

Appraisal of laboratory culture experiments on benthic foraminifera to assess/develop paleoceanographic proxies

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The laboratory culture studies, carried out on benthic foraminifera, with the aim to refine paleoceanographic/paleoclimatic or environmental application of benthic foraminifera, have been reviewed. The review includes studies, which refined the understanding of factors that bring out changes in benthic foraminiferal abundance, morphology and chemical composition (of the test). Additionally, studies dealing with taxonomic aspects of benthic foraminifera have also been discussed, since such studies have significantly improved application of benthic foraminifera for stratigraphic correlation.

Most of the laboratory culture studies on benthic foraminifera in the early days were carried out to monitor the complete life-cycle of selected species. Such studies revealed presence of morphologically different stages in the life-cycle of single species. Thus the forms that were earlier recognized as different species were later on clubbed as developmental or ontogenetic stages of single species. Interesting relationship between mode of reproduction and coiling direction were also observed. Later on, with the growing application of foraminiferal characteristics for past climatic and oceanographic reconstruction, benthic foraminifera were maintained under controlled physico-chemical conditions in the laboratory. Such studies helped to refine the differences in the foraminiferal characteristics from physico-chemically different environments, as observed in the field. As it was proposed that the amount and type of food material is the major factor that controls the benthic foraminiferal population, numerous studies were carried out to assess the response of benthic foraminifera to different type and amount of food and oxygen concentration. Surprisingly limited laboratory culture studies have been carried out to understand the factors that govern the chemical composition of the benthic foraminiferal tests. It probably reflects the difficulties in simulating the conditions under which physico-chemical parameters can be kept constant throughout the experiment. Towards the end of 20th century application of molecular systematic analysis techniques on foraminifera started and such studies refined the evolutionary history and taxonomic position of foraminifera as well as helped recognize cryptic species. However, despite a large number of culture studies being carried out on benthic foraminifera with their paleoceanographic/paleoclimatic application in focus, still much more efforts are needed to understand the parameters affecting the benthic foraminiferal abundance, morphology and chemical composition.

[**Key words:** Foraminifera, paleoceanography, paleoclimate, laboratory culture]

Introduction

Foraminifera, unicellular, preferentially marine microorganisms, are one of the most efficient indicators of their ambient environment. Changes in abundance, species assemblage, morphology and chemical composition of benthic foraminifera have long been applied to reconstruct the climatic and oceanographic conditions during the earth's geologic past, as well as to assess the modern changes in the coastal regions due to increasing anthropogenic influence^{1,3}. Laboratory culture studies on benthic foraminifera have also been carried out soon after the discovery of potential application of benthic

foraminiferal characteristics for the paleoclimatic reconstruction. Laboratory culture studies were started because the studies from field have not always provided a definite clue about the factors governing the specific foraminiferal assemblage⁴⁻⁶. Though large number of laboratory culture studies have been carried out on benthic foraminifera covering different aspects, here we review the findings of those laboratory culture studies that helped to understand the effect of different ecological parameters on benthic foraminiferal abundance, morphology and chemical composition, as observed in the field, as these are the benthic foraminiferal parameters used for paleoclimatic/paleoceanographic reconstruction (Table 1). Additionally, those studies have also been included that were carried out on cellular part of the foraminifera, and helped refine the evolutionary

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history and taxonomic position of the foraminifera, as well as to identify cryptic species. Such studies have significantly improved the application of foraminiferal characteristics in stratigraphic correlation, especially for hydrocarbon exploration studies. Studies that refined the species identification have immensely improved the application of foraminiferal chemical composition (stable isotopic and elemental) for paleoceanographic studies as large differences have been noticed in the stable isotopic and elemental composition of the closely related species belonging to same genus. Thus the review is divided into different sections as:

1. Studies carried out to understand the factors affecting abundance and morphology
2. Studies that helped understand the factors affecting chemical composition
3. Studies that refined evolutionary position of foraminifera
4. Studies that helped to identify cryptic species
5. Miscellaneous studies that refined application of benthic foraminifera for past climatic/oceanographic reconstruction.

In order to emphasize the need and relevance of this review work, current status of reviews done till date, which discussed similar aspects, is provided in the next section.

Previous reviews

Earlier Lister⁷ compiled the studies covering the biological aspects of foraminifera but the results were mainly based on the field observations. Later on, efforts were made to provide a comprehensive review of the factors affecting the abundance and growth of species, as well as its response to various ecological parameters based on the samples collected from the field⁸. Murray⁹ compiled the biological aspects of foraminifera and their potential application for paleoecological studies, but the findings included observations made both in the field and laboratory culture. A comprehensive review of ecological parameters affecting the benthic foraminiferal morphology was provided by Boltovskoy *et al.*⁵. But, here also, most of the studies included were based on the field observations. Subsequently, the paleoceanographic significance of studies carried out to understand the biological aspects of benthic foraminifera was compiled and discussed by Gooday¹⁰. In this study, results from laboratory culture of benthic foraminifera were included to some

extent, much emphasis was given to the influence of food and oxygen conditions on the benthic foraminiferal communities. Thus, a complete review of the studies carried out to understand the specific effect of a single, or a combination of few ecological parameters on benthic foraminifera under laboratory culture, is not available.

As the culturing of foraminifera increased with advancements made in the techniques to maintain benthic foraminifera under laboratory conditions, a brief historical account of developments in the benthic foraminiferal culturing techniques is given in the next section.

Laboratory culturing techniques through ages

Though laboratory maintenance of benthic foraminifera started from the first half of the 19th century and number of studies were published during the later half of the 19th century, it was not until the mid of 20th century that ecological experiments were conducted on benthic foraminifera maintained in laboratory culture. Myers^{11, 12} discussed various methods and precautions to be taken during collection and maintenance of benthic foraminifera from the littoral zone in the laboratory. Arnold¹³ and Slater¹⁴ provided a comprehensive review of the various methods to culture benthic foraminifera and proposed a simple system for laboratory maintenance of benthic foraminifera. Subsequently, Lee *et al.*¹⁵ and Arnold^{16,17} provided a detailed description of the methods of collection and maintenance of living foraminifera in the laboratory, as a part of their research on growth and physiology of foraminifera in the laboratory. An updated account of the developments made in the laboratory culturing methods for benthic foraminifera was given by Anderson *et al.*¹⁸. Recently, Hintz *et al.*¹⁹ described a new setup to maintain benthic foraminifera under controlled physico-chemical conditions under laboratory conditions. It will help to carry out studies to understand the specific physico-chemical and biological factors affecting chemical composition of the foraminiferal tests, one of the most frequently used foraminiferal characteristic.

Most of these studies discussed the methods for maintaining shallow water benthic foraminifera under laboratory conditions. Though limited success was reported in maintaining deep-water benthic foraminifera under normal laboratory conditions²⁰, successful maintenance of deep-sea foraminifera

Table 1—Foraminiferal culture studies on benthic foraminifera for paleoclimatic implications

