

How will Benthic Foraminifera Respond to Warming and Changes in Productivity: A Laboratory Culture Study on *Cymbaloporeta plana*

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Abstract

The anthropogenic activities are likely to cause global warming. The global warming will affect marine productivity and thus food availability for marine organisms. Both, the seawater temperature and food availability, affect benthic foraminifera, the most abundant marine calcareous microorganisms. Therefore, a laboratory culture experiment was conducted on *Cymbaloporeta plana* to understand the coupled effect of temperature (25°C, 27°C, 30°C) and food (102±5, 203±9, 305±14, 407±18, 508±23 diatom cells). At all temperatures, the growth increased with increase in food. The specimens subjected to 27°C temperature attained the maximum growth and those subjected to 25°C, were the smallest. All specimens fed with 508±23 cells reproduced, irrespective of temperature. Out of all the specimens without food, 40% at 27°C, and 20% at 25°C reproduced, whereas, specimens subjected to 30°C, did not reproduce. The 100% reproduction at 27°C suggests that it is the optimum temperature for growth and reproduction. All the specimens at 30°C and without additional food, died, whereas at 25°C and 27°C, the mortality was 80% and 60%, respectively. The limited growth and reproduction with decreasing food, clearly indicates that food availability also controls the growth and reproduction of shallow water benthic foraminifera *C. plana*. Therefore, warming coupled with decreasing productivity will severely affect the growth and abundance of shallow water benthic foraminifera.

Key Words: *Cymbaloporeta plana*, Culture Experiment, Temperature, Food, Reproduction

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Introduction

The anthropogenic activities have warmed the world by 0.85°C since the year 1880 (IPCC, 2013). The warming has severely affected the oceans. The oceans, especially the upper 75 m have warmed at a rate of 0.11°C per decade since 1971, and the trend is likely to continue under the business as usual scenario (Levitus et al. 2000, Gleckler et al. 2012, IPCC, 2013). The warming affects the marine primary productivity and thus the food availability in the oceans (Goes et al. 2005, Roxy et al. 2016). The changes are more pronounced in the marginal marine regions of the tropical oceans (Kwiatkowski et al. 2017). The ocean warming and associated changes in productivity affect the marine organisms, with the response varying from species to species (Brierley & Kingsford 2009, Ashton et al. 2017, Kleisner et al. 2017). A more pronounced effect is envisaged in tropical marine species as they are already living close to their upper thermal tolerance limits (Nguyen et al. 2011). Out of a wide diversity of marine organisms, foraminifera, unicellular protozoans with an exoskeleton, abundant in marginal marine regions (Saraswat & Nigam 2013), are likely to be severely affected. The calcareous foraminifera are an important link in the carbon cycle (Schiebel 2002, Barker et al. 2003). Any change in foraminiferal population or behavior, as a result of warming or availability of food, can affect the global carbon cycling and thus has far-reaching implications. Therefore, it is important to understand the effect of warming and food availability on foraminifera.

In coastal areas, though temperature and salinity are the important parameters that govern the growth and reproduction of foraminifera (Boltovskoy et al. 1991, Murray 2006, Nigam et al. 2006, 2008, Saraswat et al. 2011; Lei et al., 2016), food is also equally important for these minute organisms to flourish. Foraminifera collect its food with the help of pseudopodia and the food material is ingested through the aperture. Foraminifera feed on phytoplanktons, diatoms, coccolithophores, dinoflagellates, algae, spores, algal gametes, other sarcodina, radiolarian (Winter 1907, Sandon 1932, Myers 1935, 1937, 1943A, Jepps 1942, Arnold 1954, Bradshaw 1955, 1957, Nyholm 1955, Hedley 1958, Lee et al. 1961, Murray 1963, Lee et al. 1966, Lee & Pierce 1963, Boltovskoy 1969, Lengesfeld 1969, Muller & Lee 1969, Lipps & Valentine 1970, Christiansen 1971, Rottger 1972, Ross 1972, Boltovskoy & Wright 1976, Kathal 1998). The seasonal difference in foraminiferal population and assemblage (Gooday 2003, Gooday & Lambshead 1989), suggested that changes in the type and amount of food may be one of the factors responsible for the changes in the foraminiferal population. The seasonal changes in water temperature, nutrient, salinity and dissolved oxygen alter the type and amount of organic matter (food) available for foraminifera and thus affect foraminiferal population and diversity. The food preference of species belonging to the same genus may vary. Laboratory culture studies

suggest that changes in the foraminiferal diversity and abundance were brought by the amount of food and the response was species-specific (Heinz et al. 2001). The differential food preference affects the relative abundance of a particular species and thus the species assemblage, under different environments.

