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Effects of Temperature on the Dimensions of the Lorica of the Marine Choanoflagellate *Acanthocorbis camarensis*

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Yuh-ling Lee Chen, Jia-Chi Sheu and Seiko Hara (1997) Effects of temperature on the dimensions of the lorica of the marine choanoflagellate *Acanthocorbis camarensis*. *Zoological Studies* **36**(2): 115-122. This paper presents the effects of temperature on the dimensions of the lorica and the length of the costal strip of the longitudinal costa in a laboratory cultured marine choanoflagellate, *Acanthocorbis camarensis*. Four temperatures, 15 °C, 25 °C, 30 °C, and 35 °C, were tested. Flagellates raised at higher temperatures had a smaller lorica and shorter costal strip than those cultured at lower temperatures. The temperature effect on the lorica dimension of a choanoflagellate is here clearly demonstrated for the 1st time.

Key words: Temperature, Choanoflagellate, Lorica dimension.

Choanoflagellates are a group of colorless protozoa possessing a single flagellum surrounded by a ringed collar at the anterior end of the protoplast. They are heterotrophic and feed on bacteria, detritus (Leadbeater and Manton 1974, Leadbeater and Morton 1974), and picoplanktonic autotrophs. Thus they are important in making marine particulate organic carbon available to higher consumers of the food web. Acanthoecidae, one of the 3 families of choanoflagellates, exist only in marine or saline waters (at concentrations of 40 g/kg in the Red Sea, Thomsen 1978). They have a basket-like lorica composed of siliceous costae outside of the protoplast. Numerical characteristics and dimensional aspects of the lorica are important features in the taxonomy of Acanthoecidae.

Members of Acanthoecidae thrive in all latitudes of the earth, from the Antarctic (Buck 1981) to tropical waters (Thomsen and Boonruang 1983). Considerable variation in the dimensions of the lorica within the same species collected from various geographical areas has been reported (Manton and Oates 1979, Manton et al. 1980). *Parvicorbicula socialis* collected from Denmark (Thomsen 1973) and Japan (Hara 1984) were found to have 2 costal strips in their longitudinal costa. The same species from the Arctic and Antarctic Oceans has 3 costal strips (Manton et al. 1976). Decreases in the size of the lorica in lower density seawater or higher water temperatures in the same geographical area have been reported for *Crucispina cruciformis* (Hara and Takahashi 1987) and *Stephanoeca supracostata* (Hara et al. 1996). These observations indicate that temperature variation, which is one of the prominent factors that vary concurrently with latitude and season, may play a role in affecting the lorica morphology of Acanthoecidae species.

In this study the effects of temperature on the dimensions of the lorica and the length of the costal strip of the longitudinal costa were evaluated using laboratory-cultured marine choanoflagellate, *Acanthocorbis camarensis*. The results show that flagellates kept at higher temperatures had smaller lorica and shorter costal strip than those cultured at lower temperatures.

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MATERIALS AND METHODS

Culture of choanoflagellates

Surface water samples were collected from the coast of Kaohsiung, Taiwan (120°15'E, 22°40'N) in December 1993. The water temperature and salinity were 23.8 °C and 32.6‰, respectively. Large plankton and particles were removed by filtering the water through a plankton net (20 μm pore size). Yeast extract (2 μg/ml, DIFCO, Detroit, USA) and proteose pepton (10 μg/ml, DIFCO) were added to the filtered water as nutrients to enhance the growth of bacteria. Bacteria in turn support the growth of choanoflagellates. Polixenic culture of choanoflagellates was adopted in the study because of the universal difficulties in their monoculture. The culture was acclimated in darkness at 25 °C before the experiment.

