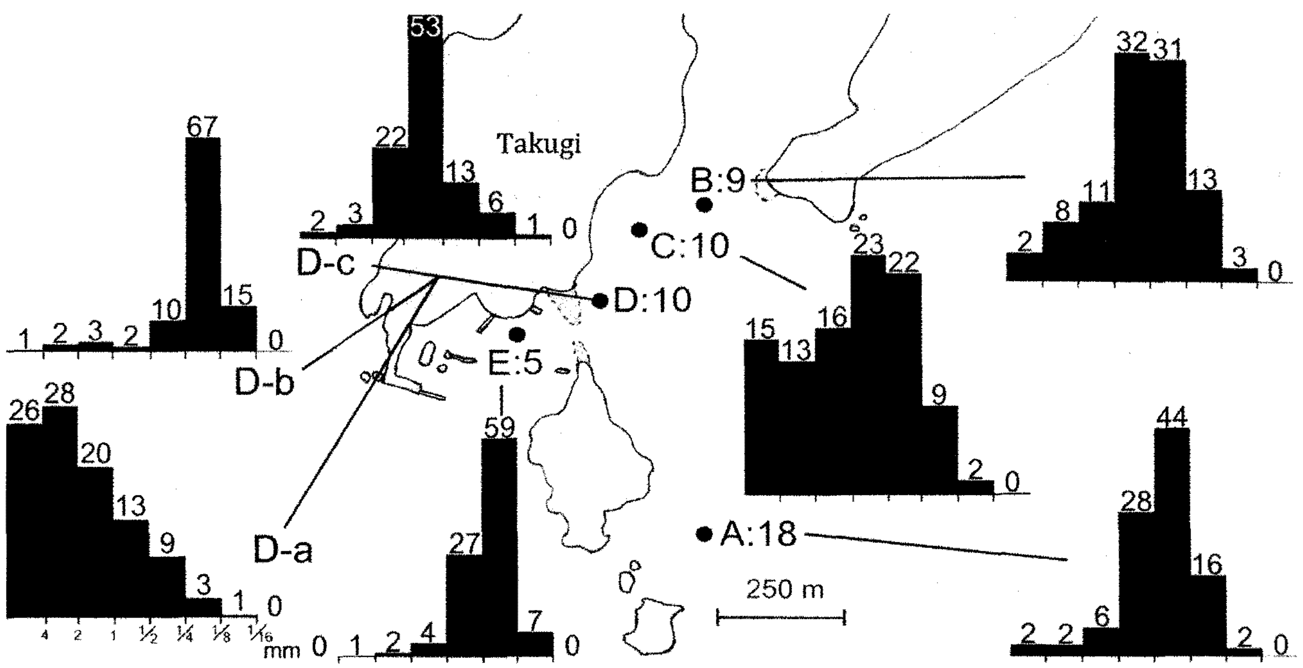

FIGURE 2. Map of the Dogo region of the Oki-Islands, showing stations studied (●) with water depth, and histograms of the substratum particle size distribution; numbers in histograms indicate percent dry weight (see also Table 1).

draw fresh water from sediment surface were observed. In order to check the effectiveness of an apical funnel, a spatangoid whose apical tuft spines were cut off was allowed to burrow in fine-grained sand in an aquarium and its behavior was observed.

Mode of burrowing is closely related to test shape, particularly the shape of plastron and postero-ventral part (Kanazawa 1992). Focusing on this test morphology and related function of spines, burrowing behavior of the spatangoids was examined in aquaria. The activity in the sediment was observed when the urchin appeared at a side wall of an aquarium. The sediments taken from their habitats were used for the experiments, and each echinoid was allowed to burrow not only in the native sediment but also in non-native sediment in different grain size.

The behaviors of the spatangoids under water disturbance were examined in an aquarium. The currents were produced manually by waving a hand in the aquarium, and sediment overlying a burrowing echinoid was washed away at a rate of 6–10 cm per minute. The behavior of the urchin was recorded by a video camera. Righting and re-burrowing behaviors on the sediment were observed in an aquarium. Each animal was placed in an upside-down position on the sediment surface and its speed of righting and re-burrowing was measured.

Results

Habitat condition. The investigated area is located in a protected bay surrounded by capes and islands and is usually calm except at times of storm. In the Oki-Islands as well as other coastal regions of the Japan Sea, strong storms come in winter: ripple marks about 5 cm high and 20–30 cm wave length formed by storm disturbance were frequently observed on the sea floors at depths shallower than 10 m and sometimes at depths from 10 to 18 m during winter and early spring. Dead tests of *P. alta* were often found on sediment surfaces at depths shallower than 10 m in spring and numerous dead tests of *M. spatagus* were observed once at the station B at a depth of 9 m in April 2008. In other seasons ripple marks were rarely observed on the bottoms at depths deeper than 5 m except after a typhoon.

Spatangoids in their habitats. Only *Lovenia elongata* was observed in a variety of habitats in different conditions, while the other five species were found in distinct habitats, depending on substratum and water depth (Table 1).

