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Basal-disc creeping combined with rotation, an undescribed behaviour with preferred directionality in bivalve-inhabiting hydrozoans (Cnidaria: Hydrozoa: Leptomedusae)

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A creeping movement, which often results in clockwise or counterclockwise bodily rotation, is described for ordinary zooids of two species of bivalve-inhabiting hydrozoans, Eutima japonica Uchida and Eugymnanthea japonica Kubota, attached to artificial hard substrata (polystyrene and glass) in the laboratory. Time-lapse video recordings furthermore showed that the non-transparent half of the flat, ellipsoidal pedal disc always faces forward during this motion, with no lateral or backward creeping during either day or night. Because an ordinary zooid generally crept in a circle of small radius, the zooid's body rotated as the creeping proceeded. One full rotation of a zooid of either species took about 5–6 hours on average at 21–25°C. The direction of rotation of an individual zooid was nearly constant irrespective of developmental state, this being true for zooids with or without a medusa bud on the hydrocaulus or a daughter zooid on the pedal disc, those with a normal or a double hydranth, or those consisting of a bare hydrocaulus. Asexually produced tiny daughter zooids quickly became well separated from their mother zooids. The attachment site of the latter did not shift much as they rotated, but daughter zooids and other tiny free zooids creep along a nearly straight line, thereby markedly shifting their position. This may contribute to the prevention of crowding of zooids in the restricted space between soft body parts in the host bivalve's mantle cavity.

Keywords: Hydrozoa, zooids, bivalve-inhabiting, creeping and rotation

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INTRODUCTION

The bivalve-inhabiting hydrozoans belonging to the genera *Eugymnanthea* and *Eutima* are particularly unusual among thecate hydroids in being solitary with no periderm. They thus differ morphologically from all other colonial thecate hydroids, which have well-developed hydrothecae and gonothecae. In connection with their symbiotic life habit within the mantle cavity of bivalves such as mussels and oysters, the pedal disc of bivalve-inhabiting hydroids is transformed into a flat, ellipsoidal disc, by means of which the zooids attach to the soft parts of the host (Cerruti, 1941; Crowell, 1957; Kubota, 1983; El-Bossery *et al.*, 1997). Furthermore, two species of *Eugymnanthea* exhibit a unique degree of passivity inasmuch as they display no escape reaction against mechanical or light stimulus, and also no contraction response to food capture or satiation. The body remains uncontracted, and the tentacles extended, irrespective of the presence of captured food, even when the gastric cavity is

full (Miglietta *et al.*, 2006). This passivity is thought to be correlated with their protected life-style.

Crowell (1957) was the first to report a creeping movement of the hydroid stage of a bivalve-inhabiting hydrozoan, namely in *Eugymnanthea inquilina* Palombi from Naples, Italy, on ciliated epithelium removed from the host bivalve *Mytilus galloprovincialis* Lamarck. No further observations on such movement have been reported. In the present paper, a new feature of the movement of zooids is reported for two other species of this group, *Eutima japonica* Uchida and *Eugymnanthea japonica* Kubota, which are parapatrically distributed in Japan (Kubota, 1992, 2000). The autoecological significance of this behaviour is discussed.

MATERIALS AND METHODS

Two hydrozoan species associated with the bivalves *Mytilus galloprovincialis* Lamarck, *Barbatia virescens* (Reeve), and *Crassostrea vitrefacta* (Sowerby) were collected from Hokkaido to Okinawa Prefecture, Japan (Figure 1). The collection data have been presented in previous reports on the life cycle, biogeography, and systematics of these two species (Kubota, 1991, 1992; Kubota *et al.*, 2005), except for *Eutima*

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japonica Uchida from Matsushima, Miyagi Prefecture. This was collected on 4 April 1986 and its infraspecific form (the 'northern' form) was determined by laboratory culture of medusae (S. Kubota, unpublished data; Kubota, 1985). The materials used in the first phase of the present study thus included two infraspecific forms of *Eutima japonica* (the 'northern' and 'intermedia' forms) collected from four localities in Japan (Figure 1: 1, 2, 3, 6), and *Eugymnanthea japonica* from three localities (Figure 1: 4, 5, 7), all having been collected during 1985–1991.

