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WHEN DOES ENVIRONMENTAL VARIABILITY BECOME ENVIRONMENTAL CHANGE? THE PROXY RECORD OF BENTHIC FORAMINIFERA

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ABSTRACT

There are three possible approaches to investigating environmental change using organisms as proxies: comparison of spatial surveys from different time periods, time-series studies, and high resolution studies of cores. Because they have a preservable shell and are abundant, benthic foraminifera are the best meiofaunal group for giving a proxy record of past marine and marginal marine environments. Through the analysis of: changes in abundance of marker species; the introduction of new species or serious loss of previously existing species; changes in species diversity, dominance and abundance which extend well outside the established limits of variability; it is possible to document the extent of environmental changes that have taken (or are taking) place.

1. INTRODUCTION

The aim of ecological studies is to establish the relationship between the biota (community structure of populations of living organisms including standing crop, species abundance, species diversity, etc.) and the attributes of the environment (physical, chemical, biological). Such studies may be *spatial* involving a suite of samples collected over a geographic area during a very short time interval (days), or *temporal* where samples are collected from one (or more) sites over an extended period of time (ideally several decades). Spatial studies give a snapshot over a broad area. Temporal studies give a near-continuous record of a very small area.

Both approaches yield data with a lot of ‘noise’ that may obscure the overall patterns not only within the community structure but also in its relationship to the environment. On a short timescale, conditions may appear to be unchanging and this has given rise to the concept of ecological stability (for a critique see Grimm,1996). In reality, there may be changes which operate at such a slow rate that they are not obvious. These have been described as the *invisible present* (Magnusson, 1995). However, such slow changes become apparent when time-series studies are carried out over period of years or decades as, for instance, the 50 year long Russell cycle observed off southern England (Cushing and Dickson, 1976). Also, there may be time lags of longer than one year between a disturbance and the ecological response although the duration will depend on the frequency of reproduction of the organisms involved (and this is commonly only a few months in the case of foraminifera). Time lags may possibly lead to misinterpretation of cause and effect.

Those organisms that have preservable hard parts have the potential to leave a fossil record in stratigraphic sequences. Such records embrace both space *and* time. Geologists are used to interpreting the fossil record to show changes of environment through time. They are also aware that change is normal in the history of the Earth. The principal difference between the ecological and geological approaches to change is the timescale: ecologists are normally concerned with changes on much shorter timescales than geologists.

However, it is possible to combine the two approaches by carrying out high resolution studies of faunal change (as a proxy for environmental change) on cores of sediment containing well-preserved microfossils where it is possible to date individual sediment horizons using radiometric methods. The advantage of this approach is that it provides a means to reconstruct past environments from times prior to the documentation of ecological data (for example, over the past few hundred years) and prior to the onset of significant human interference. This is particularly important in those instances where recent anthropogenic disturbance has caused environmental change for it is then possible to determine what conditions were like before disturbance and thereby establish its full effects. Geologists can also provide an insight into the effects of environmental change on early human activity (see for instance, Reinhardt, *et al*., 1994; Stanley and Warne, 1997, on the relationship between Holocene sea-level changes and the early utilisation of deltas).

Thus, there are three possible approaches to investigating environmental change using organisms as proxies: comparison of spatial surveys from different time periods, time-series studies of selected sampling areas, and high resolution studies of cores.

2. THE CONCEPT OF ENVIRONMENTAL CHANGE

Over the last decade or so there has been popular concern about changing climate. This stems partly from fear that the climate may cool to give another ice age or that it may warm through the accumulation of so-called greenhouse gases. But the fear is mainly that man’s activities are adversely affecting both the climate and the natural environment as a consequence of pollution. Biologists and geologists are now actively investigating the contemporary effects of man’s activity on living organisms and environments.

In spite of the growing literature on the subject of environmental change, and especially its potential effects on humans, it is very hard to find a definition of what constitutes an environmental change. It is first necessary to consider variability in the environment. Variability is fluctuation about a mean and takes place on different timescales: diurnal or semidiurnal; seasonal; and cycles over a period of years/decades. Such variability can be considered as short term change. True environmental change requires that the variability occurs about a mean which itself has changed through time. But there may still be uncertainty in distinguishing variability from change. For instance, there may be progressive change in variability either on a single trend or with small cycles superimposed on larger cycles (Fig. 1). It is probably best to consider that there is a continuum from short-term variability to longer term change but the problem remains of where to draw the boundary between variability and change.

