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Introduction

1.1 Objectives and strategy

Ecology is the study of the causes of patterns of distribution and abundance of organisms. It is concerned with interactions between individuals and their physical and chemical environment, interactions between individuals of the same species and between species. Ecology may be investigated through field studies, laboratory experiments and mathematical modelling. Foraminifera are generally small (<1 mm) although some exceed 1 cm and most have a shell or test which may be preserved in the fossil record. These attributes make foraminifera extremely valuable as they provide not only a contemporary but also a historical record of previous environments. They are therefore of interest both to biologists and geologists.

The primary objective of this book is to present a state-of-the-art synthesis of ideas and data on foraminiferal ecology that will be of value to those carrying out new studies or wishing to interpret new data from modern or ancient environments. In this book similarities are stressed because it is very easy to overlook the broad picture if the focus is on small differences. All applications of benthic foraminifera involve an understanding of their ecology (Chapter 10).

1.2 Taxonomic scope of foraminifera

The foraminifera form an order (Foraminiferida) in the Phylum Protista: 'Cytoplasmic body enclosed in a test or shell of one or more interconnected chambers . . . ' (Loeblich and Tappan, 1987, p. 7). It has recently been argued that there are naked forms (without a test) (Pawlowski *et al.*, 1998) but such forms do not leave a fossil record. Molecular geneticists are investigating

both the antiquity of the group and whether or not it is monophyletic but no definitive answers have yet been reached (see review by Pawlowksi, 2000).

Although biological species are defined on the ability successfully to reproduce sexually, foraminiferal species are defined primarily on wall structure, chamber and test shape, and the position of the aperture(s); hence they are morphospecies. The life cycle is known for no more than 30 species and several patterns have been observed with the basic cycle appearing very ancient (Goldstein, 1997, 1999). One of the problems faced by those studying foraminifera is inconsistent use of species and generic names (Boltovskoy, 1990). Generic terminology is stabilised by using taxonomic treatises such as that of Loeblich and Tappan (1987); however, that is now almost two decades old so inevitably there have been revisions. Some highly variable species that are difficult to separate on morphology seem even more complex from a molecular genetic perspective as there are cryptic species that have no morphological expression (e.g., *Ammonia*, Holzmann, 2000; Hayward *et al.*, 2004). There is clearly a need to integrate studies of morphospecies, life cycles and molecular genetics in order to determine true taxonomic relationships. So far this has been done only for a small group of glabratellids (Tsuchiya *et al.*, 2000). At present, foraminiferal ecology is based entirely on morphospecies but no doubt this will change in the future as the impact of molecular genetics becomes greater.

1.3 Historical development of ecological studies

The scientific discoveries of one generation are built upon the foundations laid by earlier workers. Although most of the ideas and data discussed in this book are from recent decades we should not overlook the contributions made by those who started our subject, many of whom earned their living in business or in other fields of science or medicine. Although fossil foraminifera had been recorded in the fifth century BC they were regarded as small molluscs or worms. The first modern foraminifera were described by Beccarius in 1731 but the collective term 'foraminifera' was not introduced until 1830 (Loeblich and Tappan, 1964). The study of foraminifera started as a hobby for eighteenth century gentlemen who examined various small objects under the newly introduced microscopes. In Britain, the first were Boys, a surgeon and naturalist, and Montagu. In the nineteenth century major contributions were made by Williamson, Professor of Natural History at Manchester; Carpenter, Professor of Medical Jurisprudence and Registrar of the University of London; and H.B. Brady, pharmacist who studied the Challenger expedition foraminifera in retirement. In the twentieth century Heron-Allen, a solicitor and

polymath, and Earland, civil servant, formed a team producing numerous publications in the period 1913–43. In Austria, two keen collectors (Fichtel and Moll) described material from the Mediterranean and the Indian Ocean. In France, similar pioneering studies were made by d'Orbigny from various Atlantic localities, and in Germany by Ehrenberg and Rhumbler. In the USA, Flint was a pioneer but it was particularly Cushman and his co-workers who described numerous new taxa from a wide range of environments in the period 1909–48. All these authors concentrated on taxonomy, a necessity that had to precede true ecological studies; however they all reported on the occurrence of forms in different environments and habitats. The British school (Williamson and Carpenter) believed in a broad species concept, allowing for greater morphological variation than d'Orbigny and later workers such as Brady and Cushman. However, it has subsequently been shown that there is considerable morphological variation spanning several genera in *Cibicides lobatulus* (Nyholm, 1961) so perhaps species concepts should not be too narrow.