The food availability also affects the morphology of foraminifera. The extreme scarcity of food leads to the cessation of growth and reproduction in certain species while the unfed specimens of certain other species grow equally well or better than the specimens that were supplied with food at regular intervals (Bradshaw 1961, Lee et al. 1991). However, the scarcity of food leads to longer survival rate as the reproduction was delayed (Hemleben & Kitazato 1995). A similar observation concerning temperature was also made (Bandy 1963, Lewis & Jenkins 1969). The shell size of several benthic foraminifera increased with decreasing temperature. But the response is again species specific as the shell size of a few other foraminifera decreases with decreasing temperature (Phleger & Hamilton 1946, Theyer 1971). In view of the species-specific preferences, the response of different benthic foraminifera to both the temperature and food availability has to be assessed to understand the impact of warming and associated changes in productivity, on foraminifera.

2 Methodology

Both the seaweed attached to the partially submerged rocks, and the top sediments from the shallow waters of Dias Beach, Goa, India, were collected to isolate living benthic foraminifera (Fig. 1). The ambient seawater temperature at the sampling site was 27.5°C. The seaweed was stirred in seawater to detach the living benthic foraminifera. The detached material and sediments were sieved by using 63 µm and 1000 µm sieve to concentrate living benthic foraminifera. The 63-1000 µm fraction was collected in beakers, soaked in seawater and brought to the laboratory for further processing. Benthic foraminifera *Cymbaloporeta plana* were isolated from the samples with the help of a stereozoom microscope (Olympus SZX16) and transferred to multi-well culture dishes. The living status of the specimens was confirmed by movement, collection of food material or extended pseudopodia. The living specimens were then divided into three batches and maintained in duplicate sets, at different temperatures (25°C, 27°C and 30°C). The salinity of the media in all the culture sets was maintained constant (35 psu). The pure culture of diatom *Navicula* sp. was used as food. A continuous laboratory culture of diatoms was maintained throughout the experiment. To isolate diatoms, seawater was collected from the study area, brought to the laboratory and filtered with 10 µm mesh to concentrate diatoms. From this concentrated sample, *Navicula* sp. were isolated and transferred to filtered sea water and kept under the light. After a few days, only the *Navicula* sp. was again isolated and transferred to

F2 media. This procedure was repeated six to eight times to get a pure culture of *Navicula* sp. For diatom culture, F2 media was prepared by following Guillard & Ryther (1962).

The specimens collected from the field and kept at all three temperatures, reproduced. The juvenile specimens of *C. plana* with 4 to 5 chambers were picked from the stock cultures maintained at different temperatures (25°C, 27°C and 30°C). The isolated juvenile specimens were subjected to the same temperature from which it was picked, to prevent the experimental shock which the specimens would experience if they were directly transferred to different temperatures. Additionally, these specimens subjected to three temperatures (25°C, 27°C and 30°C) were also provided different amount of food (no additional food, 102±5, 203±9, 305±14, 407±18, 508±23 diatom cells). The diatoms (100 µl, 200 µl, 300 µl, 400 µl, 500 µl) were fed to foraminifera. The number of cells in unit aliquot of diatom culture was counted every time, before feeding foraminifera, to maintain consistent food supply throughout the experiment. No food was added to one set of *C. plana* specimens. All the cultures were maintained at 12 h light and 12 h dark interval. The experiment was conducted in replicate, with each set containing 5 specimens. A total of 5 specimens were kept in each well of the 6 well culture trays. The replicate sets were maintained in the same incubator. A total of 180 specimens were used for the experiment. The coiling direction, number of chambers and the maximum diameter of all the specimens were noted in the beginning. The salinity, temperature, dissolved oxygen and pH of the food as well as the media was measured every time the media was changed. The maximum diameter of the individuals was measured weekly, and the number of specimens reproduced and died during the experiment was also recorded. The specimens that died without reproducing, were considered to calculate mortality.

3 Results

A significant growth (defined as the increase in maximum diameter), was noted in all the specimens kept at all three temperatures (25°C, 27°C and 30°C) (Fig. 2, Table 1). Interestingly, the growth of specimens increased with increasing amount of food. The specimens subjected to 27°C, however, attained the maximum growth. At 200 µl or more food (203±9 cells), the specimens kept at 25°C grew the least (Fig. 2). At less than 200 µl of food (203±9 cells), the specimens kept at the warmest temperature (30°C) were the smallest. The specimens with no additional food did not grow much, irrespective of the temperature. An extensive pseudopodial activity along with movement was observed right from the start of the experiment. During the experiment, the specimens fed with food responded more quickly than the specimens with less or no additional food.

The reproduction was frequent in the specimens. All the specimens fed with 500 μ l of diatoms (508 ± 23 cells), reproduced, irrespective of seawater temperature (Fig. 3). Almost all the specimens supplied with 400 μ l of food (407 ± 18 cells) also reproduced, except those maintained at 25°C temperature, wherein only 80% of the specimens reproduced. In case of specimens supplied with 300 μ l food (305 ± 14 cells), all the specimens maintained at 27°C temperature reproduced, whereas only 80% reproduction was observed in the specimens kept at 25°C and 30°C temperature (Fig. 3). Out of all the specimens maintained without food, 40% of those kept at 27°C temperature, and 20% of those subjected to 25°C temperature, reproduced (Fig. 3). None of the specimens, without additional food, kept at 30°C temperature, reproduced (Fig. 3). *Cymbaloporeta plana* accumulated a lot of organic matter all around its test just before addition of new chambers or when the specimen was about to reproduce (Fig. 4). During asexual reproduction, the juveniles require food to form its initial two to three chambers, before being released from the parent cell or the cyst. The food material collected by the parent cell helps to feed the juveniles. The growth stages and chamber formation in *Cymbaloporeta plana* are illustrated in (Fig. 5).