It is also customary for the layman to think of environmental change solely in terms of chemical or physical parameters but biological changes also affect the environment. For instance, the sudden blooming of an organism has consequences for other organisms (competition for space and nutrients, potential source of food, etc.). Similarly, the arrival of a new species or the local extinction of a species has potential consequences for the rest of the biota. It is also a commonly held view that change must be bad but that is not necessarily true. For instance, the addition of small amounts of nutrients to a system may be beneficial and the breakdown of a barrier between a lagoon and the open sea may improve water circulation with consequent advantages for at least part of the biota.

3. FORAMINIFERA AS PROXIES OF CHANGE

Benthic foraminifera are abundantly present in modern and ancient marine sediments. There are numerous case studies which have demonstrated their utility in documenting present environments (summarised in Murray, 1991) and a few have documented changes over recent decades. Furthermore, although much remains to be learned about the ecology of benthic foraminifera and the taphonomic processes which affect their preservation in the fossil record, they are nevertheless the best meiofaunal group for giving a proxy record of past marine and marginal marine environments. This is because not only are they are abundant but, unlike other meiofaunal organisms such as nematodes and tiny crustaceans, they have a test/shell which is capable of preservation in the subsurface sedimentary record.

Because of space limitations, it has been necessary to be selective in the choice of examples from the literature but, wherever possible, reference has also been made to reviews which give more comprehensive lists of references (e.g., Murray, 1991, on ecology; Alve, 1995, on pollution, Alve, in press, on colonisation). For time-series studies, those used are based on living assemblages (stained with rose Bengal), collected over a period of two years or more.

4. METHODS

4. 1. Sampling Methodology

A pre-requisite for ecological studies is that sampling must be carried out very carefully. Although benthic foraminifera are known to live infaunally to a depth of several centimeters in most environments, the majority live within the top 1 cm and it is imperative that there should be no loss of this layer during the sampling process. Many authors study the >63 µm size fraction but others use >40, >125 or even >250 µm. When comparisons are being made between two or more studies or between different times of sampling, care must be taken to base this on the same size fractions otherwise errors will arise (Schröder, et al., 1987).

4.2 Methods of data analysis used in this review

The attributes of foraminifera which are related to ecology include univariate measures (where the data for the whole sample are expressed as a single figure such as species diversity or standing crop of the whole assemblage) or multivariate measures (where similarities are computed between two or more samples as in cluster analysis, principal component analysis, multi-dimensional scaling, etc.). It is important to note that while stability or a change in a univariate measure in one area may be of ecological significance, two completely unrelated areas may have the same univariate value. For example, two areas may have exactly the same range of species diversity or standing crop yet not have a single species in common. By contrast, multivariate methods utilise all the assemblage data.

One way ANOVA, covariance, and correlation (covariance of 2 data sets divided by the product of their standard deviations; values close to one indicate a close relationship) have been calculated for published data using Excel 5.0. Non-metric multidimensional scaling (MDS) plotted in two dimensions is used here to recognise groups of samples that are similar (lie close to one another on an MDS plot) and to distinguish samples which are dissimilar (lie in different parts of the MDS plot). The calculations have been carried out with the PRIMER package (Clarke and Warwick, 1994) using the Bray-Curtis coefficient of similarity (the most widely accepted measure of similarity used in ecological studies) and with no transformation of the data.

5. MODERN EXAMPLES OF ENVIRONMENTAL VARIABILITY AND CHANGE

These can be divided into three groups: short-term (seasonal) repetitive variability; long-term variability/change; non-cyclic change.

5.1. Short-term, seasonal, repetitive variability

In order to define the range of short term variability of the environment, it is necessary to have time-series data both on the ecological parameters and the organisms.

5.1.1. Variability in standing crop

There are relatively few studies where foraminiferal samples from the same locality have been taken monthly over a period of one or more years. However, these provide important data on the variability of the standing crop both during a year and from one year to another (Table 1). The intertidal and very shallow water examples, with the exception of Bahrain, are all from temperate settings.The annual ranges of variability are large in each area and the data contain much ‘noise.’ One way of overcoming this for any one station is to make comparisons between years based on the mean monthly values plus or minus their standard deviations. This shows that there is generally some overlap from one year to the next. However, analysis of variance (single factor ANOVA, 5%

confidence, Table 2) shows that only the Exe data are statistically similar for the two whole year data sets whereas the pairs of years for Bahrain, Bottsand and Puerto Deseado are significantly different as are those for the deeper sites in the Baltic Sea. The data for Hamana Lake, Japan are based on a comparison of the four common sampling months over two years and have a high degree of similarity.