After 2-d acclimation, the choanoflagellate culture was divided and transferred to each of 8 sterilized 250 ml flasks, containing 250 ml medium, and kept at 25 °C. Two of the 8 flasks were transferred to separate incubators, each set at one of the 4 test temperatures (15 °C, 25 °C, 30 °C, and 35 °C). A 15-ml aliquot from each flask was taken and fixed with 1% (v/v) neutralized formaldehyde at days 0, 4, and 7 after the experiment began. The morphology of *Acanthocorbis camarensis*, a dominant species in the culture, was examined under a transmission electron microscope (JEOL JEM-100S).

TEM examination

For TEM observation, cells were washed by concentrating the 15-ml aliquot to 1 ml by centrifugation at 3000 g for 10 min, and washing with distilled water to remove salts from the sample. This procedure was repeated 5 times. A fixed volume of the concentrated material was transferred by a micropipet onto a Formvar-coated copper grid and dried at 40 °C or room temperature for 1-2 h. The grids were shadowcast with chromium and examined with the TEM. Two to 3 grids of each sample were examined.

Cell density of *A. camarensis* in each flask was calculated by the cell number on grids times its volume. Lengths of costal strips and various positions of lorica (Fig. 1) including the width of the 1st transverse costa (L(1)), the width of the 2nd transverse costa (L(2)), the height of the anterior chamber (L(3)), the height of the posterior chamber of the lorica (L(4)), the length of the 1st costal strip (S(1)), and the length of the 2nd costal strip (S(2)) of the anterior projection were measured. Three costal strips of each of S(1) and S(2) were randomly selected from 1 cell and measured. A flagellate with lorica containing a cell body was classified as a living cell while that without a cell body or with a simple cluster of costal strips was classified as dead.

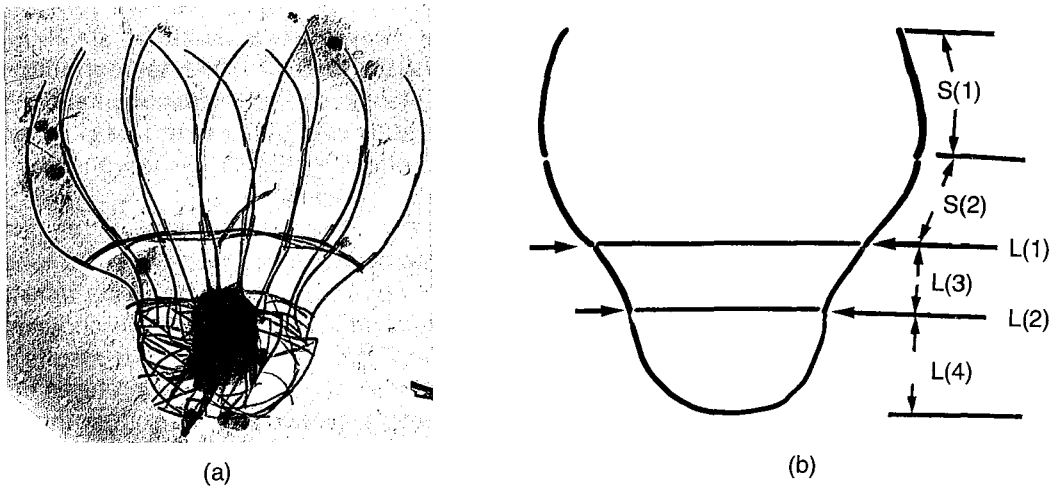

Fig. 1. (a) *Acanthocorbis camarensis* under transmission electron microscope (× 3782) and (b) various parts of lorica and costal strips measured for morphological comparisons of lorica. L(1), width of 1st transverse costa; L(2), width of 2nd transverse costa; L(3), height of anterior chamber; and L(4), height of posterior chamber of lorica; S(1), length of 1st costal strip; and S(2), length of 2nd costal strip of the anterior projection.