Lovenia elongata (Fig. 5A) was found at water depths of 5 to 18 m (stations A, B, C, D-b, E). The animals burrowed in various kinds of sediments from fine- to coarse-grained sand with the apex 2 to 3 cm below the sediment surface. Many individuals were observed in fine-grained sand of the station E where other sea urchins were rarely found. The burrowing depths of small and large individuals did not differ. In the winter storm seasons from November 2007 to April 2008 and from January 2009 to May 2009 no decrease in number of individuals was observed for any station (Fig. 3).

Pseudomaretia alta (Fig. 5B) was found at water depths of 9 to 18 m (stations A, B, C, D-c). It burrows in medium- to coarse-grained sand with the apex 2 to 3 cm below the sediment surface. The burrowing depth for small and large individuals did not differ. In the winter storm seasons from November 2007 to April 2008 and from January 2009 to May 2009, a remarkable decrease in number of individuals was observed at station C at a depth of 10 m, while no such decrease occurred at station A at a depth of 18 m (Fig. 4).

Metalia spatagus (Fig. 5C) and ***Brissus agassizii*** (Fig. 5D). These spatangoids lived in gravely coarse-grained sand at water depths of 9 to 18 m (stations A, B, C, D-a). Large individuals more than 5 cm test length burrowed 10 to 15 cm deep below the sediment surface, while small ones burrowed only about 5 cm deep. Although the number of observed individuals was few, in these species, a decrease in number of individuals was found in winter storm seasons.

Echinocardium cordatum and ***Moira lachesinella*** These echinoids were rarely found in the investigated area. They were observed only at station E, burrowing 10 to 15 cm deep in fine-grained sand. Changes in number of individuals could not be studied due to the scarcity of these species (4 speci-

TABLE 1. Habitats of the spatangoids studied. Abbreviations: m-c, medium- to coarse-grained; g, gravelly; c, coarse-grained; m, medium-grained; f, fine-grained. In each species the number and percentage of individuals show the cumulative figure for three-year investigation.

Station	**Depth**	**Substratum**	**Sea grass**	**Species observed**					
	(m)			*L. elongata*	*P. alta*	*M. spatagus*	*B. agassizii*	*E. cordatum*	*Moira lachesinella*
A	18	m-c sand	scarcely	17 (4%)	161 (50%)	33 (22%)	4 (5%)	0	0
B	9	g m-c sand	patchily	91 (20%)	23 (8%)	36 (25%)	27 (36%)	0	0
C	10	g m-c sand	all around	62 (14%)	101 (33%)	40 (27%)	14 (19%)	0	0
D-a	10	g c sand	scarcely	0 (0%)	0 (0%)	36 (25%)	29 (39%)	0	0
D-b	10	f sand	patchily	83 (19%)	0 (0%)	0 (0%)	0 (0%)	0	0
D-c	10	m sand	patchily	0 (0%)	19 (7%)	0 (0%)	0 (0%)	0	0
E	5	f sand	patchily	193 (43%)	6 (2%)	1 (1%)	1 (1%)	4	4

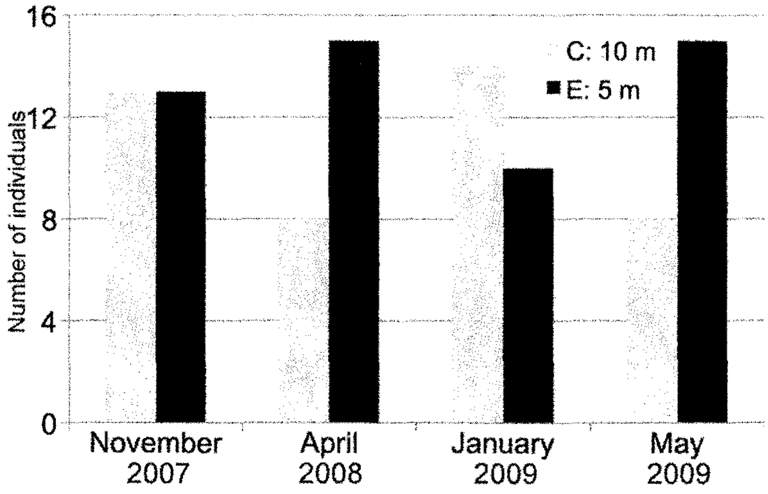

FIGURE 3. Changes in number of individuals for *Lovenia elongata* in winter storm seasons. Cumulative figures for all stations are shown.

mens collected in total during all sampling campaigns).