Observations on the soft parts of *Elphidium crispum* led to the determination of the life cycle (Lister, 1895) and since then around 30 species have been studied (Goldstein, 1999). Modern foraminiferal ecology started in the late 1930s to the 1950s with the works of Rhumbler (1935), who tried staining methods, Myers (1942), who introduced the first ideas on population dynamics, and Boltovskoy (1964), Bandy (1956) and Phleger (1951), who carried out field studies. In 1952, Walton introduced the now widely used rose Bengal staining method to differentiate live from dead in preserved samples. The introduction of the scanning electron microscope in the 1960s revolutionised our ability to illustrate foraminifera and the introduction of computers during the same period allowed the introduction of multivariate methods of data analysis. Whereas stable isotope studies of fossil foraminifera became commonplace from the 1960s, it is only in relatively recent years that they have been more widely applied to foraminiferal ecology.

Previous syntheses of foraminiferal ecology have shown the progressive increase in information and changes in which variables are thought to be significant: depth distributions (Phleger, 1960a); biogeographic distributions (Boltovskoy, 1965; Boltovskoy and Wright, 1976); the use of diversity indices and ternary plots of wall structure as features summarising the attributes of assemblages (Murray, 1973); associations related to water temperature, salinity and substrate (Murray, 1991). There have been no complete syntheses of ecology since then. Biology and ecology are briefly reviewed in Lee and Anderson (1991a). In Sen Gupta (1999) there are three chapters that discuss the role of oxygen and flux of organic material as ecological controls, and chapters on biogeography and symbiosis. Supplement 1 of *Micropaleontology* on the

theme 'Advances in the biology of foraminifera' (Lee and Hallock, 2000) is especially useful. The practical application of using foraminifera to monitor pollution is discussed in Sen Gupta (1999), Lee and Hallock (2000), Martin (2000) and Scott *et al.* (2001), while the latter also consider their use in determining past sea level and in sediment transport. Foraminiferal ecology is commonly applied in the interpretation of the Quaternary palaeoecology (Haslett, 2002).

National museums play an important role in housing collections of type and reference material as well as maintaining comprehensive libraries of relevant literature, all of which are freely available for consultation by researchers. Key foraminiferal collections are housed in the Smithsonian Institution, Washington, USA (Cushman), the Natural History Museum, London, UK (Williamson, Brady, Millett, Heron-Allen and Earland), and the Museum National d'Histoire Naturelle, Paris, France (d'Orbigny). These are essential reference collections for taxonomic purposes. As micropalaeontological studies have grown in importance, scientific societies have been established to promote the subject, especially through their publications and by arranging symposia (Cushman Foundation, Gryzbowski Foundation, The Micropalaeontological Society). All these elements are important for the education of the next generation of micropalaeontologists. Over recent decades there has been a change in employment of micropalaeontologists from oil geology and basic geological surveying to interpreting palaeoecology and palaeoceanography (especially in connection with the deep sea) and in environmental monitoring (pollution, sea level, climate change). This trend is likely to continue.

1.4 Major developments over the past decade

No aspect of science develops in isolation. The development of new instrumentation and the greater involvement of biologists have led to the introduction of new techniques, e.g., biomarker analysis (lipids, sterols), molecular genetics, fluorogenic probes for detecting live individuals without causing them harm, and remote sensing images of sea-surface chlorophyll as an index of primary production. Improvements in analytical equipment make it possible to analyse ever smaller samples with greater accuracy for stable isotopes and trace-element geochemistry. There has been more experimentation: microcosm and mesocosm experiments to address specific questions (faunal response to changing oxygen conditions or to the introduction of specified pollutants); *in situ* sea-floor experiments (colonisation of barren substrates; exclusion of predators). Time-series studies showing the response to natural variability have been carried out in environments ranging from

intertidal to the deep ocean. There is a greater understanding of sediment inorganic geochemistry especially in the top few centimetres where the majority of foraminifera actually live (redox boundary, nitrate boundary, etc.) because of the ability to make *in situ* measurements using probes. Also, it is now possible to quantify the biopolymers produced by bacteria and algae (potential food resources and important for stabilising the sediment surface against erosion). From a geological perspective, specific radiation events (^{137}Cs from nuclear-bomb testing which peaked in 1963–64; Chernobyl, 1986) and ^{210}Pb can be used to provide a timescale down core for the historical record of faunal and environmental change. All these developments are revolutionising our understanding of foraminiferal ecology and are discussed in the appropriate chapters.