Bacteria density

In order to understand the effects of food concentration on the density and morphology of the choanoflagellate, bacteria density was measured during the choanoflagellate examination. A DNA-specific dye, DAPI (4,6-diamidino-2-phenoylindole), was used to discriminate living organisms (including bacteria) from detritus under UV excitation using an epifluorescent microscope (Olympus BH-2). During the DAPI preparation, 5 ml of sample from each flask was taken and preserved with 2% neutralized formaldehyde. DNA-associated particles were then labeled by dyeing with DAPI (final concentration 0.1 μg/ml in distilled water) for 5 min, and then this was filtered through a 0.2-μm polycarbonate filter membrane (Poretics, 25 mm diameter) under a pressure of < 100 mmHg. The filter membrane was placed on top of a drop of nonfluorescence immersion oil on a microscope slide. Another drop of oil was added on the filter before it was covered with a cover glass (Hara et al. 1991). When the microscopic observation was not conducted immediately, the prepared slides were stored at −20 °C, and the examination was completed within 2 wk.

SAS package software was used to analyze the temperature effects. Duncan's new multiple range test was used to distinguish the hierarchical difference of the lorica size between temperature treatments. In all analyses, living cells were treated separately from dead ones.

RESULTS

A. camarensis was the dominant species (> 50% of living cells) and it occurred in temperatures between 25 and 35 °C after 4 and 7 d of culturing. Its dominance provided an adequate number of replications and made the statistical analysis of morphological comparisons possible. The growth of the flagellate was optimum when raised at 25 °C (Table 1), followed by 15 °C and 30 °C, and was slowest at 35 °C. The initial cell densities of living *A. camarensis* in the 4 test temperatures were between 0.44 and 1.27 cells/ml. After 7 d of culture, those incubated at 25 °C increased to 150.13 cells/ml.

Bacteria densities in the initial and end phase of the experiment were similar among temperature treatments, and were 1.3×10^6 to 1.6×10^6 /ml at the initial phase and 2.1×10^6 to 2.8×10^6 /ml at the end (Table 2). This similarity of bacteria densities across varying temperatures indicates that differential densities of choanoflagellates was possibly not caused by food abundance.

The lengths of costal strips, S(1) and S(2), of dead *A. camarensis* were shorter than those of living cells (Fig. 2). The comparisons of lorica dimensions and the lengths of costal strips, thus, were made between 2 separate categories: living

Table 1. Average (±SE) cell density (cells/ml) of living *Acanthocorbis camarensis* grown at various temperatures

Elapsed time (d)	Temperature (°C)			
	15	25	30	35
0	0.44 ± 0.31	0.48 ± 0.34	1.27 ± 0.18	0.62 ± 0.44
4	4.28 ± 0.35	32.08 ± 3.45	5.39 ± 0.65	2.13 ± 0.67
7	15.45 ± 9.38	150.13 ± 70.11	11.57 ± 3.55	0.49 ± 0.34

Table 2. Average (±SE) bacteria density (X 10^6/ml) in choanoflagellate cultures incubated at various temperatures

Elapsed time (d)	Temperature (°C)			
	15	25	30	35
0	1.34 ± 0.03	1.33 ± 0.16	1.58 ± 0.05	1.64 ± 0.05
4	1.48 ± 0.02	2.27 ± 0.13	2.77 ± 0.21	2.39 ± 0.04
7	2.07 ± 0.07	2.77 ± 0.06	2.41 ± 0.06	2.10 ± 0.64

and dead cells. The results show that flagellates, both living and dead, cultured in high temperatures had smaller loricas and shorter costal strips than those grown in low temperatures (Tables 3, 4). For example, the mean lengths of the costal strip S(1) of living *A. camarensis* after 4 d of culture in 35 °C and 15 °C were 3.5 μm and 4.2 μm, respectively. The widths of the anterior chamber (L(1)) were 8.7 μm when raised at 35 °C and 9.4 μm at 15 °C on the 4th d of the culture experiment.