Morphology and behavior in relation to respiration. *L. elongata* has an internal fasciole and an apical tuft on the dorsal side. In an aquarium, the sea urchin burrowed in fine-grained sand with the apex 1 to 2 cm below the sediment surface, constructing an apical funnel to the sediment surface. There was a water current drawn from the sediment surface into the apical funnel. No other current into the burrow was observed. When the apical tuft spines were cut off, the animal was not completely buried with the apex exposed on the sediment surface. *P. alta* has neither fasciole nor apical tuft on the dorsal side. In an aquarium, the sea urchin was entirely buried in medium- to coarse-grained sand with the apex 1 to 2 cm below the surface. On the sediment surface above the animal no water current filtering through the sediment onto the dorsal area was observed. In fine-grained sand it burrowed exposing the apex on the sediment surface. *M. spatagus* and *B. agassizii* have peripetalous fascioles and no apical tuft on the dorsal sides. In an aquarium, *M. spatagus* and *B. agassizii* burrowed about 10 to 15 cm deep below the sediment surface in coarse-grained sand. In fine-grained sand, the sea urchins burrowed exposing the petalodium on the sediment surface. When the urchins burrowed about 1 to 2 cm deep below the sediment surface, a water current filtering from the sediment surface approximately above the petal region into the burrow was observed.

Morphology and behavior in relation to burrowing. *L. elongata* has a completely flat oral side, *i.e.* an entirely flat plastron and not stern-like postero-ventral shape. The flat oral side brings the latero-ventral spines into contact with the bottom of the burrow. Their backward-directed power strokes propel the urchin forwards. The latero-ventral spines also transport the sand excavated in front to the latero-posterior end and push it into the surrounding sand because the flat ventral surface leaves no space below the test for accumulating the transported sand. This burrowing mechanism appears to be useful only in the superficial layer of sediment. In *P. alta* the posterior part of the plastron is slightly projecting, forming a somewhat stern-like shape. In this sea urchin, the plastron spines as well as the latero-ventral spines provide the principal thrust for forward locomotion. The slightly stern-shaped postero-ventral region produces a small space below the latero-ventral area of the test for accumulating the sand excavated in front and transported to the posterior, though the sand is rejected to some extent into the surrounding sediment. *M. spatagus* and *B. agassizii* have inflated plastrons and a

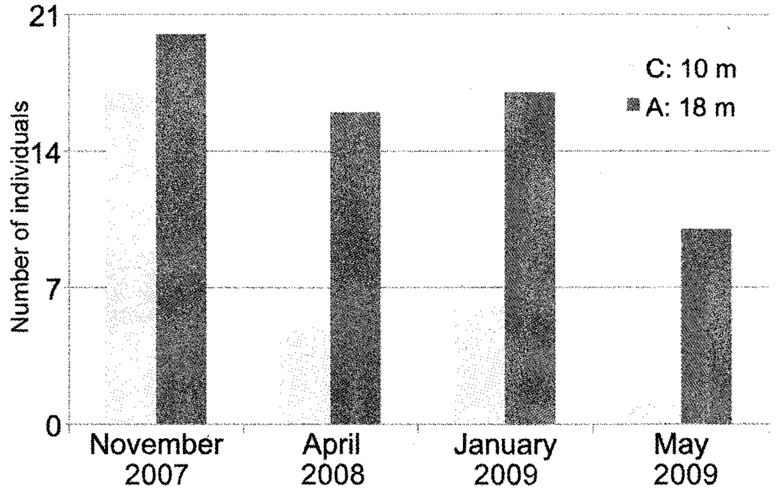

FIGURE 4. Changes in number of individuals for *Pseudomaretia alta* in winter storm seasons. Cumulative figures for all stations are shown.

remarkable stern-like postero-ventral shape. They also have a much more tuberculated plastron and larger sternal plates in comparison to *L. elongata* and *P. alta*. The elevated plastron brings the plastron spines into contact with the floor of the burrow, whereby the spines support the test. Their backward-directed power strokes provide the principal thrust for forward locomotion. The elevated plastron also provides the latero-ventral spines with a convenient space under the test to transport excavated sediment posteriorly. The stern-shaped latero-ventral region produces a large space adequate to accumulate the posteriorly transported sand below the latero-posterior area of the test without pushing it into the surrounding sediment. This morphology presumably enables the spatangoids to burrow deeply in sediment where the pressure of surrounding sediment is expected to be much greater than near the sediment surface.

Behavior under water disturbance. In aquarium experiments with *P. alta*, *M. spatagus* and *B. agassizii*, the urchin was washed out onto the sediment surface and rolled over when the sediment overlying a burrowing urchin was washed away by currents, having no chance to re-burrow. In *L. elongata*, when the dorsal side was partly exposed as overlying sediment was washed away, this urchin started to burrow more deeply and was not washed out. However, after it reached the bottom of aquarium and was no longer able to burrow deeply, the urchin was washed out and overturned. But *L. elongata* soon righted quickly and was not rolled over the sediment surface. The flat test shape with the completely flat ventral side provides the animal with significant stability in currents on the sediment surface.

Righting and re-burrowing on the sediment. In aquarium experiments, *L. elongata* can right much more quickly than the other spatangoids (Table 2): on average 10 seconds, which was about 35 times faster than the other urchins. On the dorsal side, *L. elongata* has very long and stout spines for righting. The tubercles of the spines possess deeply sunken areoles that form large bulges on the inside of the test (camellate tubercles) and provide support for the extremely long and thick muscles. The other echinoids in this study lack such spines.