The highest mortality was in specimens maintained without food and decreased with the increasing amount of food. Out of all the specimens without food, all those subjected to 30°C, 80% of the ones maintained at 25°C, and 60% specimens at 27°C, died (Fig. 6). The difference in mortality between specimens without food and those with minimum food was large. A few specimens fed with 400 μ l food (407 ± 18 cells) and maintained at 25°C, also died.

4 Discussion

The average growth increased with the increase in food, at all temperatures, suggesting that the food availability dominantly controls benthic foraminiferal growth. The number of specimens undergoing reproduction also increased as the amount of food increased. The growth in foraminifera is faster when plenty of food is available whereas when food is less the growth is comparatively slower (Myers 1943b, Bradshaw 1955; Lei et al. 2016). The foraminifera grow faster and reproduce more frequently in places where there are phytoplankton blooms. But, whenever food is scarce, growth is slower and the number of specimens undergoing reproduction, also decreases (Lee et al. 1966). The quality of the organisms used as food, also affects the feeding in foraminifera (Muller 1975). But, such a possibility is ruled out in the present experiment as all the specimens were fed the same type of food. Additionally, the chance of any adverse impact of single diatom diet on *C. plana* is also not likely as the monospecific diatom cultures grown in the laboratory were the most favourable food for foraminifera (Duffield et al. 2014). The response of *C. plana* to food is similar to another benthic foraminifera *Marginopora*

kudakajimensis. Here also the maximum growth was under illuminated, nutrient enriched and well-fed conditions (Lee et al. 1991).

The increase in pseudopodial activity with increasing quantity of food suggests, increased efforts to collect the available food. The food intake is linked with foraminiferal activity (Gross 2000). The pseudopodial response of *C. plana* to food is different than a few other species. The pseudopodial activity in a few other species decreased significantly after the foraminifera have taken enough food (Langer & Gehring 1993). Similar, species-specific response to food have also been observed in *Rotaliella heterocaryotic*, as it did quite well when supplied with heat-killed *Dunaliella*, but at the same time, *R. roscoffensis* did not (Grell 1954). Further, the encasement of test with food by *C. plana*, was also reported by Goldstein & Corliss (1994) wherein they observed that the actively feeding foraminifera surround its tests completely by the foreign material collected by the pseudopodia. Such a mode of food collection, termed as deposit feeding, is common in both the shallow water as well as deep-sea benthic foraminifera.

The high instance of mortality in specimens devoid of additional food is unlike the response of deep-sea benthic foraminifera. The field and laboratory studies showed that the deep-sea foraminifera are adapted to limited or no supply of food material for long, means starvation (Linke 1992, Graf & Linke 1992). The abundance of specimens, not fed with additional food, also increased, suggesting that most species were feeding on microbes or detritus available in the sediment (Duffield et al. 2014). The seawater provided to the specimens in the present study contained microbes. But the reduced growth, low reproduction and very high mortality in specimens devoid of additional food, clearly suggests that *C. plana* requires additional regular phytodetritus for normal growth and survival. The response to phytodetritus has also been found to vary as per the depth at which the species are found in the ocean, thus reflecting the depth zonation of benthic foraminiferal species. The response of abyssal foraminifera to the phytodetritus was different than that of the continental slope species, and foraminifera showed a retarded response as compared to the macrofauna (Witte et al. 2003). The arrival of food has increased impact on the shallow infaunal species as compared to the deep infaunal species, while a few species do not respond at all (Nomaki et al. 2005). Here also, an inter-specific difference in response to food was observed, and thus it explains the changing abundance and diversity during different seasons and in different geographical regions. Based on foraminiferal culture studies it was observed that changes in the foraminiferal diversity and abundance were brought by the amount of food and the response was species-specific (Heinz et al. 2001).