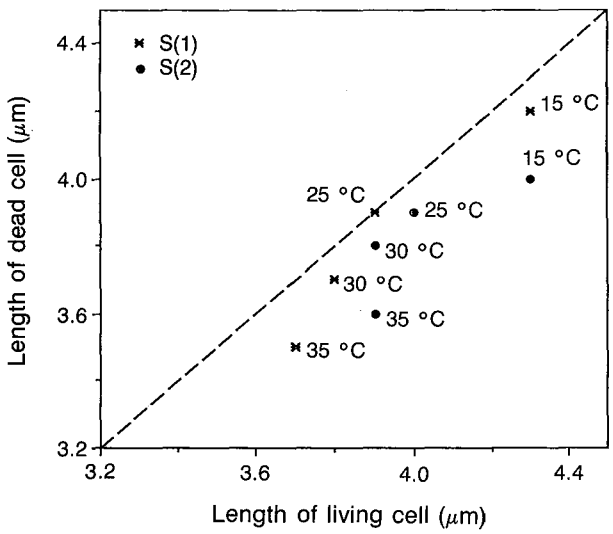

Fig. 2. Comparisons of the average lengths (μm) of 1st costal strip (S(1)) and 2nd costal strip (S(2)) of lorica between living and dead *Acanthocorbis camarensis*.

DISCUSSION

Smaller lorica width and shorter costal strips were observed in *A. camarensis* grown at a higher temperature. Similar observations have been reported and were linked to seasonal variations in Acanthoecidaean choanoflagellates, *Crucispina cruciformis* (Hara and Takahashi 1987) and *Stephanoeca supracostata* (Hara et al. 1996) collected from Seto Inland Sea, Japan. Temperature was suspected of playing an important role in affecting the lorica dimension of these choanoflagellates because bacterial number and carbon both showed little seasonal variation in the Seto Inland Sea (Iwamoto et al.1994, Imai and Yamaguchi 1997).

The size of planktonic copepods is also smaller in the summer and autumn than in the spring when it is colder (Evans and Diaz 1978). Deevey (1960) suggested that both water temperature and food supply control copepod size. The temperature effect on the lorica size of choanoflagellates, however, could not be linked to food abundance in terms of bacteria concentration. Food concentration was found to correlate with body size of

Table 3. The size (μm) of the lorica and the length (μm) of costal strips of living *Acanthocorbis camarensis* incubated at 15 °C, 25 °C, 30 °C, and 35 °C, respectively, for 4 d and 7 d. Means in the same row with different superscripts are significantly different ($p < 0.05$) according to Duncan's new multiple range test

Position of lorica	Culture period (d)	Temperature (°C)			
		15	25	30	35
First transverse costa, L(1)	4	9.4^{a} (n = 6)	8.9^{ab} (n = 10)	9.0^{ab} (n = 6)	8.7^{b} (n = 3)
	7	9.2^{a} (n = 10)	9.1^{a} (n = 17)	8.8^{a} (n = 4)	*
Anterior chamber, L(3)	4	2.4^{a} (n = 6)	2.3^{a} (n = 10)	2.3^{a} (n = 5)	2.0^{b} (n = 3)
	7	2.4^{a} (n = 8)	2.0^{b} (n = 18)	2.2^{a} (n = 7)	*
First costal strip on anterior projection, S(1)	4	4.2^{a} (n = 21)	4.1^{b} (n = 24)	3.9^{c} (n = 15)	3.5^{d} (n = 9)
	7	4.3^{a} (n = 21)	3.9^{b} (n = 24)	3.8^{c} (n = 21)	3.7^{c} (n = 3)
Second costal strip on anterior projection, S(2)	4	4.4^{a} (n = 20)	4.1^{b} (n = 24)	3.8^{c} (n = 15)	3.6^{d} (n = 9)
	7	4.3^{a} (n = 21)	4.0^{b} (n = 21)	3.9^{b} (n = 24)	3.9^{b} (n = 3)

*no data available.