Many zooids were removed from each host and kept in the laboratory at Hokkaido University in a covered, 60- or 80-ml polystyrene vessel filled with filtered natural seawater (from Oshoro, Hokkaido, and changed daily: Figure 1, 1) at a constant temperature (21–25°C), while waiting for the zooids to attach to this artificial, hard substratum (i.e. the polystyrene vessel). After they had become firmly attached, the zooids were occasionally fed with newly hatched *Artemia* nauplii, usually at night. The rearing vessel was placed in a constant position in the room.

The movement of zooids was observed once every hour in the daytime for up to 25 days, until the zooids detached

from the vessel. Attention was paid to changes in their developmental state such as production of a medusa bud or daughter zooid, or loss of a hydranth or hydrocaulus. To specify the position of each zooid and to detect its movement, two small dots were marked with a needle on the bottom of the polystyrene rearing vessel, and the distances between the centre of the hydrocaulus on the zooid's pedal disc and each of the two dots, and between the two dots themselves, were measured under a binocular microscope with an ocular micrometer. The hydrocaulus is usually placed eccentrically toward one side of the ellipsoidal pedal disc (Crowell, 1957; El-Bossery *et al.*, 1997). The creeping movement was not fast; therefore, determination of the direction of rotation required a minimum of one hour between observations. It was possible to trace successive positional changes by the orientation of the pedal disc, even if the zooid had changed its developmental state, for example with the appearance of a medusa bud or the degeneration of the upper body part. Observations were not made at night and the total time of movement is, therefore, shown as daytime hours. All observations were done within a few months after collection of the materials.

The second phase of the present study was conducted in mid-November, 2006. Creeping movements of three ordinary zooids and two tiny zooids of *Eugymnanthea japonica* associated with *Crassostrea gigas* (Thunberg) from Shirahama, Tanabe Bay, Wakayama Prefecture, Japan (Figure 1: 8), were recorded with a time-lapse video camera every two or four minutes for 16.5–29 hours, beginning one to three days after the zooids had attached to polystyrene or glass vessels. At night, the room lights were turned off and the room made dark, but a strobe flash was used every two or four minutes to record the position of the zooids. The resulting video recordings again demonstrated the same sort of undescribed creeping movement, accompanied by morphological changes in the pedal disc.

RESULTS

The time-lapse video recording of zooids of *Eugymnanthea japonica* showed ordinary larger zooids slowly rotating clockwise or counterclockwise, with only slight shifting of their attachment position as they crept along a circle of small radius, even at night. Flexibility of the pedal disc, demonstrated by changes in shape during both day and night with preferred directionality, was confirmed. Rare contraction of tentacles, hydranth, or hydrocaulus was observed. Half of the pedal disc was non-transparent and this side always faced forward during creeping. Smaller zooids, to the contrary, tended to proceed along a nearly straight path, thereby shifting their location without a distinct rotational component to the movement. Neither lateral sliding nor backward movements were observed in either the small or the ordinary zooids. Furthermore, neither change in movement nor body contractions were observed when ordinary zooids and tiny zooids met and came into contact with each other.

In the earlier study at Hokkaido University (Table 1), some zooids of both *Eutima* and *Eugymnanthea* rotated clockwise, and others counterclockwise: 25 zooids (49.0%) versus 22 zooids (43.1%) respectively in *Eutima*, and 17 zooids (43.6%) versus 17 zooids (43.6%) respectively in



Fig. 1. Localities of observed species and infraspecific forms of bivalve-inhabiting hydrozoans collected in Japan and their host bivalves. 1, Oshoro, Hokkaido; 2, Kuroiwa, Hokkaido; 3, Matsushima, Miyagi Prefecture; 4, Shimoda, Shizuoka Prefecture; 5, Shimizu, Shizuoka Prefecture; 6, Zagashima Island, Mie Prefecture; 7, Yagaji, Island, Okinawa Prefecture; 8, Shirahama, Wakayama Prefecture. 1–3: the 'northern' form of *Eutima japonica*, associated with *Mytilus galloprovincialis*. 6: the 'intermedia' form of *Eutima japonica*, associated with *Barbatia virescens*. 4, 5, 7, 8: *Eugymnanthea japonica*, associated with *Mytilus galloprovincialis* (4, 5), *Crassostrea vitrea* (7), and *C. gigas* (8).