The food alone was not the limiting factor. The response of *C. plana* to a different amount of food also varied with the ambient temperature. Even in specimens that were fed the same amount of food, both the growth as well as reproduction, were more frequent in specimens kept in warmer water. The growth of specimens kept at the warmest temperature was, however, lower than that at the medium temperature, suggesting that 27°C is the optimum temperature for growth of *C. plana*. Therefore, it is likely that initial warming will result in a prolific growth and increase in abundance of *C. plana*. A persistent warming, however, will adversely affect *C. plana*. This finding of the present study that the growth is more in specimens kept in comparatively warmer water, is supported by the studies conducted by Phleger & Hamilton (1946), Theyer (1971) and Saraswat et al. (2011). The response to temperature probably reflects the tropical shallow water habitat of *C. plana*. A few other benthic foraminifera (*Pararotalia calcariformata* and *Lachlanella* sp.) also calcified as well as grew well at extreme warm temperatures (~42°C) in thermally polluted area (Titelboim et al. 2017) suggesting that foraminifera can survive as well as grow well in warm waters. A few studies, however, contradict our findings of increased growth at warmer temperature. Increased growth in several benthic foraminifera was observed at lower temperatures as compared to the specimens subjected to higher temperatures (Rhumbler 1911, Bandy 1963, Lewis & Jenkins 1969, Arnold 1967, Nigam et al. 2008). Additionally, there is no linear increase and decrease in growth with a change in temperature, as the growth rate decreased in all the specimens of *Rosalina leei* subjected to temperature other than the optimum (Nigam et al., 2008; Kurtarkar et al. 2017), thus suggesting that the change in growth with temperature is a species specific response. Similarly, a few benthic foraminifera survive in slightly lower temperature but would ultimately die (Bradshaw 1955, 1961). This signifies the fact that the temperature tolerance of foraminifera is species specific. Some species may require warmer temperature to grow, where as a few others may proliferate only at colder temperatures. Such an observation was not made in the present study, as the lower temperature tolerance limit for *C. plana* would be much lower than the temperature to which it was subjected in this experiment. However, the food availability seems to be a very significant factor controlling the mortality of the specimens, as the majority of specimens without food, died whereas no death was reported in specimens fed with 500 µl of food.

5 Conclusions

The unprecedented increase in atmospheric carbon dioxide concentration is expected to cause global warming, which in turn may affect marine primary productivity. The marine primary productivity is the major source of food for foraminifera. Therefore, it is likely that the rising CO₂ concentration and

associated changes will affect benthic foraminifera. A laboratory culture experiment was conducted to understand the effect of different seawater temperature (25°C, 27°C and 30°C) and food availability, on a shallow water benthic foraminifera. Based on this experiment it is inferred that the growth in *Cymbaloporeta plana* increases with increased amount of food, irrespective of the seawater temperature. Out of all the specimens fed with same amount of food, higher growth was noted in specimens kept in comparatively warmer waters. Even the reproduction was favoured in warmer water. The growth, however, decreased with further warming, suggesting an optimum temperature for growth and also an adverse effect of persistent warming. Under the experimental conditions, in general, a majority of the specimens subjected to 27°C temperature reproduced, which indicates that 27°C temperature is more suitable for growth and reproduction of *C. plana*. The study shows pronounced influence of food and seawater temperature on the growth, survival and reproduction in benthic foraminifera.

Acknowledgments

The authors are thankful to the Director, National Institute of Oceanography, Goa for his support and permission to publish this work. Authors are thankful to the Department of Science and Technology, New Delhi for the financial support to RS under the National Network Programme on Climate Change and Coastal Vulnerability (DST/CCP/NCC&CV/130/2017(G)) and to SRK under the Women Scientist Scheme [SR/WOS-A/LS-145/2016(G)].

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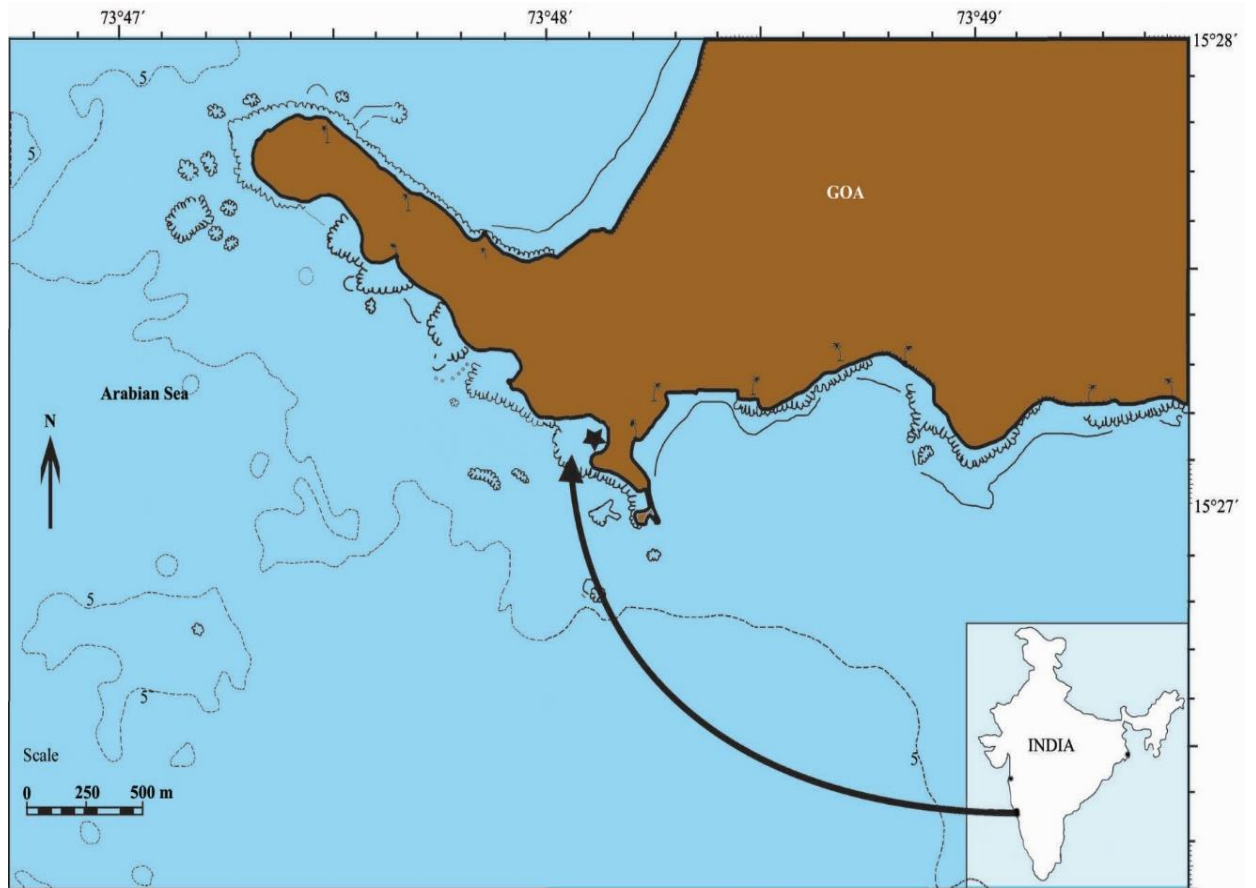