The major patterns of distribution have been determined by field studies. We can readily distinguish between brackish, marine and hypersaline assemblages, and also between environments such as marsh, lagoon/estuary, continental shelf, bathyal and abyssal; and, for shallow-water environments, whether they are from cold, temperate or warm regimes. This database is readily applicable to the fossil record but with decreasing certainty of interpretation in passing from the Quaternary back through the Cenozoic and Mesozoic to the Palaeozoic (due to evolutionary changes in faunas through time and lack of environmental analogues). Apart from field surveys there are controlled experiments, where the impact of single variables can be isolated, and these give fairly definitive answers. We can look forward to an expansion of this type of study in the years ahead. This will help to explain some of the observed field relationships and help to bridge the gap between biological and geological approaches. Indeed, interdisciplinary collaboration is essential to advance the subject. However, as observed by Hilborn and Mangel (1997, p. 13) 'In both ecology and geology, experiments may be difficult to perform and so we must rely on observation, inference, good thinking, and models to guide our understanding of the world.' Finally, modelling is a way of considering how observations or data may be explained. Two broad types of model are recognised: *mathematical models*, where attempts are made to explain processes through calculation (e.g., the impact of variables on numbers of individuals as in population dynamics); *conceptual models*, which are essentially 'what if' questions: what would happen to species *x* if the value of variable *y* is changed? Mathematical models may be deterministic (where all components have known values, so for fixed starting values the model will always produce the same results) or stochastic (where some components are random, so several outcomes are possible depending on the values used). To do good science we need to consider whether we are asking the right questions and, if so, whether

we are attempting to answer them using the best possible methods. It is important to test new ideas and to reject those that lead up blind alleys. Mathematical and conceptual models play a role in this and in advancing understanding in reality, but models should never be confused with reality itself (Hilborn and Mangel, 1997, p. 32).

1.5 The future

No doubt foraminiferal ecology will continue to play an important role in the interpretation of the geological record. Whereas geologists have the view that 'the present is the key to the past' it is now clear that this can also be turned around to help predict future events. Thus the study of past marine transgressions may help to determine the impact of future sea-level rise; past climatic warming may help to predict future responses. There are certainly lots of challenges for foraminiferal workers in the years to come and the future of foraminiferal ecology looks exciting.

2

Methods

2.1 Planning general field surveys

A key consideration is that it must be possible for the results to be compared with those obtained in other studies. As it is desirable to compare like with like, this means that there must be some standardisation of approach (e.g., using the same sieve size). The planning stage should include reviewing any previous studies on the geographic area: on foraminifera, ecology, oceanography, etc. Biologists like to take three to four replicates from each sampling area to determine patchiness and for valid statistical analyses. Most geologically oriented ecological surveys are based on single samples from each station. If possible, a preliminary survey should be carried out in order to decide on the following points.

- Take samples of adequate size; e.g., for standing crop, large enough to give more than 100 stained individuals.
- Is the study to include soft-shelled foraminifera or just those that might withstand fossilisation? If the former, then the samples will need to be examined wet. The method of examination will control the number of samples to be collected as well as the type of data collected.
- Which type of sampling equipment should be used (see below)?
- How many (or how few) sample sites should be chosen? Should replicates be taken. If so, how many? Their positioning needs very careful consideration as they should be random. For multicores and boxcores, replicates would be separate cores. Taking one or more subsamples from a single core is not true replication but pseudoreplication.

- What spatial and temporal patterns of sampling will be undertaken?
- Should sediment slices be taken down core in order to investigate abundance changes and infaunal depth stratification?
- How will the samples be preserved and, how they will be transported back to the laboratory; how long will it be before they are processed?
- Which environmental variables should be measured and how should this be done? Some require additional sediment samples (e.g., for grain-size analysis, lipid analysis or other geochemistry).
- The mathematical methods used to analyse the data should be decided at the time the sampling plan is drawn up.

Sometimes ecological studies of foraminiferal studies are part of a bigger programme so that choices of sampling pattern, number of samples, replicates, etc. are restricted. With few exceptions, the data discussed in this book have come from surveys that have not been planned according to these modern concepts.

2.2 Planning surveys to address a specific question

These should follow preliminary studies so that it is certain that the question can be addressed. Care must be taken not to prejudice the outcome. Many of the considerations listed above will apply. Additional points to consider include:

- It is essential to take replicates in order to determine variability.
- The environmental variable of prime interest should not co-vary with the only other variables measured (e.g., if oxygen is the variable of interest, it is likely to co-vary with clay content and total organic carbon (TOC) so other variables should also be measured).
- It may be necessary to collect time-series data. If so, consider short-term variability when planning the sampling interval. For instance, whether reproduction is periodic or continuous; if the former, the length of the life cycle is relevant to the sampling interval.