Sr. No.	Author & Reference	Year of Publication	Study Details
1.	Myers ¹¹	1935	The optimum temperature for <i>Patellina corrugata</i> is very near to the upper temperature tolerance limit; lower temperature leads to decreased rate of reproduction.
2.	Myers ⁸⁰	1936	Close relationship between mode of reproduction and coiling direction in <i>Spirillina vivipara</i> .
3.	Myers ⁸¹	1940	Megalospheric specimens preferentially coiled sinistrally while the microspheric ones coiled dextrally in <i>Discorbis patelliformi</i> .
4.	Myers ⁸³	1942	About 1000 <i>Elphidium crispum</i> tests per square foot are contributed annually to the sediments; larger tests evade degradation during ingestion by macrofauna.
5.	Arnold ¹⁰²	1952	Desiccation experiments showed that a part of tubuliferous ring may get preserved after fossilization and help in identification from fossil assemblage.
6.	Arnold ¹⁰³	1953	Observed live specimens of <i>Allogromia laticolaris</i> in the laboratory and inferred morphological differences in gamonts and agamonts; helped in clubbing of previously different species under single species.
7.	Arnold ¹³	1954	<i>Discorinopsis aguayi</i> and <i>Discorinopsis vadesens</i> can survive extremes of temperature only if subjected for a short period.
8.	Bradshaw ⁴	1955	Different rotalid species have different food preferences; comparatively lower temperature results in reduced growth rate; both higher and lower than normal salinity has adverse effect on the growth of rotalids.
9.	Bradshaw ⁵⁷	1957	Temperature and salinity below and above tolerance limits, lead to cessation of growth in <i>Streblus beccarii</i> (Linné); within the temperature tolerance limit, growth increases with temperature; lower temperature and extreme salinity leads to delayed reproduction.
10.	Nyholm ¹²⁴	1958	Observed that previously considered separate taxa were in fact different ontogenetic stages of <i>Cibicides lobatulus</i> .
11.	Bradshaw ³²	1961	Higher temperature lead to the increased growth rate and quick reproduction, however the specimens were smaller than the ones grown at lower temperature; effect of temperature and pH on benthic foraminifera was linked with seawater salinity; scarcity of food lead to the decreased growth and reproduction; antibiotics adversely affected the benthic foraminiferal species; only extremely high hydrostatic pressure was fatal; oxygen consumption was species specific and was controlled by the seawater temperature.
12.	Lee <i>et al.</i> ¹⁵	1961	The response of benthic foraminifera to a combined diet of diatom, filamentous algae and bacteria varied from species to species.
13.	Freudenthal <i>et al.</i> ⁶³	1963	Developed a tidal system for laboratory studies on eulittoral foraminifera and found that the higher salinity is correlated with early reproduction.
14.	Lee <i>et al.</i> ⁸²	1963	Close link between mode of reproduction and coiling direction with gamont specimens being preferentially dextrally coiled while the agamonts being sinistral.
15.	Murray ¹²⁵	1963	Performed various ecologic experiments on foraminifera.
16.	Sliter ¹²⁶	1965	Laboratory experiments on the lifecycle and ecologic controls of <i>Rosalina globularis</i> d'Orbigny.
17.	Angell ⁶⁸	1967	<i>Rosalina floridana</i> can recover the dissolution of the tests incurred while subjected to seawater with acidic pH; however no evidence of any special mechanism to regenerate the test.
18.	Schnitker ²³	1967	At sexual maturity under laboratory culture, offsprings of <i>Triloculina linneiana</i> attained only the one-eighth the size of the parent and were morphologically distinctly different than the parent.
19.	McEnery & Lee ⁶⁷	1970	Incorporation of radionuclides of Ca, Sr, P and S was proportional to the growth rate of <i>Rosalina leei</i> and <i>Spiroloculina hyalina</i> ; both the species have the capability to regenerate the test.
20.	Röttger ⁵⁶	1972	Low intensity and darkness lead to cessation of growth activity; growth pattern changed after the specimens were subjected to normal light again. Lower temperature resulted in reduced rate of chamber formation but does not affect the size of chambers or shape of the test.
21.	Röttger & Berger ²²	1972	Very high light intensity lead to decreased growth rate and tests grown under such conditions were morphologically distinct.

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Table 1—Foraminiferal culture studies on benthic foraminifera for paleoclimatic implications—*Contd.*

Sr. No.	Author & Reference	Year of Publication	Study Details
22.	Lee & Muller ³⁵	1973	<i>Allogromia laticollaris</i> , <i>Rosalina leei</i> , and <i>Spiroloculina hyalina</i> are selective feeders and can adjust to the seasonal changes in the food availability.
23.	Frankel ¹²⁰	1974	<i>Trochammina ochracea</i> attaches to the cavities in the surfaces and may be missed during counting.
24.	Schnitker ¹²⁷	1974	Mature and nearly mature specimens are incapable of adjusting to different temperature regimes; physiological acclimatization takes place during and possibly after reproduction over a span of generation; clone culture lead to morphological variations.
25.	Muller ¹²⁸	1975	Assessed temperature, salinity and pH limits for <i>Allogromia laticollaris</i> , <i>Rosalina leei</i> and <i>Spiroloculina hyalina</i> ; type and amount of food affect the food intake.
26.	Lee & Bock ¹²⁹	1976	In two species of symbiont bearing soritid foraminifera, feeding is by far the more important process at midday; both species added about 4% of their weight in additional calcium each day; light did not enhance the rate of calcification.
27.	LeFurgey & St. Jean ⁶⁹	1976	Species diversity was approximately 20% higher and average number of living foraminifera was approximately 5 times greater in control ponds than in the effluent ponds.
28.	Röttger & Spindler ¹³⁰	1976	Studied the optimum condition for growth of <i>Heterostegina depressa</i> including the light intensity and the symbiotic algae; described the embryonic and nepionic developmental stages of the living individuals.
29.	Salami ¹³¹	1976	Studied the feed preference optimum for growth and reproduction (salinity range and temperature range), mode of reproduction, chamber addition, differences in size, number and arrangement of nuclei etc of <i>Trochammina cf. T. quadriloba</i>
30.	Ross ¹³²	1977	Size of the animal depends on the composition of food available; reproduction is adapted to seasonal changes in food.
31.	Schwab ¹³³	1977	Described the biology (size, colouration, behaviour and the ability to rapidly change shape) of a new foraminifera belonging to genus <i>Boderia</i> and family Lagynidae.
32.	Erez ⁸⁸	1978	Carbon isotopic composition of the foraminifera becomes more depleted under increased rate of photosynthesis by attached symbiont algae.
33.	Hallock ¹³⁴	1978	Studied the rate of carbon fixation by <i>Amphistegina lessonii</i> (in the light as well as in dark) and noted that carbon fixation in light was consistently higher than that in the dark.
34.	Rottger ¹³⁵	1978	Unusual multiple fission in the gamont of the larger foraminifera <i>Heterostegina depressa</i> ; observed regeneration following multiple fission during which a small residue of protoplasm remained within the vacated test.
35.	Angell ¹³⁶	1979	Studied the crystal growth during chamber development in <i>Rosalina floridana</i> ; also studied the calcium and carbonate uptake during the same developmental periods using tracer method.
36.	Lee <i>et al.</i> ¹³⁷	1979	The symbiosis is responsible for the comparatively larger size of the symbiont bearing benthic foraminifera.
37.	Lopez ⁵⁰	1979	The food intake varies as per the density of chloroplast; the chloroplast abundance varies as per changing light-dark conditions.
38.	Lee ⁴⁹	1979	Nutrition and physiology of foraminifera from littoral, sub littoral to temperate zones is discussed.
39.	Lee <i>et al.</i> ⁵²	1980	<i>Amphisorus hemprichii</i> and <i>Amphistegina lobifera</i> were photoinhibited above 200 klx illumination, while photoinhibition in <i>Amphistegina lessonii</i> and <i>Heterostegina depressa</i> occurred at lower than 10 klx light intensity.
40.	Hallock ⁵⁴	1981	Effect of light on growth rates of <i>Amphistegina lessonii</i> and <i>Amphistegina lobifera</i> are studied in the laboratory as well as the field conditions.
41.	McEnery & Lee ¹³⁸	1981	Three species of larger foraminifera <i>Amphistegina lobifera</i> , <i>Amphisorus hemprichii</i> and <i>Heterostegina depressa</i> were studied for their endosymbiotic associations and also fine structure analysis.
42.	Williams <i>et al.</i> ⁹¹	1981	Identified significant disequilibrium in carbon and oxygen isotopic fractionation in <i>Heterostegina depressa</i> and attributed it to the vital effects that varied with changing light intensity and age.
43.	Duguay ¹³⁹	1983	Calcium incorporation and photosynthetic carbon fixation was examined in three species of benthic foraminifera that harbor symbiotic microalgae.