Table 4. The size (μm) of the lorica and the length (μm) of costal strips of dead *Acanthocorbis camarensis* incubated at 15 °C, 25 °C, 30 °C, and 35 °C, respectively, for 4 d and 7 d. Means in the same row with different superscript are significantly different ($p < 0.05$) according to Duncan's new multiple range test

Position of lorica	Culture period (d)	Temperature (°C)			
		15	25	30	35
First transverse costa, L(1)	4	9.1^{a} ($n = 1$)	9.5^{a} ($n = 6$)	9.5^{a} ($n = 5$)	9.0^{a} ($n = 8$)
	7	9.4^{a} ($n = 4$)	9.3^{a} ($n = 7$)	8.9^{ab} ($n = 8$)	8.3^{b} ($n = 9$)
Anterior chamber, L(3)	4	2.3^{a} ($n = 1$)	2.2^{a} ($n = 6$)	2.5^{a} ($n = 5$)	2.1^{a} ($n = 8$)
	7	2.3^{a} ($n = 4$)	2.2^{ab} ($n = 7$)	2.2^{ab} ($n = 8$)	2.0^{b} ($n = 9$)
First costal strip on anterior projection, S(1)	4	5.2^{a} ($n = 3$)	4.0^{b} ($n = 18$)	3.6^{c} ($n = 9$)	3.6^{c} ($n = 21$)
	7	4.2^{a} ($n = 12$)	3.9^{b} ($n = 24$)	3.7^{c} ($n = 9$)	3.5^{d} ($n = 22$)
Second costal strip on anterior projection, S(2)	4	4.4^{a} ($n = 3$)	4.0^{b} ($n = 18$)	3.9^{c} ($n = 12$)	3.8^{d} ($n = 21$)
	7	4.0^{a} ($n = 12$)	3.9^{b} ($n = 24$)	3.8^{c} ($n = 12$)	3.6^{d} ($n = 24$)

zooplankton (Klein Breteler and Gonzalez 1982, Warren et al. 1986). At increasing food concentrations 2 adult calanoid copepod species grow to a significantly larger size (Klein Breteler and Gonzalez 1988). However, Corkett and McLaren (1978) suggested that the size of *Pseudocalanus* is dictated by temperature alone, while a shortage in food supply only prolongs its development period, but does not reduce the eventual adult size. The uniform bacterial concentrations among temperatures through the cultivation periods in our study indicate that the influence of variations in food concentration may be limited. On the other hand, the high concentration of bacteria in our study ensured a safe comparison of the temperature influence at excessive food concentrations. With low food levels it would have been difficult to make meaningful comparisons since the effects of food concentration and temperature on size variation may have been confounded.

It is well known that temperature has an important influence on body length of cladocerans and copepods in areas where food is abundant throughout the year (McLaren 1978, Ohman 1985). The pronounced effect of temperature on the size distribution of the sea anemone, *Haliplanella luciae*, also suggests that temperature is the primary environmental factor regulating both fission rate and organism size (Minasian 1982). In our study, no direct link was found between growth rate and size variation under different temperatures. Growth rate of *A. camarensis* was highest at 25 °C among the test temperatures. However, the size of the lorica was largest at 15 °C.

During cell growth, reactive silicate is taken up by cells to form costal strips. Once the biogenic silica of costal strips comes into contact with an aqueous medium it begins to dissolve and produce free reactive silicate. Thus both uptake and dissolution occur simultaneously in actively growing cultures (Leadbeater and Davies 1984). Differential absorption rates of silica were found in diatoms cultured in different temperatures of 8 °C, 13 °C, 18 °C, and 23 °C (Paasche 1980). *Skeletonema costatum* and *Thalassiosira pseudonana* were shown to have the highest silica concentration at 13 °C while *Chaetoceros affinis* and *Rhizosolenia fragilissima* have their highest concentration at 8 °C and *Cerataulina pelagica* at 23 °C. No published data were found concerning the differential absorption rate of silica with temperature by choanoflagellates. Therefore, whether the small size of choanoflagellate lorica was caused by a slow silicate absorption rate, and/or by a fast silica dissolution rate at high temperature needs further study. Progressive dissolution of costal strips occurs during the stationary and early death phases (Leadbeater and Davies 1984). Shorter costal strips were observed in dead than in living *A. camarensis* in our study.