Fig. 1: The location of Dias Beach, Goa, India (marked by star), from where living benthic foraminifera were collected. The inset map shows the location of the sampling site on the western margin of India. The 5 m bathymetric contour is marked by dotted line. The coconut tree symbols mark the location of other beaches in the vicinity. The zagged contour represents rocky shore.

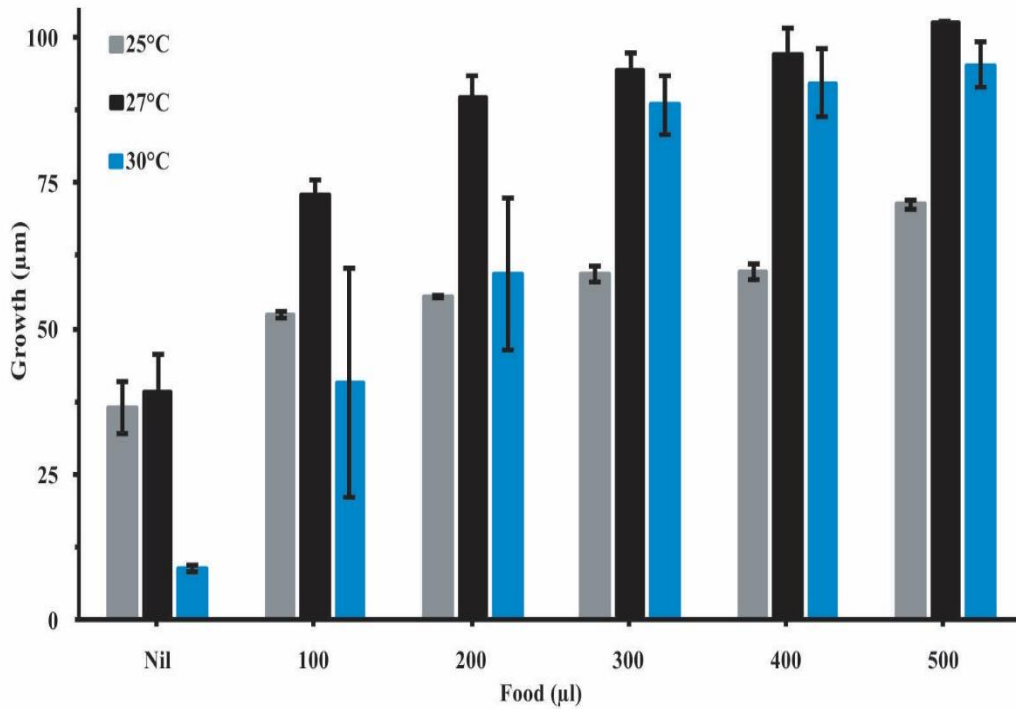


Fig. 2: The growth (average of the maximum diameter of all the specimens maintained at a particular condition) in *Cymbaloporetta plana* (Cushman) at different temperature and food concentration. The error bar represents the standard deviation of growth in replicate sets.