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44.	Zimmerman <i>et al.</i> ¹⁴⁰	1983	<i>Heterostegina depressa</i> tests, secreted at increased light levels are depleted in heavier isotopes of oxygen and carbon, probably under the influence of symbiont photosynthetic activity.
45.	Bowser & Bloodgood ¹⁴¹	1984	Phase contrast light microscopy and membrane surface marker studies on two protozoan systems including that of <i>Allogromia laticollaris</i> and <i>Ammonia</i> sp. indicated that surface motility does not occur by a surf-riding/surf boarding mechanism.
46.	Kuile & Erez ⁵¹	1984	Growth rate decreases under dark conditions in symbiont bearing foraminifera; shell thickening occurs under turbulent conditions.
47.	Biekart <i>et al.</i> ¹⁴²	1985	Existence of two biologically different types of megalospheric <i>Heterostegina depressa</i> in laboratory cultures as well as Hawaiian sediments.
48.	Delaney <i>et al.</i> ¹⁴³	1985	Temperature dependence for the minor elemental composition of foraminiferal shells was investigated in the laboratory and by analysis of several planktic and one benthic foraminiferal species from sediment trap and sediment core samples.
49.	Hallock <i>et al.</i> ⁵⁵	1986	Influence of environment, especially availability of light and water motion on the test shape of <i>Amphistegina</i> .
50.	Röttger <i>et al.</i> ¹⁰⁴	1986	Proposed that the earlier considered schizont of <i>Heterostegina depressa</i> , in fact belonged to a new species.
51.	Kuile & Erez ¹⁴⁴	1987	Uptake of inorganic carbon and internal carbon cycling in symbiont bearing benthic foraminifera.
52.	Kuile <i>et al.</i> ¹⁴⁵	1987	Attempted to define the role of feeding in the carbon metabolism of the host-symbiont system in larger symbiont bearing foraminifera.
53.	Röttger ¹⁰⁵	1987	Describes and illustrates a new species of <i>Heterostegina</i> (<i>H. apogama</i> , n.sp.) based on the reproductive as well as morphological characteristics.
54.	Goldstein ¹⁴⁶	1988	Reported the alternation of generations in the life cycle of <i>Saccamina alba</i> Hedley.
55.	Grell ¹⁴⁷	1988	Reported the extreme heteromorphy in the alternative generations of monothalamous foraminifera <i>Heterotheca lobata</i> .
56.	Kuile & Erez ¹⁴⁸	1988	Established the existence of an internal inorganic carbon pool in the perforate foraminifer <i>Amphistegina lobifera</i> using ¹⁴ C tracer method.
57.	Buzas ¹⁴⁹	1989	No effect of mineralogically different sediments on the colonization potential of foraminifera.
58.	Buzas <i>et al.</i> ¹⁵⁰	1989	Conducted experiments on predation, substrate preference and colonization of benthic foraminifera at the Shelf break off the Ft. Pierce inlet, Florida.
59.	Röttger <i>et al.</i> ¹⁰⁸	1990	The gamonts and schizonts of <i>Calcarina gaudichaudii</i> vary in their test size, size of the proloculus and number of chambers.
60.	Röttger <i>et al.</i> ¹⁰⁶	1990	Observed the formation of megalospheric schizonts by a microspheric agamont for the first time, which verifies part of the hypothesis of biologic trimorphism.
61.	Boltovskoy ¹⁵¹	1991	Conducted laboratory experiments to study the destruction of foraminiferal tests.
62.	Faber & Lee ¹⁵²	1991	Studied the effect of feeding on the growth of foraminifera.
63.	Kuile & Erez ¹²¹	1991	Presence of internal carbon pool for calcification and partial contribution of carbon to this pool from the organic matter respiration.
64.	Lee <i>et al.</i> ³³	1991	Response to food was species specific as few species grew more when fed while others showed increased growth when provided with no food; symbiont bearing species could not survive prolonged darkness; additional nitrate and phosphate does not change the growth rate under certain conditions.
65.	Linke ³⁹	1992	Two survival strategies in benthic foraminifera based on the ATP content and metabolic rates, namely, the one that maintained uniform rate throughout the year, and those that showed seasonally varying ATP turnover rate.
66.	Pawlowski & Lee ¹⁰⁷	1992	Showed that <i>Rotaliella elatiana</i> has a classical heterophasic lifecycle, with a regular alternation of diploid agamontic phase and a haploid gamontic phase.
67.	Bernhard ⁴⁶	1993	No evident statistically significant effect of changing oxygen condition on the survival or ATP pool of foraminifera.
68.	Goldstein & Moodley ¹⁵³	1993	Life cycle of <i>Ammonia beccarii forma tepida</i> includes both sexual and asexual phases and is probably best characterized as a facultative alternation of generations.
69.	Wray <i>et al.</i> ¹¹¹	1993	Discussed the extraction and enzymatic characterization of foraminiferal DNA.

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Sr. No.	Author & Reference	Year of Publication	Study Details
70.	Chandler <i>et al.</i> ¹⁵⁴	1994	Utility of sediment microcosm cultures for the study of ontogenetic and sediment microhabitat effects on isotopic composition of benthic foraminifera.
71.	Goldstein & Corliss ¹⁵⁵	1994	Organic detritus, associated sediments as well as bacterial cells act as food for deep-sea and shallow-water species.
72.	Pawlowski <i>et al.</i> ⁹⁸	1994	Identified two species of <i>Glubratella</i> from eight morphotypes collected from the field, by using molecular systematic analysis.
73.	Pawlowski <i>et al.</i> ¹¹²	1994	Inferred that foraminifera branch close to the plasmodial and cellular slime molds in the eukaryotic evolutionary tree, which is in contrast to the fossil records.
74.	Alve & Bernhard ¹⁵⁶	1995	Studied the vertical migratory response of benthic foraminifera to controlled oxygen concentrations ranging from well-oxygenated to dysaerobic conditions in experimental mesocosm.
75.	Bresler & Yanko ⁷⁹	1995	Presence of unidentified organic compounds decreased the toxic effect of heavy metals on the <i>Pararotalia spinigera</i> and <i>Rosalina macropora</i> ; potential application of foraminifera for pollution monitoring owing to their response to xenobiotics.
76.	Hemleben & Kitazato ³⁴	1995	The culture without food survived for longer duration but reproduced less than the ones maintained under continuous food supply.
77.	Kitazato ¹²³	1995	<i>In situ</i> recolonization experiments to understand the possible substrate preferences of deep sea benthic foraminifera; faunal density was much lower and mainly confined to the natural sediment deposited over the artificial substrate.
78.	Linke <i>et al.</i> ¹⁵⁷	1995	The response of deep sea benthic foraminifera to a simulated sedimentation was assessed in a strip-board microorganism by using TEM (Transmission Electron Microscopy) Organic Carbon, Adenosine Nucleotide, ETS assay and line observation.
79.	Pawlowski <i>et al.</i> ¹¹³	1995	Identified three species of <i>Ammonia</i> based on the partial sequences of large subunit ribosomal DNA from six morphotypes of <i>Ammonia</i> ; all the six morphotypes had distinct LSU rDNA.
80.	Wray <i>et al.</i> ⁹⁹	1995	Concluded that the foraminifera were derived from a heterokaryotic flagellated marine protist, probably sometime in the later Proterozoic, based on the cytological features and the DNA sequences of <i>Ammonia</i> .
81.	Bernhard & Alve ⁴⁷	1996	Survival rate of <i>Adercotryma glomeratum</i> , <i>Psammosphueru bowmuni</i> and <i>Stainforthia fusiformis</i> subjected to anoxic conditions does not vary much from the control specimens; however the ATP concentrations were significantly lower. <i>Bulimina marginata</i> behaved differently.
82.	Chandler <i>et al.</i> ⁸⁹	1996	Determined the sediment microhabitat effects on carbon isotopic signatures of microcosm-cultured benthic foraminifera <i>Ammonia beccarii</i> .
83.	Holzmann <i>et al.</i> ¹⁵⁸	1996	Sequence variations in the large- subunit ribosomal RNA gene of <i>Ammonia</i> (foraminifera, Protozoa) and their evolutionary implications.
84.	Nigam <i>et al.</i> ¹⁵⁹	1996	Food and type of media controls the growth in <i>Rosolina leei</i> .
85.	Pawlowski <i>et al.</i> ¹⁰⁰	1996	Foraminifera were probably the first eukaryotes to branch off from the main eukaryotic tree.
86.	Fahrni <i>et al.</i> ¹⁰⁹	1997	<i>Miliammina fusca</i> is porcellaneous and not agglutinated as suggested before.
87.	Holzmann & Pawlowski ¹¹⁴	1997	Identified two species of <i>Ammonia</i> based on the molecular, morphological and ecological evidence.
88.	Pawlowski <i>et al.</i> ¹⁰¹	1997	Confirmed monophyletic origin of foraminifera.
89.	Holzmann <i>et al.</i> ¹¹⁷	1998	Identified two <i>Ammonia</i> sp based on the differences in the partial sequencing of large subunit ribosomal DNA, but the species could not be identified morphologically.
90.	Moodley <i>et al.</i> ⁴²	1998	Few foraminifera can survive under anaerobic conditions; soft-shelled foraminifera are less tolerant to anoxia.
91.	Moodley <i>et al.</i> ¹²²	1998	Sulphidic conditions resulted in significant reduction of foraminiferal density; none of the species reproduced under sulphidic conditions.
92.	Wilson-Finelli <i>et al.</i> ⁹⁰	1998	While <i>Cibicides pachyderma</i> incorporated the changing carbon isotopic signal of the medium, <i>Uvigerina peregrina</i> ¹⁸ O was relatively enriched, in contrast to the field studies.
93.	Alve & Olsgard ⁷³	1999	Extreme copper contaminated sediments does not defer foraminifera from colonization; no correlation between copper contamination and abundance of abnormal specimens.