In re-burrowing experiments it took on average 1 minute for *L. elongata* to disappear under the sediment, which was about 8 times faster than the others. All the spatangoids use the latero-ventral spines for burrowing into sediment, but only *L. elongata* has particularly long, stout spines with

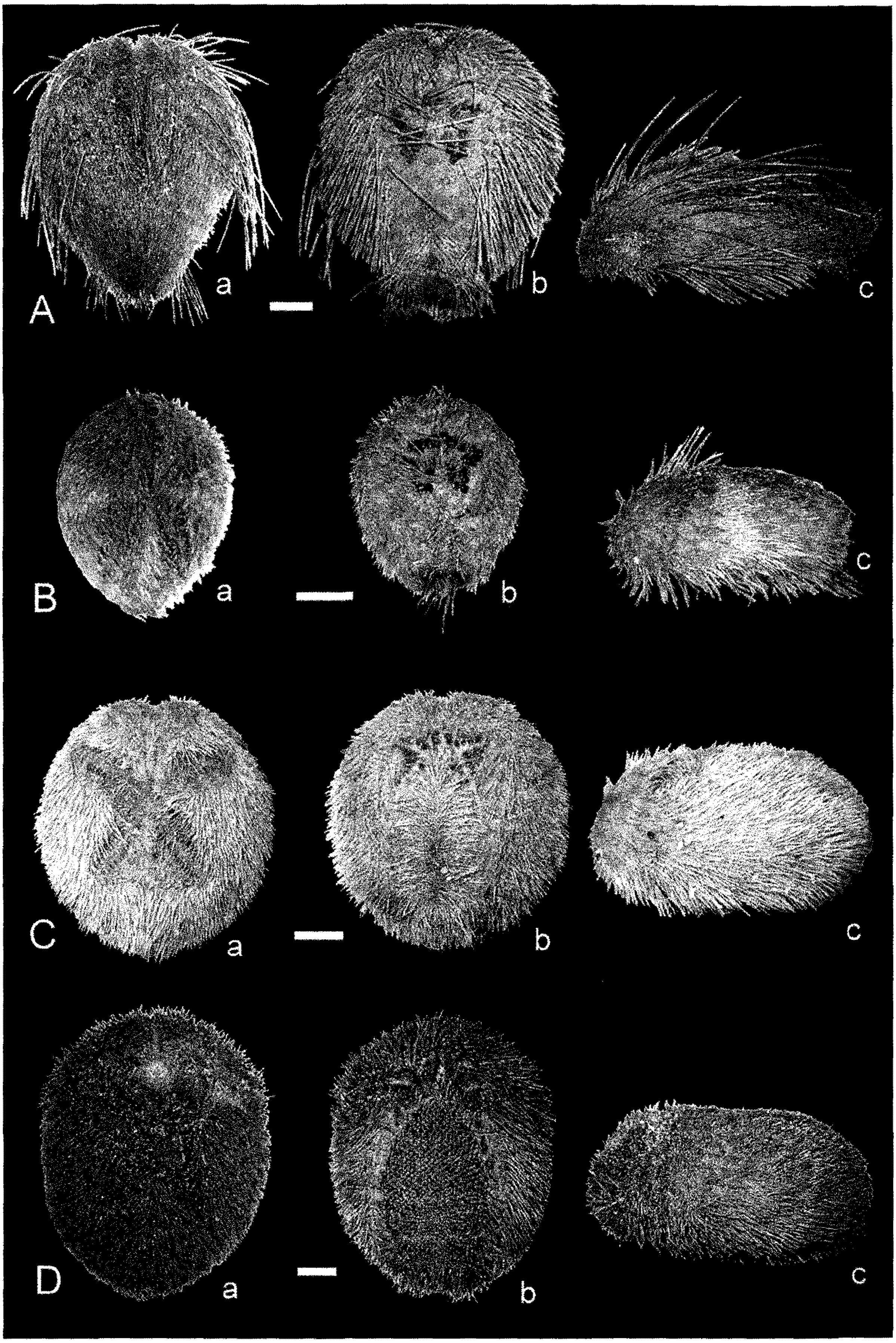

FIGURE 5. Spatangoids examined in this study. A, *Lovenia elongata* (64 mm long); B, *Pseudomaretia alta* (44 mm long); C, *Metalia spatagus* (70 mm long); D, *Brissus agassizii* (76 mm long): a, dorsal side; b, ventral side; c, lateral side. Scale bars equal 10 mm.

deeply sunken tubercles like its long dorsal spines. In the other echinoids, the latero-ventral spines are much smaller and their tubercles are not sunken, providing no support for long thick muscles. The completely flat ventral side of *L. elongata* also facilitates the movement of the latero-venral spines to excavate the sediment beneath the test rapidly because all the spines are in contact with the sediment surface. Additionally, the ventro-lateral areas in *Lovenia* are enlarged compared to the other echinoids studied here and also bear more muscular spine attachments.