Much of the noise in the monthly records can probably be attributed to patchiness in distribution patterns. Of the examples discussed above, a survey of patchiness has been carried out only at Puerto Deseado. This revealed great variation both on 10 cm and 1 m sample spacing (Boltovskoy and Lena, 1969b). For example, in their area 1, with 23 samples spaced at 1 m intervals, the observed range was 61-280 individuals per 9 cm^2 or 27 cm^3 (mean 148, SD 74). Thus, in this area it is remarkable that any pattern can be observed from one month to the next when only a single sample was taken each month as in the surveys by Boltovskoy (1964) and Boltovskoy and Lena (1969a).

Time-series data also reveal whether there is any cyclicity in standing crop. In 1965 in Bottsand Lagoon (Fig. 2A), there was a spring low followed by a summer-winter peak but the latter was not present in 1966 (Lutze, 1968). Covariance correlation is low (0.17) indicating little similarity and is not significant. However, the two main species showed different patterns. *Elphidium williamsoni* (*Cribroelphidium articulatum* of Lutze) had a pattern closely resembling that of the whole standing crop but *Miliammina fusca* showed much the same range of variabilty throughout the period without any obvious cyclicity. In the Exe estuary (Fig. 2B), there were lows for *Nonion depressulus* in June-August in all three years sampled (Murray, 1983); covariance correlation is 0.39 and not significant. The two studies of Puerto Deseado (Fig. 2C, D) produced conflicting results. From 1961-1963 there were peaks in the standing crop of *Elphidium macellum* from November to May (southern summer) and lows in the winter (Boltovskoy, 1964). However, in the continuation of the survey, where the whole assemblage was studied, the peaks of standing crop were during April-November 1964 (southern winter) but the pattern was not repeated in 1965 and consequently the covariance correlation is very low (-0.12). Boltovskoy and Lena (1969a) were unable to account for these differences.

The standing crop of individual species in the intertidal zone in Bahrain also show different patterns from one year to the next (Basson and Murray, 1995). Whereas the numbers of *Ammonia beccarii* remained much the same throughout the study period, *Elphidium advenum* increased about fourfold in 1992-93, while *Brizalina pacifica* and *Nonion* sp. suddenly increased 30 to 100 times in August 1992 and remained high thereafter. There was a parallel increase in diversity. This poses the question: does this reflect natural variability or was it an environmental change? At present the cause of these abundance increases remains unknown since the only enviromental variables measured were temperature and salinity and no other environmental data were available.

The Lim channel is an arm of the Adriatic Sea in Istria. Daniels (1970) made a transect of stations from the open sea (35 m) to the landward end (5 m) and sampled over a 14 month period. The three seaward stations had the highest standing crops (range 321 - 1227 per 10 cm^2, means 714, 679, 800, SD 272, 302, 304 respectively), the innermost two stations had the lowest values (range 104 - 722 per 10 cm^2, means 353, 320, SD 101, 200) while central stations had intermediate values.

Until recently, it was commonly believed that the deep sea is a very stable environment with virtually no environmental variability. However, this is now known to be incorrect. Bottom photography has shown that there is often quite a considerable amount of bioturbation creating microhabitats which provide scope for patchiness in meiofaunal distribution and abundance. Furthermore there are benthic storms (Kaminski, 1985) and disturbance from turbidity currents (Vénec-Peyré and Le Calvez, 1986). But perhaps the most important discovery is that the deep sea experiences seasonality. This comes as pulses of food (termed phytodetritus) derived from the phytoplankton (Gooday and Lambshead, 1989).