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Table 1—Foraminiferal culture studies on benthic foraminifera for paleoclimatic implications—*Contd.*

Sr. No.	Author & Reference	Year of Publication	Study Details
94.	Stouff <i>et al.</i> ⁶⁴	1999	Increased number of abnormal <i>Ammonia beccarii</i> and <i>Ammonia tepida</i> specimens under hypersaline conditions; abnormalities similar to those reported from similar environments in field.
95.	Stouff <i>et al.</i> ⁶⁵	1999	Though abnormal specimens were also present under normal conditions, hypersaline conditions lead to the increased abundance of abnormal specimens.
96.	Gross ⁴⁵	2000	Species-specific effect of change in temperature, oxygen and food quantity on the migrational activity.
97.	Gustafsson <i>et al.</i> ⁷⁸	2000	Introduction of small amount of Tri-n-Butyltin lead to increased population density, probably due to reduced predation; higher concentration had adverse effect.
98.	Holzmann ¹⁶⁰	2000	Deciphered the subspecies of <i>Ammonia</i> through molecular systematics.
99.	Moodley <i>et al.</i> ²⁹	2000	<i>Ammonia</i> responded best to the freshly added phytodetritus.
100.	Nigam & Caron ⁵⁹	2000	The pairing, probably a requisite for sexual reproduction in <i>Rosalina leei</i> , was affected by the seawater temperature.
101.	Toyofuku <i>et al.</i> ⁹³	2000	Concluded that monospecific Mg/Ca can be used to infer paleotemperature, based on culture of <i>Planoglabratella opercularis</i> (d'Orbigny) and <i>Quinqueloculina yabei</i> Asano under controlled conditions; salinity does not have significant effect on the foraminiferal Mg/Ca.
102.	Tsuchiya <i>et al.</i> ¹¹⁵	2000	Ribosomal DNA sequence studies show that the single specimens of <i>Glabratellidae</i> are genetically less diverse as compared to <i>Ammonia</i> .
103.	Havach <i>et al.</i> ⁹²	2001	Ba/Ca and Cd/Ca partitioning coefficients of <i>Bulimina marginata</i> , <i>Cibicidoides pachyderma</i> and <i>Uvigerina peregrina</i> were within the range observed from the field.
104.	Heinz <i>et al.</i> ⁴³	2001	Benthic foraminiferal abundance increased under increased food supply and oxygen; the within sediment migration was controlled by the availability of oxygen.
105.	Heinz <i>et al.</i> ¹⁶¹	2002	Time series experiment to investigate the response of cultures deep sea benthic foraminifera to simulated phytodetritus pulses under stable oxygen concentrations.
106.	Moodley <i>et al.</i> ³⁰	2002	Differential response of benthic foraminifera to induced phytodetritus.
107.	Pawłowski <i>et al.</i> ¹¹⁸	2002	Identified 49 Allogromids species belonging to 28 genera/families, from the 27 morphotypes, collected from Explorers Cove, McMurdo Sound, Antarctica, based on 135 partial small-subunit ribosomal DNA sequences.
108.	Cadre <i>et al.</i> ⁶	2003	Temporary acidification of the environment can cause morphological abnormalities in the <i>Ammonia beccarii</i> foraminiferal tests during recalcification.
109.	Saraswat <i>et al.</i> ¹⁶²	2003	Proposed that three species of <i>Pararotalia</i> (<i>P. nipponica</i> , <i>P. ozawai</i> , <i>P. taiwanica</i>) are probably one, based on base pair length of 12 S mitochondrial gene.
110.	Duijnstee <i>et al.</i> ¹⁶³	2003	Anoxic conditions lead to the comparatively shallower dwelling depth for most of the species.
111.	Tsuchiya <i>et al.</i> ¹¹⁶	2003	Identified two different species of <i>Planoglabratella opercularis</i> by sequencing internal transcribed spacers of ribosomal DNA.
112.	Ward <i>et al.</i> ⁷²	2003	<i>Haynesina germanica</i> did not consume sewage derived particulate organic matter; it might have fed only bacteria associated with sewage POM.
113.	Witte <i>et al.</i> ³⁶	2003	Abyssal foraminiferal response to phytodetritus was delayed and distinct from continental slope foraminifera.
114.	Fujita ¹⁶⁴	2004	Field colonization experiment using artificial substrate was conducted to examine the small scale distribution of algal symbiont bearing larger foraminifera on reef rubble.
115.	Geslin <i>et al.</i> ⁴⁴	2004	<i>Globobulimina affinis</i> , <i>Hoeglundina elegans</i> , <i>Pyrgo murrhina</i> , <i>Uvigerina peregrina</i> , <i>Uvigerina mediterranea</i> can all live in the oxic sediment layer, whereas <i>G. affinis</i> can also live under anoxic conditions; oxygen concentration regulates the microhabitat.
116.	Maréchal-Abram <i>et al.</i> ⁹⁶	2004	Reported cadmium partitioning coefficient value close to one for <i>Ammonia beccarii</i> under one set of conditions, and opined that cadmium does not segregate in the foraminiferal carbonate from the surrounding water; deviation in other sets was attributed to presence of food material.
117.	Saraswat <i>et al.</i> ⁷⁶	2004	Incorporation of mercury in the ambient environment of <i>Rosalina leei</i> lead to retarded growth and abnormal specimens.
118.	Williams & Hallock ⁵³	2004	The growth rate of <i>Amphistegina</i> increased in blue light while was not affected by ultra-violet light towards the lower end.

Contd...

Table 1—Foraminiferal culture studies on benthic foraminifera for paleoclimatic implications—*Contd.*

Sr. No.	Author & Reference	Year of Publication	Study Details
119.	Ernst <i>et al.</i> ²⁸	2005	Though oxygen availability affected the short term vertical distribution and density of benthic foraminifera, food content was responsible for shaping the long-term benthic foraminiferal assemblages.
120.	Langezaal <i>et al.</i> ³¹	2005	<i>Allogromia laticollaris</i> and <i>Ammonia beccarii</i> could distinguish between food (living and dead bacteria) and non-food (inorganic particles) material; inter- and intra specific variation in the uptake rate and final digestion of food.
121.	Nomaki <i>et al.</i> ³⁷	2005	Shallow infaunal species (<i>Uvigerina akitaensis</i> , <i>Bulimina aculeata</i>) assimilated more carbon as compared to the intermediate (<i>Textularia kategatensis</i>) and deep infaunal species (<i>Chilostomella ovoidea</i>); response varied as per the food and season.
122.	Nomaki <i>et al.</i> ³⁸	2005	Vertical migration in response to addition of food; response decreased from shallow infaunal to deep infaunal species; <i>Chilostomella ovoidea</i> does not respond at all.
123.	Cadre & Debenay ⁷⁵	2006	Copper contamination resulted in delayed chamber formation and reproduction, thus reducing the abundance of two species of <i>Ammonia</i> ; abnormal tests increased in number.
124.	Ernst <i>et al.</i> ⁷⁴	2006	Faunal density decreased significantly in oil induced microcosms; few species reproduced quickly under polluted environment.
125.	Hintz <i>et al.</i> ⁹⁴	2006	Large difference in the Mg, Ba, Cd, Sr versus Ca partitioning coefficients of <i>Rosalina vilardeboana</i> and <i>Bulimina aculeata</i> .
126.	Hintz <i>et al.</i> ⁹⁵	2006	Sr/Ca partitioning coefficient of <i>Bulimina aculeata</i> was not affected by the ontogenetic development, whereas large variation was observed in Mg/Ca partitioning between different individuals, as well as at different developmental stages in the same individual.
127.	Nigam <i>et al.</i> ⁶⁶	2006	<i>Pararotalia nipponica</i> (Asano) shows reduced growth at lower salinities and tests start dissolving at very low salinity.
128.	Nomaki <i>et al.</i> ⁴⁰	2006	Recognized three types of food preference, viz. (1) fresh phytodetritus selectively (phytophagous species); (2) fresh phytodetritus selectively but sedimentary organic matter as well when phytodetritus is absent; and (3) sedimentary organic matter at random (deposit feeders).
129.	Topping <i>et al.</i> ⁷¹	2006	No direct effect of sewage-derived particulate organic matter (POM) on the food sources and diets of <i>Ammonia beccarii</i> and <i>Haynesina germanica</i> ; sewage POM was not used as food source.
130.	de Nooijer <i>et al.</i> ⁹⁷	2007	Copper partitioning coefficient was constant in <i>Ammonia tepida</i> and symbiont-bearing <i>Heterostegina depressa</i> over a large range of seawater Cu/Ca and was not affected by the seawater salinity, temperature or presence of symbionts.
131.	Grimm <i>et al.</i> ¹¹⁹	2007	Reported highly divergent genotypes among <i>Chilostomella</i> collected from different geographical locations, based on sequencing of 3' region of the small subunit ribosomal RNA (SSU rDNA), 5.8 subunit and the internal transcribed spacers.