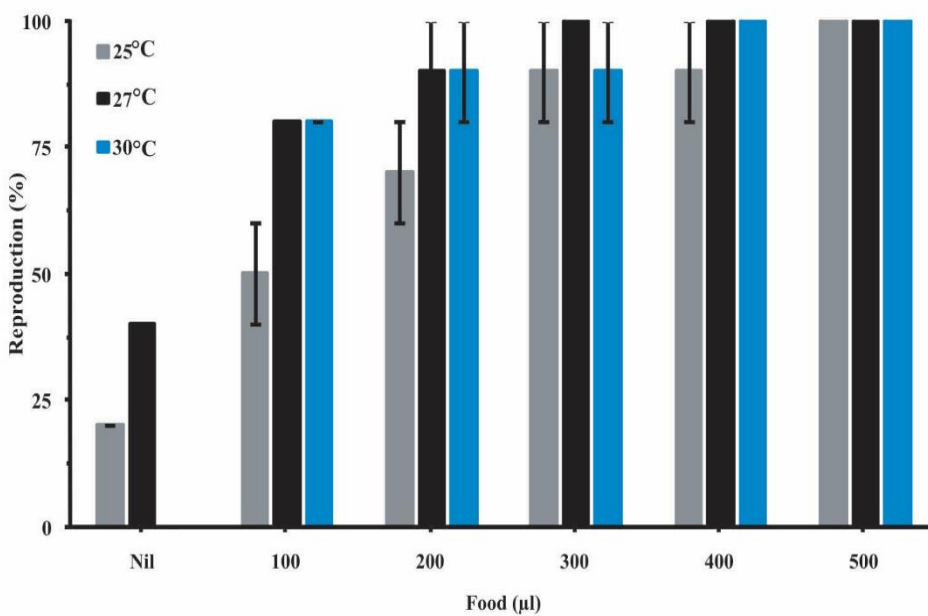


Fig. 3: The percentage of *Cymbaloporetta plana* (Cushman) specimens that reproduced at different temperature and concentration of food. The error bar represents the standard deviation of reproduction in replicate sets.

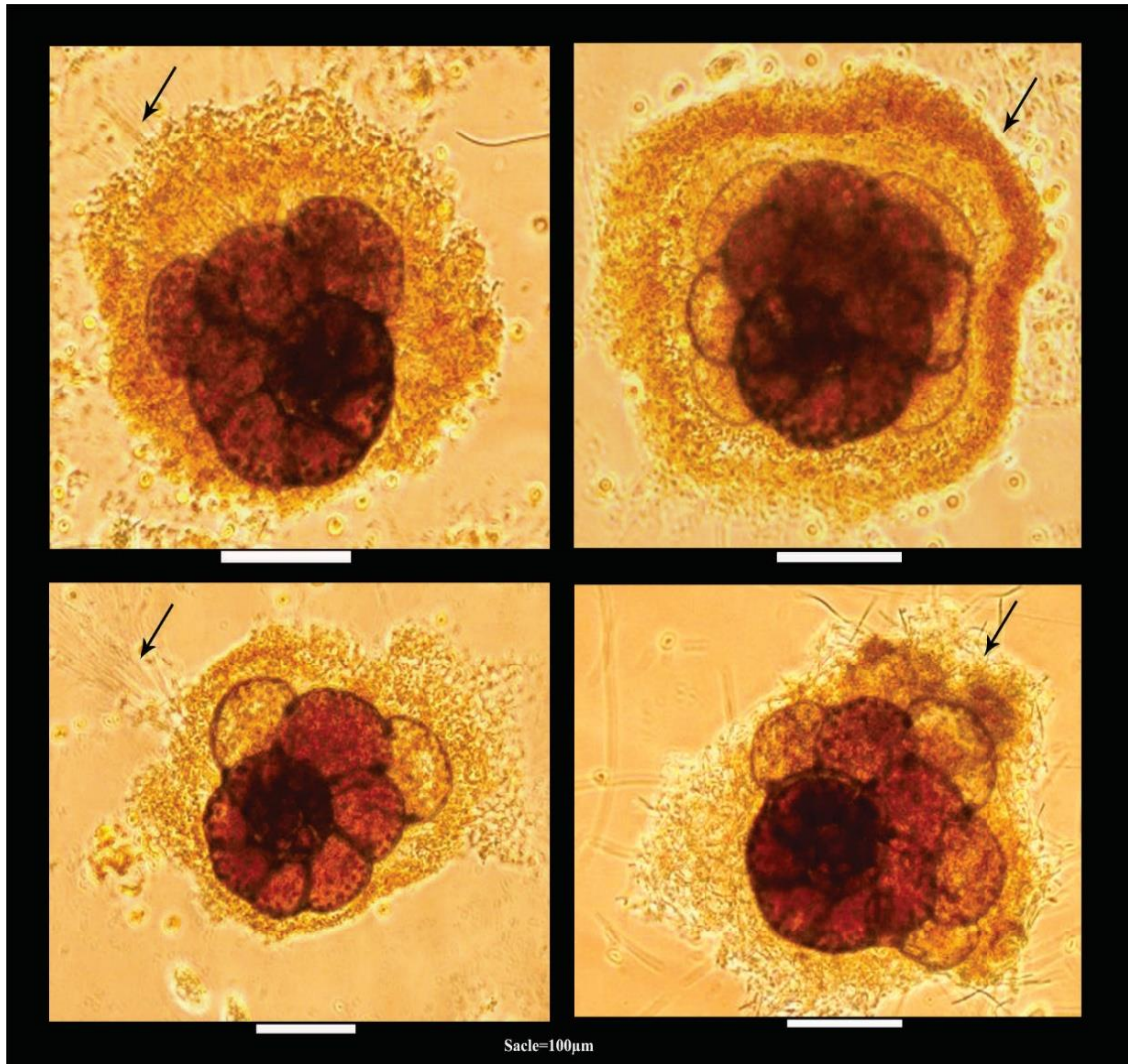


Fig. 4: The cyst of food material formed by *Cymbaloporella plana* (Cushman), with the help of pseudopodia, at the time of chamber formation.