Eugymnanthea. A few zooids changed their direction of creeping and rotating: four out of 51 zooids of *Eutima* (7.8%) and five out of 39 zooids of *Eugymnanthea* (12.9%). In any population examined, unidirectional movement, either clockwise or counterclockwise in a given case, prevailed over movement in both directions (binomial test, **: $P < 0.01$, *: $P < 0.05$ in Table 1), except for the 'intermedia' form of *Eutima japonica* from Zagashima Island (binomial test, not significant: $P > 0.05$).

During the long continuous runs conducted at Hokkaido University, the direction of rotation did not change for most of the zooids. For up to 12 days, in the daytime 12 out of 15 zooids of *Eutima* and three out of ten zooids of *Eugymnanthea* maintained unidirectional rotation. For example, a zooid of *Eutima* from Oshoro rotated clockwise for a total of 61 observed daytime hours over 12 days, and a zooid of *Eugymnanthea* from Yagaji Island, Okinawa, rotated counterclockwise for a total of 31 observed daytime hours over four days (Table 2). The other three zooids of *Eutima* and seven zooids of *Eugymnanthea* rotated in both directions, but one direction was dominant.

The direction of rotation of an ordinary zooid of either species was nearly constant in the daytime for up to 12 days even when it produced either a daughter zooid on the pedal disc or a medusa bud on the hydrocaulus (Table 2: P-Pp-Pm). Furthermore, after a medusa had been released from a zooid of *Eugymnanthea*, the direction of rotation of the latter remained nearly constant, i.e. 26 daytime hours counterclockwise versus one daytime hour clockwise (Table 2: Pm-P). Even after the hydranth (ordinary one or extraordinary double ones) and the hydrocaulus of a zooid of *Eutima* had degenerated, the direction of rotation was still nearly constant for 3-11 days (Table 2: Pm-Mp; P-Pd; Ph-P'; Ph-P'-P'd).

In any individual in any developmental stage, unidirectional movement, either clockwise or counterclockwise, prevailed (Table 2, binomial test, **: $P < 0.01$, *: $P < 0.05$),

Table 2. Direction of rotation of individual zooid of two hydrozoan species associated with bivalves, observed in the daytime for 3-12 days in the laboratory.

Species and form locality	Total time of movement (h)		Period observed (days)	Developmental state and/or temporary change of state during observation
	Clockwise	Counter-clockwise		
<i>Eutima japonica</i>				
'Northern' form				
Oshoro	61**	0	12	P-Pp-Pm
	0	19**	3	Pm-Mp
	38**	0	7	P
Kuroiwa	31**	0	7	P
	21**	0	5	Ph
	0	33**	7	P
	0	31**	7	P
	0	24**	7	P
	0	23**	6	P
	0	19**	5	P
Matsushima	17**	0	5	P
'Intermedia' form				
Zagashima Island	19**	1	4	P-Pd
	0	63**	11	Ph-P'
	8	20*	8	Ph-P'-P'd
	2	6 ^{ns}	3	Ph
<i>Eugymnanthea japonica</i>				
Shimizu	19**	0	3	P
	3	47**	12	P-Pp-Pm
Yagaji Island	32**	6	9	P
	29**	5	8	P
	27**	2	5	P
	20**	0	3	P
	0	31**	4	Pm
	1	26**	8	Pm-P
	1	15**	3	P
	2	13**	3	P

P, zooid without medusa buds or daughter zooids; Pp, zooid with a daughter zooid; Ph, zooid with double hydranths; Pm, zooid with a medusa bud; Pd (P'd), zooid without hydranths and most parts of hydrocaulus; P', zooids with one hydranth degenerated from the initial Ph state; Mp, well-developed medusa bud on a degenerated zooid (hydranth and most parts of hydrocaulus degenerated). Binomial test: **, $P < 0.01$; *, $P < 0.05$; not significant (ns), $P > 0.05$.

Table 1. Frequency (%) of direction(s) of movement of zooids, mostly those without medusa buds, of two hydrozoan species associated with bivalves, observed for a short period in the daytime (for up to two days) in the laboratory.