Table 5. Comparison in the height of the lorica (μm) or the height of the chamber (μm) of some choanoflagellates collected from Taiwan and locations at higher latitudes

Choanoflagellate	Position	Taiwan (μm)	Other countries (μm)	References[a]
Acanthocorbis apoda	Lorica	12.3-14.3	16.0 (Norway)	(1)
Acanthoeca spectabilis	Chamber	4.3- 4.9	17.0 (Norway)	(1)
Cosmoeca ventricosa	Lorica	14.6	23.0-31.0 (Denmark)	(2)
			30.0 (Finland)	(2)
			32.0 (Greenland)	(2)
Cosmoeca phuketensis	Lorica	10.0	8.0-9.0 (Mediterranean)	(2)
Crinolina aperta	Lorica	22.1-23.7	45.0-50.0 (Canada)	(3)
Diaphanoeca sphaerica	Lorica	30.7-55.7	22.5-30.0 (West Greenland)	(4)
Diaphanoeca undulata	Chamber	15.2	20.0 (West Greenland)	(4)
Pleursiga echinocostata	Lorica	11.9	7.5-10.0 (Norway)	(5)
Stephanoeca diplocostata	Lorica	11.4-11.8	18.0 (Norway)	(6)
			20.0 (USA)	(7)

[a](1) Leadbeater 1972; (2) Thomsen and Boonruang 1984; (3) Manton et al. 1975; (4) Thomsen 1982; (5) Espeland and Throndsen 1986; (6) Leadbeater 1973; (7) Thomsen et al. 1991.

Further comparisons were made of the size of the lorica or the height of the lorica chamber in the same species of choanoflagellates collected from higher latitude waters and Taiwan. Nine species showed size variations (Table 5). Six of the 9 species show a smaller lorica size in samples collected from Taiwan than those from higher latitudes. For example, the height of the lorica of *Cosmoeca ventricosa* from Taiwan was 14.6 μm which is much smaller than for those collected from higher latitudes such as Denmark (23.0-31.0 μm), Finland (30 μm), and Greenland (32.0 μm) (Thomsen and Boonruang 1984). However, the other 3 species showed a larger lorica size in the Taiwan samples than for those from higher latitudes (Table 5). These comparisons are based on data of specimens whose dead/living status was undetermined. This might contribute some errors in justifying the size difference among samples since a dead cell tended to be smaller than a living one in our study. Of course some other factors, such as food availability, may also be confounded with the temperature effect which is associated with changes of latitude since the data represent field studies. Our lab experiment under controlled conditions excluded these possible interferences. This is the 1st direct evidence showing the effect of temperature variation on the size of choanoflagellate lorica. The results also imply that temperature variations due to latitudinal differences may play an important role in affecting the size of choanoflagellate lorica. Hence attention should be focused on taxonomic and biogeographic studies in which the size of the lorica and/or the length of the costal strips are considered to be important characteristics.

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溫度對海洋襟鞭毛蟲*Acanthocorbis camarensis*骨架大小之影響

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以實驗室培養之海洋襟鞭毛蟲*Acanthocorbis camarensis*爲材料，探討溫度對其細胞骨架體型大小及骨架縱軸之矽質小段長短之影響。測試溫度包括15°C，25°C，30°C及35°C，結果顯示：高溫下培養之襟鞭毛蟲比在低溫下培養者具較小之骨架，及較短之矽質小段。此爲首次證明溫度對襟鞭毛蟲骨架大小具影響力之研究。

關鍵詞：溫度，襟鞭毛蟲，骨架大小。

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