Discussion

The study area is located in a calm protected bay, where different kinds of substrate are distributed in a narrow area. This exceptional situation basically enables six spatangoid species to live there. The bottom surfaces are disturbed at the time of storms in accordance with water depths, whereby the spatangoids are confined to their specific habitats.

Adaptation to fine-grained sand bottom in very shallow water. In field investigations, *L. elongata* exclusively lives in fine-grained sand within the study area. In aquarium observations, only *L. elongata* was completely buried in fine-grained sand, constructing a respiratory funnel formed by the apical tuft spines. However, if the apical tuft spines were cut off, the animal was no longer able to disappear under the sediment. Considering that in fine-grained sand *P. alta*, *B. agassizii* and *M. spatagus* that have no apical tuft spine burrowed exposing the petal areas on the sediment surface, the respiratory funnel must be essential for spatangoids to be buried under fine-grained sand, which has already repeatedly noted by many authors (*e.g.*, Nichols 1959; Chesher 1963; Smith 1984). However, unlike *Echinocardium cordatum* and *Moira atropos* observed by those authors, *L. elongata* has no funnel-building tube feet, so that it constructs only a short respiratory funnel about 1 to 2 cm that is slightly longer than the apical tuft spines. It is probable that this constraint allows the animal only to burrow just below the surface of fine-grained sediment.

In the field observations, the fine-grained sand bottom at a depth of 5 m where *L. elongata* lives was often disturbed by water currents. *L. elongata* has specific morphologies for quick burrowing and rapid righting. In a disturbance, this urchin presumably burrows deeper than usual before it is washed-out by currents. Even if washed out, it could rapidly right and re-burrow. *L. elongata*, thus, would survive, though it burrows just below the unstable sand surface in very shallow water environment. No decrease in number of individuals was observed for *L. elongata* in storm seasons.

Other spatangoids (*E. cordatum* and *Moira lachesinella*) found together with *L. elongata* in fine-grained sand burrow 10–15 cm deep below the sediment surface, constructing long respiratory funnels by the funnel-building tube feet. Owing to their deep-burrowing mode of life, these spatangoids would survive in storm disturbance.

	Righting	Re-burrowing
L. elongata	10 sec	1 min
P. alta	5 min	10 min
M. spatagus	10 min	11 min
B. agassizii	7 min	17 min

TABLE 2. Elapsed time for righting and re-burrowing; the average time is shown: 3 individuals for *L. elongata*, 6 for *P. alta*, 2 for *M. spatagus*, 4 for *B. agassizii*.

Although in aquaria *P. alta*, *B. agassizii* and *M. spatagus* apparently have no problem of living in fine-grained sand by exposing their apices on the sediment surface, in the natural environment these spatangoids would be undoubtedly washed out by water disturbance and die. Also, the spatangoids exposed on the sediment surface would easily become prey of many predators like fishes living in shallow waters.

Adaptation to coarse-grained sand bottom in very shallow water. In the field investigations, four spatangoids, *L. elongata*, *P. alta*, *M. spatagus* and *B.agassizii* were found from coarse-grained sand, but their respective distributions are strongly controlled by water depth except *L. elongata*. *P. alta* has no specific morphology to draw water from the sediment surface and the ventral morphology is not appropriate for deep burrowing. These morphological constraints probably confine this sea urchin just below the surface of coarse-grained sand, as observed in the habitat and the aquarium. *P. alta* was found at depths from 9–18 m, but in winter storm seasons a remarkable decrease in number of individuals was observed at depths shallower than 10 m, where dead tests of *P. alta* were frequently found in spring. No such decrease in number occurred at a depth of 18 m. *P. alta* living just below the sediment surface in unstable environment without specific morphology for righting and re-burrowing could be subject to death by storm disturbance. In the other regions in Japan, *P. alta* was usually found in habitats deeper than 20 m (Shigei 1986; Kanazawa 1992). *M. spatagus* and *B. agassizii* have morphologies appropriate to burrow deeply in sand: an inflated plastron and a stern-like postero-ventral shape for transport and accumulating sand in great pressure of surrounding sand. They, however, have neither apical tuft spines nor funnel-building tube feet to construct a respiratory funnel, though they possess peripetalous fascioles to draw water through the sediment above. Owing to these functional morphologies, *M. spatagus* and *B. agassizii* burrow deeply only in coarse-grained sand. In their habitats, large individuals were found in gravelly coarse-grained sand 10–15 cm deep below the sediment surface, where they can usually avoid being washed out to death in storm disturbance. However, numerous dead tests of *M. spatagus* were once observed during our three-year investigation, which indicates that it seems still difficult for *M. spatagus* to survive in severe disturbance caused by a very strong storm. In Toyama Bay *B. agassizii* was found burrowing 20 cm deep in gravelly coarse-grained sand in high-energy environment near the tidal zone (Kanazawa 1992). *B. agassizii* may be capable of burrowing more deeply than *M. spatagus*, which makes it possible for it to inhabit more unstable environment.