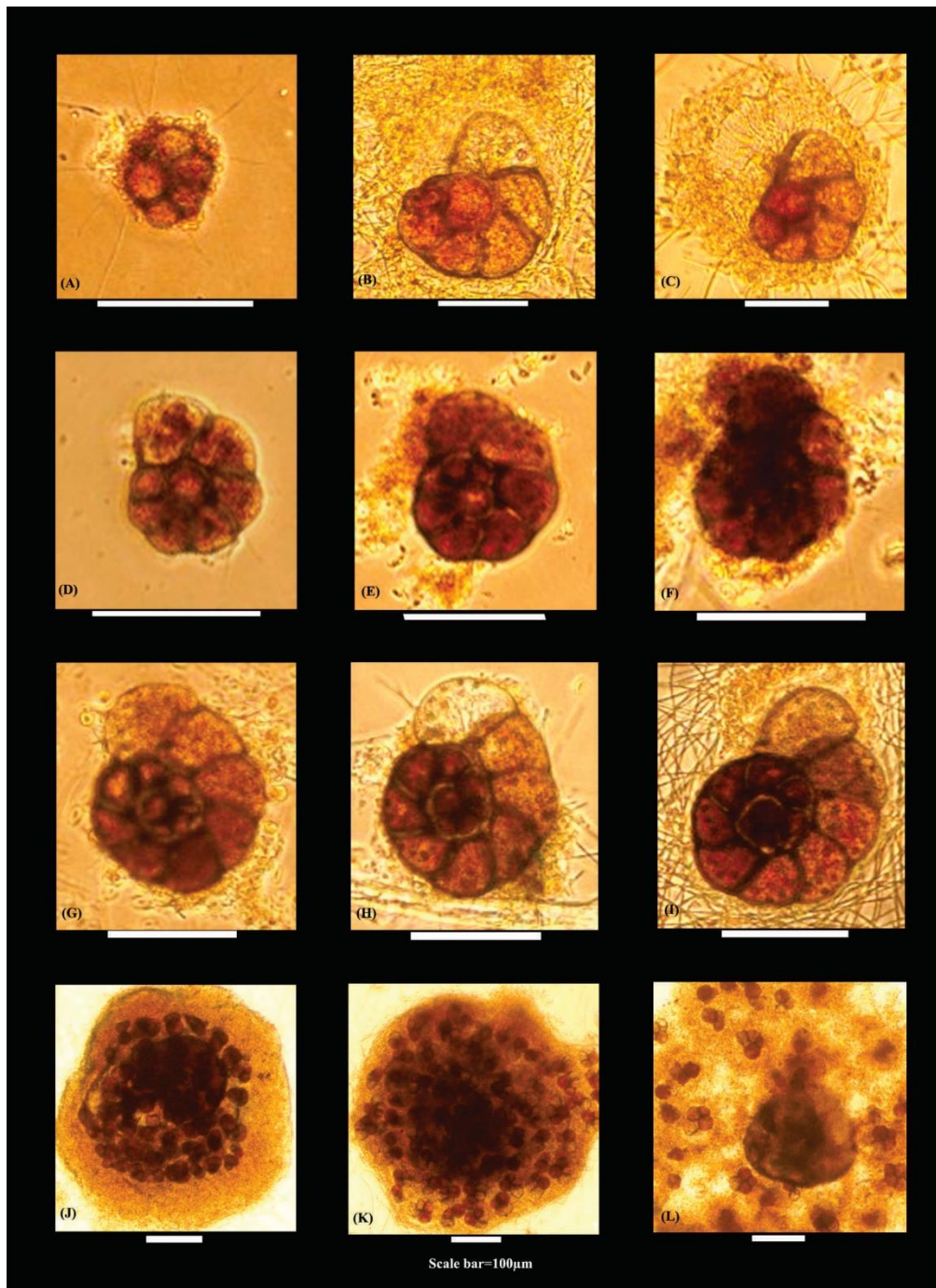


Fig. 5: The growth stages and chamber formation in *Cymbaloporetta plana* (Cushman) (A-I), juveniles inside the cyst formed by the mother cell (J), juveniles on the verge to move out of the cyst (K) and the juveniles out of the mother cell, leaving it empty (L).