under high pressure and low temperature conditions paved the way for laboratory culturing of deep-sea benthic foraminifera²¹.

However, the laboratory culture response should be taken with care as significant differences have been observed in the species behaviour under similar conditions²². Schnitker²³ observed that under laboratory culture, specimens of *Triloculina linneiana* attained sexual maturity at one-eighth the size of the parent specimens recovered from the field and were morphologically different from the parents.

1. Studies on the factors affecting abundance and morphology

Temporal changes in the benthic foraminiferal abundance and morphology are the most commonly

used foraminiferal characteristics^{1,2,24} for assessment of present and past environments. However, despite an apparent link between abundance, morphology and ecological parameters, how much change in a particular parameter will bring a specific change in the faunal characteristics, is still not clear²⁵. The morphological changes from the field have almost always been assigned to the circumstantial ecological stress including both natural extreme physico-chemical conditions and induced pollutants⁵, with a lack of understanding of precise cause of specific morphological changes. Contrasting results from the field have further complicated the issue²⁶. Therefore numerous culture studies have been carried out to understand the factors that bring out a known change in the benthic foraminiferal abundance and morphology.

A. Effect of type and amount of food

Significant seasonal differences in the foraminiferal population and assemblage^{25, 27}, lead to the belief that changes in the type and amount of food may be one of the factors responsible for the changes in the foraminiferal population. Therefore, it was imperative to understand the effect of changes in the phytodetritus on the benthic foraminiferal population.

Based on foraminiferal culture studies it was observed that long-term changes in the foraminiferal diversity and abundance were brought by the amount of food and the response was species specific. Within the same genus, certain species preferred live food whereas others were found to thrive well when fed on dead cells⁴. Ernst *et al.*²⁸ observed that the foraminiferal response to the amount of dissolved oxygen and food was species specific wherein certain species (*Stainforthia fusiformis*, *Nouria polymorphinoides*, *Hopkinsina pacifica*, *Nonionella turgida*) responded quickly to the changes in the dissolved oxygen while the others (*Caronia silvestrii*, *Epistominella vitrea*, *Acostata mariae*) responded only to the changes in the amount of food. The food uptake rate, as well as the ratio of accumulated to digested quantity of food, changed from species to species and also for different sized individuals of the same species²⁹⁻³¹. The study can help to understand the changes in the species assemblages and the abundance of certain species under changing oxygen and food conditions in the field. 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^{32,33}. However, the scarcity of food lead to longer survival rate as the reproduction was delayed³⁴. The study can help understand the reduced abundance of few species under low productivity conditions. The response to additional essential nutrients, nitrate or phosphate, was not only species specific but also was different under different light and food conditions. While *Amphistegina lobifera* does not respond to changes in nitrate and phosphate, *Marginopora kudakajimensis* showed maximum growth under illuminated, nutrient enriched and well fed conditions³³.

The type of food also affected the growth rate as well as the survival of benthic foraminifera^{15, 33}. Lee and Muller³⁵ noted that *Allogromia laticollaris*, *Rosalina leei* and *Spiroloculina hyalina* were

selective feeders preferring only few algal species. Furthermore, these species can adjust well with the changes in the microbial community structure. The essential presence of bacteria for favorable growth was reported by Lee *et al.*³³

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. Witte *et al.*³⁶ noticed that 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. Nomaki *et al.*³⁷ studied the carbon assimilation rate of benthic foraminiferal species under *in situ* experiments and noted that shallow infaunal species (*Uvigerina akitaensis*, *Bulimina aculeata*) assimilated more carbon as compared to the intermediate (*Textularia kattedgatensis*) and deep infaunal species (*Chilostomella ovoidea*). Here also, the response varied within the same species and also species to species subject to different types of food during different seasons. It thus explains the changing abundance and diversity during different seasons and in different geographical regions. The arrival of food has increased impact on the shallow infaunal species as compared to the deep infaunal species, while few species do not respond at all³⁸.

Linke³⁹ identified two survival strategies in benthic foraminifera based on the adenosine-tri-phosphate (ATP, a measure of feeding activity) content and metabolic rates, namely, the one that maintained uniform rate throughout the year and those that showed seasonally varying ATP turnover rate. The latter group of species will increase in abundance and respond well to the increased phytodetritus input. Different feeding preferences and mechanisms in benthic foraminifera were identified by Nomaki *et al.*⁴⁰, who reported that benthic foraminifera prefer at least three types of food (1) fresh phytodetritus, selectively (phytophagous species, namely *Uvigerina akitaensis*, *Bolivina spissa*, *Bolivina pacifica*); (2) fresh phytodetritus, selectively but sedimentary organic matter as well, when phytodetritus is absent (seasonal-phytophagous species, namely *Bulimina aculeata*, *Textularia kattedgatensis*, *Globobulimina affinis*); and (3) sedimentary organic matter at random (deposit feeders, namely *Cyclammina cancellata*, *Chilostomella ovoidea*). The response of benthic foraminifera to phytodetritus under controlled

laboratory culture studies has definitely helped to understand the changing abundance of different species in the field.

B. Effect of oxygen concentration

The amount of phytodetrital material reaching to the seafloor is one of the factors that regulate the concentration of dissolved oxygen in the bottom water and pore water, the regions inhabited by benthic foraminifera. Therefore, food and oxygen have been suggested as two important parameters that define the microhabitat of benthic foraminifera⁴¹. The relative influence of food and oxygen concentration on benthic foraminiferal community is debated.

Moodley *et al.*⁴² noted that several foraminiferal species can survive under anoxic conditions and soft-shelled foraminifera were comparatively less tolerant to anoxia. Heinz *et al.*⁴³ noted increased population density under high oxygen and food condition and that the migration of species within the sediments was controlled by the availability of oxygen. Geslin *et al.*⁴⁴ also noted that the oxygen concentration defined the epifaunal or infaunal habitat of benthic foraminifera and further that though few species were strictly oxic, certain others could tolerate both oxic and anoxic conditions, probably explaining the changing abundance of benthic foraminifera under changing oxygen conditions in the field. Changes in oxygen concentration also result in considerable change in the subsurface distribution of benthic foraminifera as well as the migrational capability of benthic foraminifera⁴⁵. However, Bernhard⁴⁶ did not report any statistically significant change in the foraminiferal survival rate or the adenosine-tri-phosphate content of the foraminifera subjected to different oxygen levels. But in a subsequent study Bernhard & Alve⁴⁷ reported significantly reduced ATP concentrations in species subjected to anoxic conditions.

C. Effect of light and symbionts

Symbionts are one of the essential aspects of certain benthic foraminifera and their possible influence on foraminifera has been discovered long ago⁴⁸. The photosynthetic activity of symbionts depends on the light conditions, which vary with the seasons and depth, in the marine habitats. Therefore, food intake of certain algal symbiont bearing benthic foraminiferal species is affected by the changes in the light intensity. Thus, in laboratory culture experiments carried out to understand the effect of light intensity on the benthic foraminifera, much

emphasis is given to the symbiont bearing benthic foraminiferal species.