L. elongata lives in also fine-grained sand, and it seems easy for it to inhabit coarse-grained sand, where the specific morphologies for quick burrowing and rapid righting makes it possible for it to survive storm disturbance. It is, however, uncertain why *L. elongata* prefers fine-grained sand to coarse-graind sand.

Conclusions

Spatangoids capable of burrowing deeply in sediment can principally adapt to unstable shallow water environments and are confined to specific habitats depending on their functional morphology.

The spatangoids that have fascioles and apical tuft spines with funnel-building tube feet on the dorsal sides, an inflated plastron and a stern-like postero-ventral shape, like *E. cordatum* and *Moira lachesinella*, are capable of burrowing deeply in fine-grained sand.

Spatangoids that have no apical tuft spines but peripetalous fascioles on the dorsal sides and inflated plastron and stern-like postero-ventral shape, like *M. spatagus* and *B. agassizii*, can burrow deeply in coarse-grained sand.

Spatangoids that have neither dorsal fasciole nor apical tuft spines, like *P. alta*, burrow just below the surface of coarse-grained sand. They are thus confined to somewhat deeper calm environment where the sediment surface is scarcely disturbed in a storm.

Specialized spatangoids like *L. elongata*, which has an internal fasciole and apical tuft spines on the dorsal side and the specific morphologies for quick burrowing and rapid righting (*i.e.*, large, stout dorsal spines on camellate tubercles) against disturbance of superficial sediment, can live in fine- to coarse-grained sand in unstable environment in spite of burrowing close to the sediment surface.

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浅海域に生息するブンブク類

神奈川大学大学院理学研究科生物科学専攻　**齋藤　礼弥**　(Saitoh, Masaya)

ウニ類のはぐれもの ?

ブンブク類とは、砂や泥などの堆積物中での生活に適応したウニ類である。そのため、殻上には堆積物の掘削や運搬といった作業を分担して行う機能的に異なる棘が複雑に配列し、また、堆積物中での呼吸を補助する器官が複数存在する。堆積物中での生活に適した様々な形態を持つことでブンブク類は、普通のウニ類から逸脱した形態をもつ。この様に特殊な生活様式をとるブンブク類は少数派なのかというと、そんなことは無い。現生種、化石種ともに、ウニ類全体の約25%を占め、ブンブク類はウニ類最大のグループである。

知られていないブンブク類の生態

ブンブク類は潮下帯以深の堆積物中に生息しており、調査が困難であるため、生息場所での生態学的研究は少ない。オカメブンブク(1)や *Meoma ventricosa*(2)などの、少数のブンブク類の生態について知られるのみである。これまでの研究は、各ブンブク種が、底質や水深に応じて生息することを示唆しているが、複数種が同所に生息する場所で各種がどのような生息場所を占めているのかについて調べた包括的な研究はない。日本海に位置する島根県隠岐諸島では、水深5-18mの約1km^{2}の範囲に、粒度が異なる堆積物が分布し、そこにブンブク類4種（図1）が生息している。本稿では、2007年～2011年の4年間の隠岐での潜水調査と採集したブンブクの形態と行動の観察から分かってきた浅海域でのブンブク類の生息場所を制限する要因について紹介する。

４種のブンブクの生息場所

各ブンブク種の生息場所は、**図2**と**表1**にまとめた。ヒラタブンブクは、水深5-18m の範囲で観察された。このウニは、細粒から粗粒砂までの様々な底質の表面から2-3cm の深さに潜っていた。また、このウニは、他のブンブクがほとんど生息しない地点Ｅの細粒砂底で多数観察された。ネズミブンブクは、水深9-18mの範囲で観察された。このウニは、水深10m 以深の中粒から粗粒砂の底質に多く生息し、堆積物表面から2-3cm の深さに潜っていた。ライオネスブンブクとオオブンブクは、水深9-18mの範囲で観察された。表層が礫で覆われた粗粒砂底の表面から5-15cm の深さに潜っていた。