Species and form locality	No. of zooids examined	Frequency (%) of direction(s) of movement			
		Clockwise	Counter-clockwise	Either direction	Both directions
<i>Eutima japonica</i>					
'Northern' form					
Oshoro	30	53.3	43.3	96.6	vs 3.3**
Kuroiwa	8	50.0	50.0	100.0	vs 0**
Matsushima	5	60.0	40.0	100.0	vs 0**
'Intermedia' form					
Zagashima Island	8	25.0	37.5	62.5	vs 37.5 ^{ns}
Total	51	49.0	43.1	92.1	vs 7.8
<i>Eugymnanthea japonica</i>					
Shimizu	22	40.9	54.5	95.4	vs 4.5**
Yagaji Island	17	47.1	29.4	76.5	vs 23.5*
Total	39	43.6	43.6	87.2	vs 12.9

Binomial test: **, $P < 0.01$; *, $P < 0.05$; not significant (ns), $P > 0.05$; vs, versus.

except for one zooid with a double hydranth belonging to the 'intermedia' form of *Eutima japonica* from Zagashima Island.

It took 3-9 hours for a zooid with or without a medusa bud to rotate 360 degrees (i.e. one full turn) in either direction, averaging 5.6 hours clockwise and 5.3 hours counterclockwise in *Eutima*, and 6.0 hours clockwise and 5.4 hours counterclockwise in *Eugymnanthea* (Table 3).

The distance moved across the substratum in one day was short for ordinary zooids of both species, and their position did not change much, at least during daytime, due to their rotating on nearly the same spot for a week or more (Figure 2; Figure 3: open circles). However, observations of two tiny daughter zooids of *Eutima*, which had separated from their mother zooids two hours earlier in one case and within 15 hours earlier in the other, showed the daughter

Table 3. Time for one full rotation of an individual zooid in two species of bivalve-inhabiting hydrozoans in Japan.

Species and form	Locality	Time (h) for one full rotation (No. of specimens examined)		Developmental state	
		Clockwise	Counterclockwise		
<i>Eutima japonica</i>					
'Northern' form	Oshoro	9 (1)		Pm	
		6 (1)		Pm	
		5 (1)		Pm	
		6 (5)		P	
		5 (1)		P	
		3 (1)		P	
			5 (1)		Pm
			3 (1)		Pm
			7 (1), 6 (1)*		P
			6 (3)		P
			5 (2)		P
			4 (2)		P
			3 (2)		P
			5 (1)		Ph
'Intermedia' form	Kuroiwa	6 (2)		P	
		5 (2)		P	
	Matsushima	5 (1)		Ph	
		6 (1)		Ph	
	Zagashima Island	5 (1)		Pm	
			7 (1), 6 (1)*	Ph	
			6 (1), 5 (1)*	Ph	
			7 (1)	P	
			5 (1)	P	
All combined: mean (N)	5.6 (14)	5.3 (26)			
<i>Eugymnanthea japonica</i>					
Shimizu	Yagaji Island	7 (1)		P	
			8 (1), 7 (1)*	P	
		7 (1)		P	
		6 (1)		P	
		5 (2)		P	
			8 (1)		Pm
			7 (1)		P
			5 (1)		P
			3 (1)		P
			3 (1), 3 (1)*		P
		All combined: mean (N)	6.0 (5)	5.4 (10)	

*, same specimen observed twice. For abbreviations, see Table 2.

zooids departing from the vicinity of the mother zooids as time passed (Figure 3: closed circles). The distance of separation between the daughter zooid and the mother zooid reached 4.0 and 4.8 mm, respectively, after about one day in the two cases (Figure 3).