Lee *et al.*⁴⁹ suggested that the presence of symbionts in the foraminiferal tests was responsible for the larger size attained by certain benthic foraminifera. Differences were noted in the response of symbiont bearing benthic foraminiferal species and the ones devoid of symbionts, to food. It was reported that the food intake by certain symbiont bearing benthic foraminifera was proportional to the density of chloroplast present, whose abundance changed significantly with the changing light-dark conditions⁵⁰. Kuile & Erez⁵¹ showed that the growth rate decreased significantly under dark conditions in symbiont bearing benthic foraminiferal species, whereas Lee *et al.*³³ reported that the symbiont bearing species could not survive prolonged darkness. Photoinhibition also varied from species to species. While the *Amphisorus hemprichii* and *Amphistegina lobifera* were photoinhibited above 200 klx illumination, similar phenomena was observed in *Amphistegina lessonii* and *Heterostegina depressa* at lower than 10 klx light intensity⁵². Williams & Hallock⁵³ simulated the bleaching conditions in laboratory and noted that the growth rate of *Amphistegina gibbosa* increased considerably under blue light while ultra-violet light towards the lower wavelength does not have any apparent effect on the growth rate; however, higher end UVB considerably reduced the growth.

Except the survival and growth rate, light intensity also affect the morphology of the benthic foraminiferal tests. Growth rate initially decreased and the growth stopped slowly, when *Heterostegina depressa* were subjected to very high light intensity. The reduction in light intensity resulted in reduction in growth as well as test thickness to diameter ratio of various species of *Amphistegina*^{54, 55}. Additionally the rapidly growing tests under low light conditions tend to be comparatively more fragile and weaker²². In a significant study the growth pattern of *Heterostegina depressa* changed, once it was subjected to low illumination or complete darkness. Interestingly, different specimens showed different rate and pattern of recovery from the temporary cessation of growth under low light intensity⁵⁶.

D. Effect of seawater temperature

Seawater temperature is one of the important parameters required to understand the global climatic

changes. Therefore benthic foraminiferal characteristics have increasingly been refined to track past seawater changes. In view of this many laboratory culture studies have focused on understanding the response of benthic foraminifera to changing seawater temperature.

Laboratory culture experiments show that the temperature response of benthic foraminifera as well as the lethal temperature limit is species specific³². The optimum temperature for a species may be anywhere between the lower and higher temperature extremes under which the species are reported from the field¹³. Comparatively lower seawater temperature (<10°C) resulted in lower growth rate and cessation of reproduction in few rotalid species^{57,32}. Death of specimens was the extreme effect of temperature lower than lower thermal limits, this together with the cessation of reproduction explain the reduced abundance of certain species during the colder periods⁵⁸. The growth rate was found to be significantly low in the *Heterostegina depressa* specimens subjected to low temperature. However it does not affect the size of the chambers and in turn the shape of the test⁵⁶. The growth rate increased with increasing temperature within the temperature tolerance limits but larger size was attained by specimens subjected to comparatively lower seawater temperature^{33,57}. The lower temperature has adverse effect on reproduction¹¹. Effect of seawater temperature on the sexual reproduction was explored by Nigam & Caron⁵⁹ who observed a direct relationship between pairing in *Rosalina leei* and the seawater temperature (15°C- 15.3%, 20°C- 17%, 25°C- 19.3% pairing); however no reproduction was observed in these paired specimens under laboratory culture. Change in seawater temperature also affected the migrational capability of benthic foraminifera, though the response was different for different species⁴⁵.

E. Effect of seawater salinity

Change in the seawater salinity is the major factor that controls the benthic foraminiferal population and species diversity in the coastal near-shore regions. The salinity changes in these regions are mainly controlled by the fresh water input from the adjacent continental regions. The fresh water input varies as per the changes in the rainfall intensity. Thus the temporal changes in benthic foraminiferal characteristics from the shallow water regions have

been used as potential proxy to understand monsoon intensity in the past⁶⁰. However, differences in the living and dead population lead to the belief that post-depositional taphonomic processes may alter the benthic foraminiferal diversity and distribution in the marginal marine areas⁶¹ thus altering the original signatures. As mentioned above, one important physical parameter having potential to influence the benthic foraminiferal population in the marginal marine areas is seawater salinity⁶². Therefore, laboratory culture studies have also been carried out to understand the changes in benthic foraminiferal characteristics under different salinity conditions.

Usually the salinity tolerance limit of benthic foraminifera is wider than the thermal tolerance limit⁵⁸. Both higher (30.2‰) and lower (26.8‰) than optimum salinity resulted in reduced growth, providing a possible explanation for the stunted specimens reported from the field from the regions that are subjected to increased salinity⁴. Extreme salinities (<13‰ and >40‰) also lead to delay or absence of reproduction^{32,57}. However, Freudenthal *et al.*⁶³ opined that the higher salinity (36-50‰) is correlated with early reproduction. Though abnormal specimens were reported at normal salinity (37‰) also, increased abundance of abnormal specimens was reported under hypersaline (50‰) conditions. However, the type of abnormality was different in both the cases; while the abnormalities in the specimens under normal saline conditions included a double test, protruded spiral side or abnormally arranged first few chambers, the hypersaline conditions lead to abnormal proloculus, abnormally oriented coiling plane of initial chambers, multiple whorls originating from proloculus and fusion of juveniles^{64,65}. Nigam *et al.*⁶⁶ noted that the decreased salinity (<33‰) decreased the growth rate of *Pararotalia nipponia*. Significantly lower salinity (10-15‰) lead to the dissolution of the tests, probably due to the associated decline in the seawater pH. The salinity effect studies are helpful in assessing the changing monsoon intensity based on the changes in benthic foraminiferal abundance, diversity and morphology.

F. Effect of seawater pH

The seawater pH ranges from 7.5 to 8.5, well above the acidic range. The calcareous foraminiferal tests are sensitive to seawater pH and changes in seawater pH may lead to dissolution of the calcareous tests. A

significant decline in the calcareous benthic foraminiferal diversity and abundance, after deposition of the tests, was attributed to differential dissolution probably as a result of lower than normal pH of the pore water or destruction of the tests due to current activity⁶¹. Thus efforts have been made to understand the role of seawater pH on the benthic foraminifera.

The benthic foraminiferal response to changes in seawater pH is also species specific like the other physical parameters, with few species being very sensitive to slight change in pH while other tolerating a wide pH range³². Neutral pH leads to the dissolution in the foraminiferal tests and the dissolution starts from the last chamber and slowly the complete tests start dissolving. An interesting finding is that the specimens are able to regenerate the test, if subjected to lower than normal pH for only a short duration; however the regenerated tests are abnormal⁶. McEnery & Lee⁶⁷ also reported the regenerative capability of *Rosalina leei* and *Spiroloculina hyalina*. Angell⁶⁸, based on the laboratory culture experiments on *Rosalina floridana* concluded that all those species that secrete an additional calcite layer over the whole test, every time a new chamber is formed, can recuperate from the dissolution incurred as a result of acidic pH. However, no separate specific mechanism especially to overcome dissolution or physical injury to the test was observed. These laboratory culture studies helped to understand the probable cause of increased abundance of abnormal species from certain location at present as well as at certain level in the geologic past. However, additional efforts are required to assign specific abnormalities to specific change in salinity or any other parameter.

G. Pollutants

Differences in the foraminiferal characteristics, including changes in abundance and diversity, as well as increased abundance of abnormal specimens, have been noted from polluted environments. However, most of these observations were based on the circumstantial presence of induced pollutants. Similar effect in the benthic foraminiferal diversity and abundance has also been reported from naturally ecologically stressed environments, making it difficult to apply these benthic foraminiferal characteristics to infer past environmental conditions^{5,66}. Thus laboratory culture studies have been carried out to understand the effect of pollutants on the benthic foraminiferal abundance, diversity and morphology.

Initial laboratory culture studies showed that introduction of pollutants in the ambient environment of the benthic foraminifera, especially shallow water forms, leads to significant decline in the density as well as diversity. LeFurgey & St. Jean⁶⁹ noted that the benthic foraminiferal population as well as the species diversity significantly decreased after the introduction of sewage effluents. Though clear differences have been noted in case of faunal density and morphology in the sewage affected and normal field environments⁷⁰, Topping *et al.*⁷¹ observed no effect of sewage derived particulate organic matter on the food source or diet of *Ammonia beccarii* and *Haynesina germanica*. Ward *et al.*⁷² also noted that *Haynesina germanica* does not feed on sewage derived particulate organic matter. The findings could not resolve how the sewage discharge affects the foraminifera. Additionally Alve & Olsgard⁷³ showed that the extreme copper concentration (>200ppm) also, does not defer the foraminifera from colonizing the polluted sediments. Even no correlation was observed in the abundance of abnormal specimens and copper contamination.