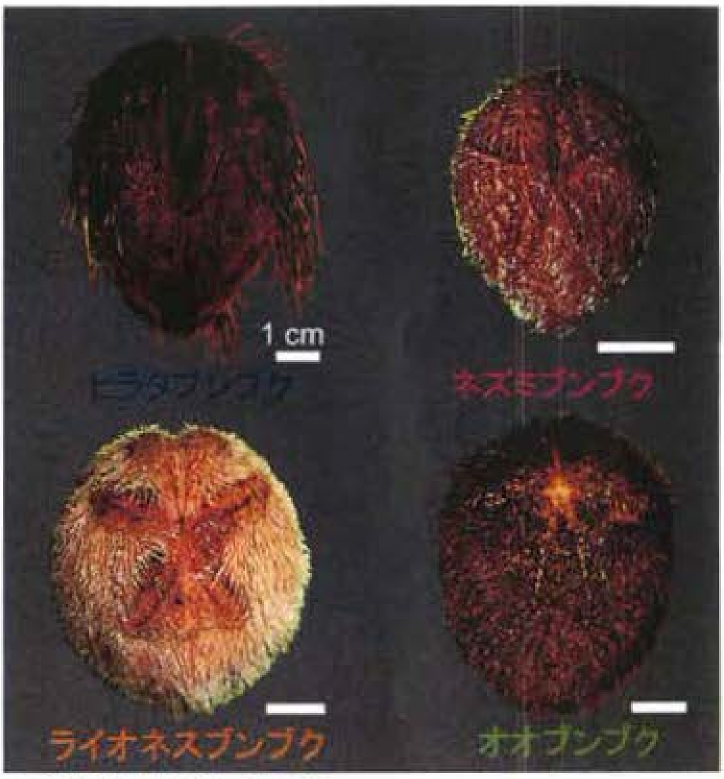

図1. 隠岐に生息するブンブク類4種

水深10m以浅では、冬後に、堆積物表層約5cmの深さまでの撹乱が観察され、表層に生息するネズミブンブクの死殻が堆積物表面で頻繁に観察された。冬前後で採集されたネズミブンブクの個体数は、撹乱が観察された水深で大幅な減少が見られた。一方、同様の撹乱を受ける環境でヒラタブンブクの個体数の減少は見られなかった。

各種が持つ呼吸補助器官

呼吸補助器官として、帯線と呼吸筒が知られている。帯線とは、繊毛を持つ微小な棘が殻上に密集して線状に配列したもので、その棘が起す水流により、ウニの周囲の水循環を良くする（**図3**）。呼吸筒とは、ブンブクが潜行する巣穴と堆積物表面とを結ぶ筒状の穴で、背側頂上のやや前方にある棘や管足により形成され、酸素に富む新鮮な海水を導く通路である。ヒラタブンブクは、背側に帯線と呼吸筒を形成する棘を持つ（**図4**）。水槽内では、ヒラタブンブクは細粒砂中に呼吸筒を形成しながら潜行し、堆積物表面から呼吸筒に向かって流れる水流が観察された。呼吸筒を形成する棘を除去すると、背側の頂上を堆積物表面に露出させたままで、完全には埋没出来なくなった。ネズミブンブクは、背側に帯線も呼吸筒を形成する棘や管足も持たず、ウニの直上の堆積物表面から堆積物内に向かって流れる水流は観察されなかった。水槽内では、このウニは中粒から粗粒砂に完全に埋没し、細粒砂では背側を堆積物表面に露出したまま潜行していた。ライオネスブンブクとオオブンブクは、背側に帯線を持つが、呼吸筒を形成する棘や管足は持たない。水槽内では、両種は粗粒砂では完全に埋没していたが、細粒砂では背側を堆積物表面に露出したまま潜行していた。また、堆積物表面から1-2cmの深さに潜っている時に、ウニの上方の堆積物表面から潜行する巣穴に向かって流れる水流が観察された。

潜る深さに関係する形態

ヒラタブンブクとネズミブンブクは、殻が扁平で下面が平らなために、掘削し

表1. 各地点の底質とそこで採集されたブンブク種の個体数。

地点	水深 (m)	底質	ブンブク種 ヒラタブンブク	ネズミブンブク	ライオネイブンブク	オオブンブク
A	18	中～粗粒砂	17(4%)	161(50%)	33(22%)	4(5%)
B	9	礫混じりの中～粗粒砂	91(20%)	23(8%)	36(25%)	27(36%)
C	10	礫混じりの中～粗粒砂	62(14%)	101(33%)	40(27%)	14(19%)
D-1	10	礫混じりの粗粒砂	0(0%)	0(0%)	36(25%)	29(39%)
D-2	10	細粒砂	83(19%)	0(0%)	0(0%)	0(0%)
D-3	10	粗粒砂	0(0%)	19(7%)	0(0%)	0(0%)
E	5	細粒砂	193(43%)	6(2%)	1(0%)	1(0%)