DISCUSSION

Crowell (1957) was the first to report the movement of zooids of a bivalve-inhabiting hydroid, *Eugymnanthea inquilina* on a near-natural substratum, i.e. a piece of the ciliated epithelium of the mantle or labial palps removed from the host bivalve at Naples, Italy. He noticed a very slow, creeping movement irrespective of the direction of beat of the bivalve's cilia, requiring an hour to travel 0.2 mm. He supposed this movement was

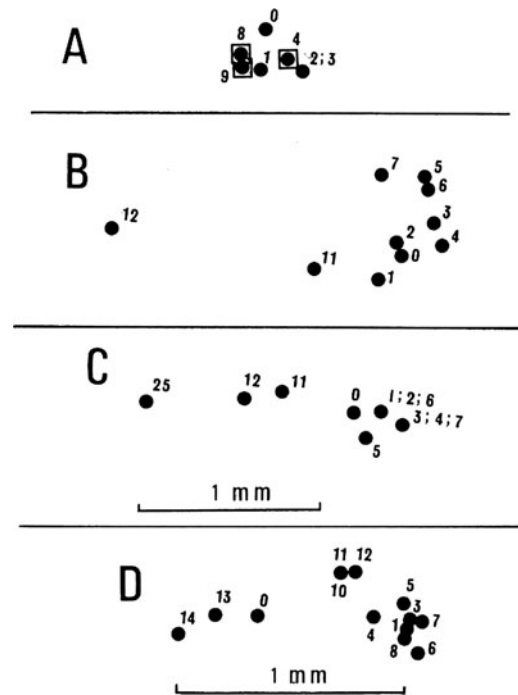


Fig. 2. Temporal change (in days) of position (shown by closed circles) by creeping in four zooids of *Eugymnanthea japonica* from Shimoda (A–C: scales are the same) and Shimizu (D). The zooids were of the ordinary form without medusa buds or daughter zooids, except for three occasions in A (circles surrounded by rectangles indicate a small medusa bud produced on the 4th–9th day).

achieved by a change in the shape of the pedal disc, although the exact means was not clarified. In *E. inquilina* from Taranto, Italy, collected in 2002 and observed under a stereoscopic microscope, similar movement with rotation was noticed in several specimens (removed from *Mytilus galloprovincialis*) that had attached to the same kind of polystyrene rearing vessel described above (S. Kubota, unpublished data; Kubota, 2004). In zooids of *Eugymnanthea japonica* found on the gills of *Mytilus galloprovincialis* at Shirahama, Wakayama Prefecture, Japan (Figure 1: 8), the pedal disc is always attached to a single gill filament by one end, while the other end is free or just touches the gill surface

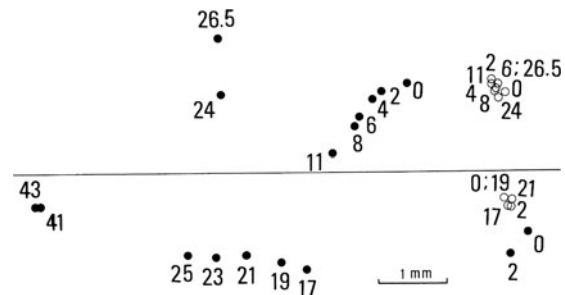


Fig. 3. Temporal change (in hours) of position of two mother zooids of *Eutima japonica* from Kuroiwa (open circles) and their newly-separated daughter zooids (closed circles: one daughter each). 0 marks the position of each daughter zooid 2–15 hours after separation from the mother zooid, when the daughter zooid was first observed. The scale is the same for both sets of observations.

(El-Bossery *et al.*, 1997). This arrangement presumably facilitates movement along the gill filament in this species.

Flexibility of the pedal disc, demonstrated by changes in shape during both day and night with preferred directionality, was confirmed by the present study's time-lapse video recordings, in which a hitherto undescribed rotational behaviour was also clearly shown. In the present study, quick and distant separation, 4.0–4.8 mm in a day, of a daughter zooid from its mother zooid was observed in *Eutima japonica* (Figure 3). Furthermore, the time-lapse video showed that smaller zooids sometimes proceed along nearly straight paths, shifting their position without distinct bodily rotation. In the restricted space between soft body parts in the mantle cavity of the host, such quick and direct movement on the part of daughter zooids could contribute to the prevention of crowding among zooids of this clonal animal. This species is sometimes present in great numbers, maximally 2034 zooids per host (Kubota, 1983). Smaller zooids of *Eugymnanthea japonica* that proceed along a nearly straight path as they creep may similarly contribute to the amelioration of crowding in the restricted space between soft body parts in the host bivalve's mantle cavity.

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