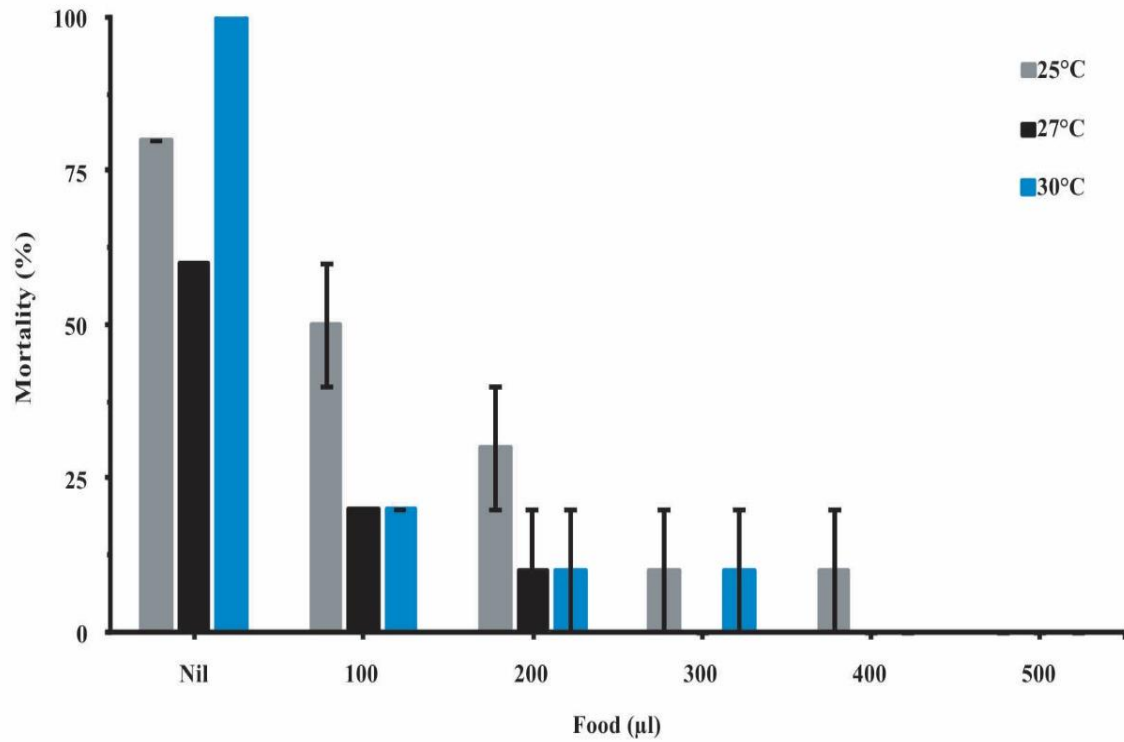


Fig. 6: The percentage of dead *Cymbaloporetta plana* (Cushman) specimens at different temperature and concentration of food. Only those specimens that died without reproducing, were considered to calculate mortality. The error bar represents the standard deviation of mortality in replicate sets.

Table 1: Average growth of benthic foraminifera *Cybaloporeta plana* (Cushman) at different food concentration and temperature. NAF means no additional food.

		25°C					
Amount of Food (µl)		NAF	100	200	300	400	500
Set 1	Initial Size (µm)	85.9	75.3	79.7	82.9	91.4	99.6
	Final Size (µm)	126.6	128.2	135.0	143.5	149.5	171.6
	Growth (µm)	40.8	53.0	55.2	60.6	58.2	72.0
Set 2	Initial Size (µm)	80.3	84.4	85.7	86.2	93.3	90.7
	Final Size (µm)	112.3	136.0	141.4	144.1	154.2	161.2
	Growth (µm)	32.0	51.6	55.7	57.9	60.9	70.4
Average Growth (µm)		36.4	52.3	55.5	59.2	59.5	71.2
StDev		4.4	0.7	0.2	1.4	1.4	0.8
		27°C					
Amount of Food (µl)		NAF	100	200	300	400	500
Set 1	Initial Size (µm)	73.9	85.7	81.9	87.7	89.2	85.6
	Final Size (µm)	119.4	161.3	168.2	179.0	182.3	187.9
	Growth (µm)	45.5	75.6	86.2	91.3	93.1	102.3
Set 2	Initial Size (µm)	95.6	89.4	82.4	84.2	91.2	88.5
	Final Size (µm)	128.6	159.3	175.5	181.4	192.5	191.1
	Growth (µm)	33.0	70.0	93.1	97.2	101.3	102.6
Average Growth (µm)		39.2	72.8	89.7	94.2	97.2	102.4
StDev		6.3	2.8	3.4	2.9	4.1	0.2
		30°C					
Amount of Food (µl)		NAF	100	200	300	400	500
Set 1	Initial Size (µm)	84.8	88.9	86.4	88.9	89.3	85.7
	Final Size (µm)	94.0	149.0	158.6	172.2	175.6	177.0
	Growth (µm)	9.3	60.2	72.2	83.3	86.3	91.3
Set 2	Initial Size (µm)	82.3	102.8	90.6	83.0	88.6	91.8
	Final Size (µm)	90.3	123.9	136.9	176.4	186.6	191.0
	Growth (µm)	8.1	21.1	46.3	93.4	98.0	99.2
Average Growth (µm)		8.7	40.6	59.3	88.3	92.1	95.2
StDev		0.6	19.5	12.9	5.0	5.8	4.0