2.3 Types of sampler, taking and handling samples

A wide range of sediment samplers is illustrated and described in Mudroch and McKnight (1994). It is essential that the sampler used will take a representative sample without the loss of the surface veneer of sediment. For samples taken under water, this means that the sample must be sealed in the

sampler on the sea floor otherwise there will be loss through 'washing' as the sampler is raised through the water column and from the water to the boat. For this reason, dredges, grabs and gravity corers are not very satisfactory as there may be loss of the surface layer on impact, and they do not seal once the sample has been taken. The ideal samplers for cohesive sediments are corers that have sealing devices and are lowered into the sediment gently so as to cause minimum disturbance and loss. Examples are the multiple corer (Barnett *et al.*, 1984), box corer (Mudroch and McKnight, 1994), and the Craib corer (Craib, 1965). These collect cores of sediment with the overlying few centimetres of bottom water. The cores can be subsampled at selected intervals (as described below) to study distributions below the sediment surface. However, corers do not always work well in non-cohesive (sandy) sediments. A sampling device that slices off the top 1 cm of sediment and seals it on the sea floor was designed to overcome this (Murray and Murray, 1987). In the intertidal zone, samples can be taken with a plastic ring of chosen height or with a core tube. The ring can be pressed into the sediment so that its upper surface is level with the sediment surface, a plate slid underneath and then the sample can be lifted out. Alternatively, the core tube can be pushed into the sediment and the base sealed with the plate.

To subdivide a core into sections the following equipment is needed: a clear plastic core tube, a shorter section of tube graduated with marks to determine sample thickness, a piston that fits the tube and a stand to hold the piston in a vertical position beneath the core (Figure 2.1). The core can be extruded into the graduated section to the desired height and the sediment sliced off using the plate. By repeating this procedure, a core can be sectioned into slices of chosen thickness. To avoid contamination it is essential to wash the plate and the graduated section of tube before each slice is taken.

2.4 Collecting live individuals

It is very easy to collect living foraminifera from the intertidal zone, especially from muddy sediments. Scrape off the top few millimetres of sediment making sure that no underlying anoxic material is included. The choice of sieve size will depend on the objectives of the study. While in the field, use ambient water with a pressure spray to wash out most of the mud. Place the residue in a container with some ambient water and keep it at the appropriate temperature during transit to the laboratory. Once there, spread the material thinly in a petri dish with water of ambient temperature and salinity and examine it under a binocular microscope. It will be easy to see tests with coloured contents and these are most likely to be alive. They can be removed

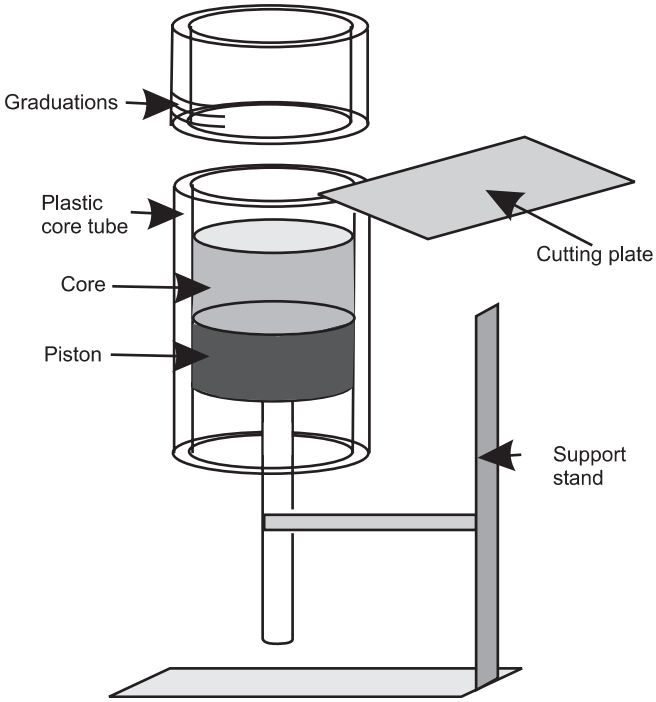

Figure 2.1. A schematic representation of the method used to subdivide a sediment core into slices.

with a pipette and placed in a small dish for examination. More detailed descriptions of field methods, and for the setting up of containers for maintaining foraminifera in the laboratory, are given in reviews by Arnold (1974) and Anderson *et al.* (1991).

2.5 Distinguishing live from dead foraminifera

A wide variety of methods of distinguishing living from dead foraminifera have been devised. In an excellent review, Bernhard (2000) differentiated between non-terminal and terminal methods and discussed their advantages and disadvantages. These techniques are listed below but only those commonly used are discussed in any detail and not all the arguments presented by Bernhard are reproduced here. The choice of technique depends on the objectives of the study. For experiments, it is clearly necessary to use non-terminal techniques. For most of the distributional studies reviewed in this book, sediment samples were collected and preserved. Forms that were alive at the time of collection were distinguished from those that were dead