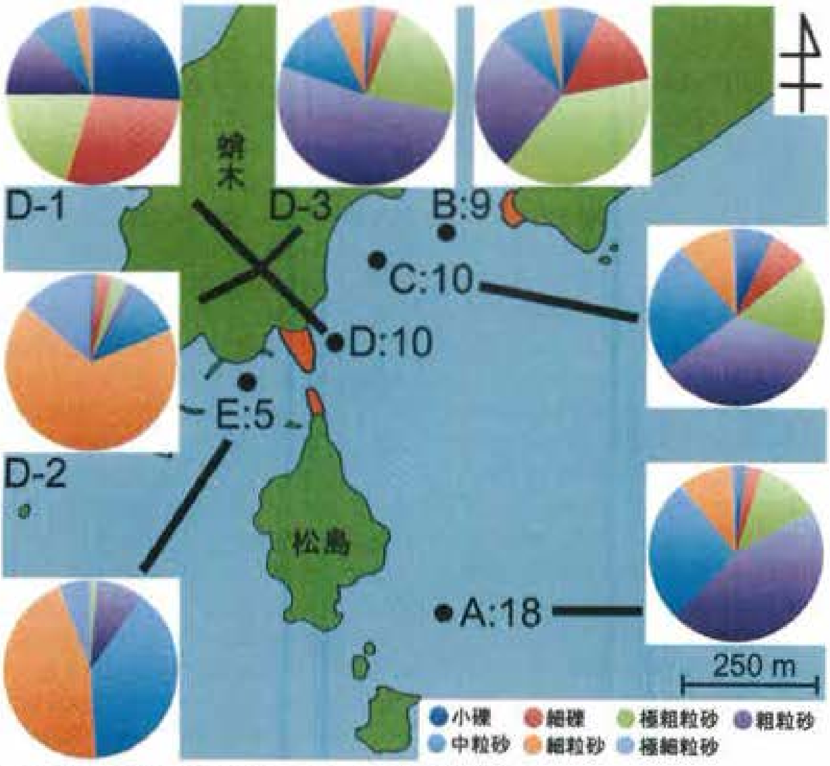

図2. 隠岐の調査地点（数値は水深（m）を表す）と堆積物粒度。

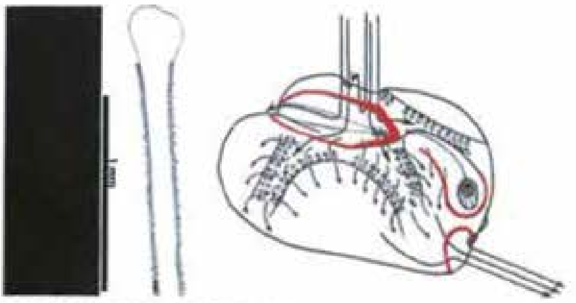

図3. 左図：帯線上の繊毛を持つ棘。
右図：帯線（赤）が起こす水流（3を改変）。

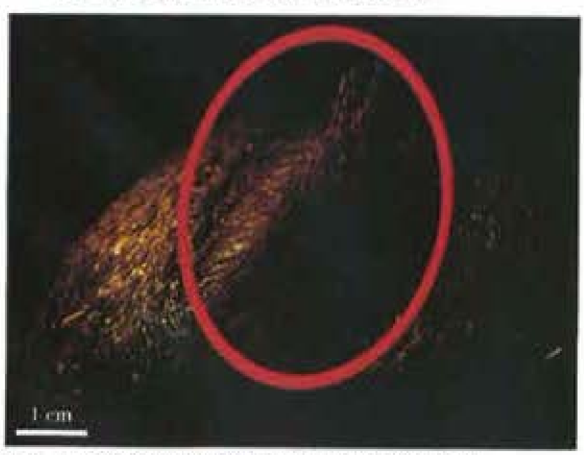

図4. ヒラタブンブクの背側にある呼吸筒を形成する棘。

た砂を充填するための隙間を作り出せず、堆積物表層にのみ潜行出来る。一方、ライオネスブンブクとオオブンブクは、膨らんだ卵形の殻をもち、掘削した砂を充填するための隙間を腹側の下に作り出し、堆積物中に深く潜る事が出来る(4)。

水底の攪乱に対する行動

水槽内でブンブクが堆積物に潜った状態で、水流を起こしてウニの上の堆積物を掘り返した場合の行動を観察した。ネズミブンブクとライオネスブンブク、オオブンブクでは、堆積物と一緒にウニは洗い出され、堆積物表面を転がって、二度と潜れなかった。一方、ヒラタブンブクでは、背側が露出するとより深く潜行し、洗い出されなかった。しかし、それ以上潜る事が出来ない水槽底面まで到達すると、洗い出されて、ひっくり返った。それでも背側の長い棘を使ってすぐに起き上がり、堆積物表面を転がる事は無かった。つまり、ヒラタブンブクは例外的に急速な埋没と起き上がりにより、攪乱による洗い出しを避けるが、他のブンブクは大抵堆積物中に深く潜ることで洗い出しを避けていると思われる。

浅海域への適応

ブンブク類は、主に、堆積物中に深く潜る事により、不安定な浅海環境に適応し、またどの呼吸補助器官を持つかによって、生息可能な堆積物粒度と潜る深さが決まる。ライオネスブンブクやオオブンブクは、背側に呼吸筒を持たないが水流を起す帯線を持ち、砂の運搬と充填に適した殻形をもつため、海水の通りが良い粗粒砂底に深く潜行出来る。ネズミブンブクは、背側に帯線も呼吸筒も持たないため、粗粒砂底の表層に潜り、嵐などによる攪乱が少ない、水深がやや深い穏やかな環境に生息する。ヒラタブンブクは、背側に帯線と呼吸筒を共に持ち、堆積物表層の攪乱に対し、素早い埋没を可能にする特殊な形態を持つため、細粒から粗粒の幅広い粒度の砂に潜行でき、また不安定な堆積物表層に生息出来る。

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文献

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