However, further laboratory culture studies showed the effect of pollutants on the reproduction in benthic foraminifera. Few species reproduce quickly, when subjected to oil polluted seawater⁷⁴. However, in another study Cadre & Debenay⁷⁵ observed significant reduction in the growth rate as well as reproduction, in *Ammonia* (*Ammonia beccarii* and *Ammonia tepida*) under high copper (200µg/l) contaminated conditions. Number of juveniles also reduced considerably and more number of abnormal tests was observed. Saraswat *et al.*⁷⁶ and Ernst *et al.*⁷⁴ also noted increased number of abnormal forms under polluted conditions (experimentally induced mercury and oil pollution respectively). The studies clearly explain the field based findings by Yanko *et al.*⁷⁷, reporting decreased faunal density, more number of stunted and deformed benthic foraminiferal specimens from polluted environments.

However, in an interesting study, Gustafsson *et al.*⁷⁸ noted that the foraminiferal abundance increased after the introduction of small amount (0.02 mmol/g) of Tri-n-butyltin, probably due to the adverse effect of TBT on predators. However, increased TBT concentration (2.00 mmol/g) resulted in an adverse effect on benthic foraminifera. An example of interaction between different types of pollutants and resultant effect on foraminifera was seen by Bresler &

Yanko⁷⁹. It was observed that the presence of unidentified natural organic compounds in the seawater medium decreased the toxic effect of heavy metals on the benthic foraminifera. It can probably explain the noted differences in the foraminiferal response at different locations that have similar levels of heavy metal pollution.

H. Effect of reproduction on the test morphology

Species identification in foraminifera is entirely based on the morphology. Morphological basis of species identification has led to the recognition of individuals with slight morphological differences as separate species, while individuals with large differences have sometimes been clubbed as same species. Initial laboratory culture studies revealed a link between mode of reproduction and morphological differences between different ontogenetic stages of the individuals of the same species. Though, the differences in number of chambers, proloculus size and overall test size were noted in almost all the species maintained in laboratory throughout their life-cycle, Myers⁸⁰ observed a potential link between the mode of reproduction and coiling direction in *Spirillina vivipara*. Later on Myers⁸¹ reported that megalospheric specimens preferentially coiled sinistrally while the microspheric ones coiled dextrally in *Discorbis patelliformi*. In a similar study Lee *et al.*⁸² observed that the coiling direction in *Rosalina floridana* was affected by the nutrition and life-cycle, with gamontic generations being predominantly dextral while the agamonts being preferably left coiled. As, such morphological changes might possibly be attributed to climatic changes, laboratory culture studies helped to outline the effect of mode of reproduction on coiling direction of individuals of certain species.

I. Other factors affecting the abundance and morphology

Besides the studies discussed above, that refined the understanding of various factors which affect benthic foraminiferal diversity, abundance and morphology; laboratory culturing of benthic foraminifera also revealed certain other factors/processes that may influence the benthic foraminiferal characteristics as observed in the field. Myers⁸³ observed that the large tests of *Elphidium crispum* evade destruction during the ingestion by larger macrofauna and calculated that ~1000 tests per

square foot per year are contributed to the sediments. Reproduction occurred only during the beginning of March. An interesting finding was that the growth during different seasons can be differentiated on the basis of change in chamber morphology, thus providing a potential technique to infer the relative strength or duration of different seasons during the geologic past.

2. Studies that helped understand the factors affecting chemical composition

Though, stable isotopic and elemental composition of benthic foraminiferal tests has been developed as potential technique to infer past seawater temperature, salinity, productivity etc, a complete understanding of factors affecting the chemical composition of the tests is still lacking^{84,85}. Thus laboratory culture studies have been carried out since long to understand the role of different physico-chemical parameters on the chemical composition of the foraminiferal tests. Much of the information about the effect of different physico-chemical parameters and vital factors on the foraminiferal chemical composition has been obtained by culturing benthic foraminifera under controlled laboratory conditions and has thus refined the paleoclimatic/paleoceanographic application of benthic foraminiferal chemical composition.

A. Studies carried out to understand the factors affecting stable oxygen and carbon isotopic composition of the tests

Though stable isotopic composition of foraminiferal test was considered as potential proxy for past seawater temperature, salinity, productivity and circulation changes depending upon the location and type of species, disequilibrium in the precipitation of CaCO₃ by benthic foraminifera, as compared to the ambient seawater, was noted by many workers^{86,87}. Thus laboratory culture studies under controlled physico-chemical conditions were carried out to understand the various factors that control the stable oxygen and carbon isotopic composition of benthic foraminifera.

Erez⁸⁸ assigned the disequilibrium between foraminiferal and seawater carbon isotopic composition to the incorporation of lighter carbon resulting from the increased photosynthesis by symbiotic algae. Not only the bottom water but also the pore water carbon isotopic composition significantly influences the carbon isotopic signal of

the benthic foraminifera. But the carbon isotopic composition of benthic foraminifera is different than both the pore water and bottom water carbon isotopic composition⁸⁹. Wilson-Finelli *et al.*⁹⁰ noted that the carbon isotopic signal of *Cibicidoides pachyderma* reflected the changing seawater chemistry to some extent. The oxygen isotopic composition of one of the most frequently used benthic foraminiferal species *Uvigerina peregrina* was found to be consistently enriched relative to the medium, thus questioning the use of its oxygen isotopic composition for paleoceanographic studies. Similarly *Buliminella marginata* and *Discorbinella* sp. were not able to record the oxygen isotopic signal of the seawater at all. Williams *et al.*⁹¹ reported significant disequilibrium in carbon and oxygen isotopic fractionation in *Heterostegina depressa*, which changes as per the light intensity and age. As the species has symbionts, the disequilibrium was suggested as a result of exchange of carbon and oxygen during various metabolic activities of symbiont and host.

In comparison to planktic foraminifera limited studies have been carried out to understand the factors controlling the stable isotopic composition of the benthic foraminifera, probably because of the difficulty in maintaining the constant physico-chemical parameters throughout the duration of the experiment under laboratory conditions.

B. Studies carried out to understand the factors affecting elemental composition of benthic foraminiferal tests

Like the stable oxygen and carbon isotopic composition, the elemental ratios of the foraminiferal tests has also been established as potential proxies for paleoceanographic and paleoclimatic interpretation. Laboratory culture studies were carried out to understand the factors controlling the partitioning of these elements in the foraminiferal tests as well as to develop numerical relationship between physical parameter and concentration of element in the foraminiferal tests.

The Ba/Ca, Cd/Ca partitioning coefficient for *Bulimina marginata*, *Cibicidoides pachyderma* and *Uvigerina peregrina* under laboratory culture was nearly similar to that obtained from core-top calibrations in the field. However, large uncertainty was reported in Cd/Ca incorporation, probably reflecting the habitat effect. Huge water pressure does

not play any role in the trace element partitioning in the benthic foraminifera⁹². Toyofuku *et al.*⁹³ established the application of Mg/Ca of *Planoglabratella opercularis* (d'Orbigny) and *Quinqueloculina yabei* for paleotemperature reconstruction based on laboratory culture study. The salinity had insignificant effect on the Mg/Ca incorporation in the studied species.

However, laboratory culture experiments have not always been able to resolve the uncertainties as reported from the field. The uncertainty in the Mg, Sr, Cd, Ba versus Ca partitioning in *Bulimina aculeata* was as large or even more than that reported from the field. Additionally the inter-individual variation was larger than the analytical precision. Inter-species variability was also observed as the partitioning coefficients for *Rosalina vilardeboana* were significantly different than that of *Bulimina aculeata*⁹⁴. The ontogenetic development has element specific effect on the partitioning in benthic foraminifer. While the Sr/Ca partitioning co-efficient remained uniform throughout the different stages of development of *Bulimina aculeata*, large variation was observed in Mg/Ca partitioning co-efficient⁹⁵. Maréchal-Abram *et al.*⁹⁶ reported Cd/Ca partitioning coefficient value of 1 for *Ammonia beccarii* under one set of conditions. However deviation was reported in other sets and was attributed to the presence of foreign food material. In a recent study, de Nooijer *et al.*⁹⁷ reported that the copper partitioning coefficient in two benthic foraminiferal species was constant over a large range of seawater Cu/Ca concentrations and was not affected by the change in temperature and salinity of the seawater. As one of these species has symbionts, the similarity in the copper partitioning co-efficient of these two species showed that presence of symbionts does not affect the Cu partitioning in these species. The study has far reaching implications for the heavy metal pollution monitoring in coastal areas by using benthic foraminiferal elemental composition.

3. Studies that refined evolutionary position of foraminifera

An important application of benthic foraminifera is for correlation of oil bearing stratigraphic datums from different parts of the world. This application arises from the large geographic but short geologic range of benthic foraminiferal species. One application of molecular systematic analysis is the

comparison of genetic make up of a group with others in order to find closeness or differences that in turn provide idea about the evolution of the group.

Pawlowski *et al.*⁹⁸, based on the sequencing of large subunit rDNA of four benthic species (*Ammonia tepida*, *Rosalina vilardeboana*, *Glabratella erecta*, and *Trochammina* sp.), inferred that the foraminifera evolved along with the plasmodial and cellular slime molds, much earlier than that suggested by the fossil record. However, in a subsequent study, based on the molecular systematic analysis of *Ammonia* sp., Wray *et al.*⁹⁹, showed that the foraminifera originated from heterokaryotic flagellated marine protist, probably sometime in the later Proterozoic. The findings were in contrast to the previously held belief that foraminifera originated from amoeba like ancestor. Later on Pawlowski *et al.*¹⁰⁰ confirmed the early foraminiferal evolution among the eukaryotic group, based on the sequencing of small sub unit rDNA genes of three species of foraminifera (*Ammonia beccarii*, *Trochammina* sp. and *Allogromia* sp.) and suggested that Wray *et al.*⁹⁹ attributed a wrong sequence to foraminifera. Later on close similarity in the partial sequences of 3' end of the small subunit rRNA gene (SSU rDNA) in 22 different species belonging to all major foraminiferal groups lead to the conclusion that foraminifera are monophyletic in origin¹⁰¹. The studies have significantly refined the evolutionary status of foraminifera and thus their application for stratigraphic correlation studies.

4. Studies that helped to identify cryptic species

Species level identification is the basic requirement for almost all foraminiferal characteristics based proxies for paleoclimatic/paleoceanographic reconstruction. Significant differences are reported in response of different species belonging to same genus, to the physico-chemical parameters, as has been discussed above. Marked differences have also been noted in the preferred microhabitat of species. Thus efficient application of foraminiferal characteristics to environmental conditions during geologic past requires that the species be identified properly.

As discussed above numerous attempts were made to resolve the slight morphological changes in certain individuals through laboratory maintenance of species throughout the life-cycle, in order to help in species identification. In an interesting study Arnold¹⁰² observed that a particular structure in *Grovia*

oviformis sustains desiccation and thus can be used as an aid in identification of the species from fossil assemblages. The morphological differences in gamonts and agamonts of a species, as well as within gamonts and agamonts of same species (*Allogromia laticolaris*) after several generations were observed by Arnold¹⁰³. It paved the way for clubbing of previously different species into single species. However, Röttger *et al.*¹⁰⁴ and Röttger¹⁰⁵ based on laboratory observations, proposed that the so called schizonts of *Heterostegina depressa* were in fact a new species. But the hypothesis was later retracted¹⁰⁶. Pawlowski & Lee¹⁰⁷ also used laboratory culturing to identify morphologically different gamonts and schizonts for many species, which otherwise may be considered as two different species. In a contrasting study previously considered separate species of *Cibicides* were found to be different ontogenetic stages of *Cibicides lobatulus*. In a similar study Röttger *et al.*¹⁰⁸, identified morphological differences, including the number of chambers, test size and size of the proloculus, between gamont and schizonts of *Calcarina gaudichaudii*. Fahrni *et al.*¹⁰⁹ used the immunoblotting of actin to suggest that *Miliammina fusca* belong to porcellaneous rather than agglutinated foraminifera.

Except for the apparent morphological changes observed between the different ontogenetic stages of the same species, molecular systematic analysis of benthic foraminifera has recently been started to identify cryptic species. The genetic make-up of each individual is characteristic. The differences increase with the increasing taxonomic level. It thus helps in identification of species or genus, based on the parentage of differences in the genetic make-up of the individuals. The extraction and enzymatic characterization of foraminiferal DNA lead the way for application of molecular systematic analysis for identification of foraminiferal species and for tracing the evolutionary history of foraminifera^{110,111}. Pawlowski *et al.*¹¹² showed potential application of molecular systematic analysis techniques for species identification and grouped eight different morphotypes of *Glabratella* in two different species. Pawlowski *et al.*¹¹³ though found distinct differences in the partial sequences of large subunit ribosomal DNA of all six morphotypes of *Ammonia*, collected from the field, identified three distinct species of *Ammonia*. Later on Holzmann & Pawlowski¹¹⁴ identified two distinct species of *Ammonia* based on the molecular analysis

and also recognized morphological and ecological differences among these two species. Tsuchiya *et al.*¹¹⁵ used ribosomal DNA analysis technique to infer the status of different morphotypes of *Glabratellidae* and observed that the *Glabratellidae* specimens were genetically less diverse as compared to the *Ammonia* specimens. By using sequences of internal transcribed spacers of ribosomal DNA, Tsuchiya *et al.*¹¹⁶ identified two different species of *Planoglabratella opercularis*, and later on supplemented the findings of molecular analysis, with geographic distribution of the species. Thus the molecular systematic analysis technique can be effectively used to differentiate between morphotypes of benthic foraminifera.

Though the molecular systematic analysis helped to identify distinct cryptic species from morphotypes of the same species and these species could be identified based on morphological differences, Holzmann *et al.*¹¹⁷ identified two *Ammonia* species based on the differences in the partial sequencing of large subunit ribosomal DNA, but the species could not be identified morphologically. Similarly, Pawlowski *et al.*¹¹⁸ identified 49 Allogromid species belonging to 28 genera/families, from the 27 morphotypes collected from the Antarctic waters. In an interesting study Grimm *et al.*¹¹⁹ recovered genetic material of entirely different non-calcareous taxa from the *Chilostomella* tests, suggesting that it may lead to wrong identification of the tests as belonging to *Chilostomella* during live-staining techniques. The studies have far reaching implications for species identification in foraminifera.

5. Other studies that refined application of benthic foraminifera for past climatic/oceanographic reconstruction

Except the studies mentioned above, during the course of laboratory culture of benthic foraminifera, certain other factors have also been found to influence the foraminiferal abundance and morphology and leave a perceivable effect on faunal composition. Frankel¹²⁰ observed that *Trochammina ochracea* occupies the cavities in the sediment surface and may be missed during the counting of foraminifera. Kuile & Erez¹²¹ proposed the presence of internal carbon pool for calcification and partial contribution to this internal carbon pool by the organic matter respiration. However, the amount of carbon contributed by the organic matter respiration to the internal carbon pool varied from species to species. Moodley *et al.*¹²²

observed the adverse effect of sulphidic conditions on the foraminiferal density and reproduction. Though the foraminifera could tolerate short-term exposure to sulphidic conditions, persistent exposure lead to significant decline in the foraminiferal density and almost complete cessation of reproductive activity. Studies carried out to understand the substrate preference of benthic foraminifera did not give encouraging results as Kitazato¹²³ observed that faunal density in the artificial substrates was order of magnitude lower than the normal field conditions and that too most of the species were confined to the freshly naturally deposited, few cm thick sediment layer overlying the artificial substrate.

Conclusion

After reviewing the benthic foraminiferal culture studies it is noticed that the proper understanding of parameters affecting the morphology of benthic foraminifera is still lacking. Exact mechanism that leads to deformities in the benthic foraminiferal tests is yet to be explored. A collective effort is needed to understand the specific effect of different pollutants, so that the benthic foraminiferal response can be used efficiently in the field. Similarly the factors affecting the foraminiferal isotopic composition, especially the carbon isotopic composition are still not known fully. The calibration equations have to be developed to infer quantitative paleoclimatic information from the benthic foraminifera.

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