Since almost all deep sea life is ultimately dependent on food from the plankton, the arrival of an increased quantity of phytodetritus triggers a biological response particularly among bacteria and protozoa. Gooday (1993) has shown that there are certain foraminifera which opportunistically exploit phytodetritus (so-called 'phytodetritus species', mainly *Epistominella exigua* and *Alabaminella weddellensis*). They have a small test size (generally less than 200 and 150 µm respectively) and live throughout the year in the top 1 cm of sediment. When the seasonal pulse of phytodetritus arrives on the ocean floor they colonise it, reproduce and increase in number. For instance, at 1350 m in the Porcupine Seabight west of Ireland phytodetritus species were present in the sediment in April 1982 and July 1982 (means 20 and 110 per 3.5 cm^3 respectively) and, during

July, when there was a layer of phytodetritus on top of the sediment, there were a further 166 within the phytodetritus (data recalculated from Gooday and Lambshead, 1989). At an abyssal site in the NE Atlantic (depth of 4550 m) the mean abundance of phytodetritus species in April 1988 in two sediment cores taken when no phytodetritus was present was 14 per 3.5 cm^3 whereas in July 1986 following a phytodetritus pulse, the mean of three sediment cores was 22 per 3.5 cm^3 and 183 for the phytodetritus layer (Gooday and Turley, 1990, plus supplementary data from A. Gooday).

At a permanent research station in Sagami Bay, Japan, situated beneath the oxygen minimum zone in Pacific Deep Water at 1450 m water depth, the temperature, salinity and bottom water oxygen concentrations are stable throughout the year. However, the standing crop of the benthic foraminifera varied from 200 - 2800 per 10 cm^2 over a four year period. The low values occurred during the summer (200-500 per 10 cm^2) and the high values in the spring (1500-2000 per 10 cm^2) when there was an input of phytodetritus to the sea floor (Ohga and Kitazato, 1997). Furthermore, the foraminifera migrated vertically in the sediment as the redox boundary shallowed following the arrival of the phytodetritus. There were juvenile individuals of the shallow infaunal species *Textularia kattegatensis* and *Bolivina pacifica* in spring and this suggests that they reproduced following the arrival of phytodetritus.

The San Pedro Basin on the USA Californian borderland has a sill depth of 715 m. Box cores collected at different seasons showed that there was essentially the same group of species making up the >150 μm assemblage although the rank order varied slightly from one season to another. The depth distribution within the sediment remained constant throughout the sample period (Silva, *et al*., 1996).

Monthly sampling of four stations over one year in the Clyde Sea, Scotland, showed variations in standing crop from 0-200 individuals per 10 cm^3 on coarse sand at 8 m to 800-3600 per 10 cm^3 on muddy sediment at 38-46 m (Hannah and Rogerson, 1997; samples prepared by elutriation so individuals smaller than 63 µm are included, Hannah, pers. comm. Feb. 1998). From analysis by ANOVA the authors concluded that season had no significant effect on the size of the standing crop.

To summarise, all the above studies reveal considerable short-term variability including changes from one year to the next which mask any underlying cyclicity. Also, most time-series are too short to detect secular changes.

5.1.2. Variability in assemblages

For the Exe estuary, MDS plots of the individual years 1979, 1980, and the data for both years combined show a broad scatter with no order from one month to the next. This can be interpreted as confirming that there is essentially one assemblage showing considerable variability through time. On the other hand, MDS plots of the Bahrain data reveal two groups which are separated and within each of which there is no order (Fig. 3). One group includes February 1991 - July 1992 (dark field) and the other August 1992 - February 1993 (light field). Thus, the faunal change (increase in *Brizalina* and *Nonion*) has clearly affected the whole assemblage.

5.1.3. Variability in the dominant species

The rank order of species may be constant or change from month to month. Examples of constancy include the Exe estuary (*N. depressulus*, Murray, 1983), Puerto Deseado (*Buliminella elegantissima*, Boltovskoy and Lena, 1969a), the Plym estuary (*Haynesina germanica* except for one month, Castignetti, 1996), and Bahrain (average of replicates, *A. beccarii* except for two months out of 26, Basson and Murray, 1995). Examples of changing dominance include the Bottsand Lagoon, Lim channel, and the southern North Sea.

In Bottsand Lagoon, *Elphidium williamsoni* (= *Cribrononion articulatum* of Lutze, 1968) was dominant in 1965 but throughout most of 1966 the dominant form was *Miliammina fusca*. The differences between the two species is that the standing crop of *M. fusca* had much the same variability throughout the two years whereas *E. williamsoni* was much more abundant in 1965 than in 1966. In Lim channel, Istria, the seaward stations were dominated by *Nonionella opima* but, with passage towards the landward end, the dominance became more variable (Daniels, 1970).

In some areas of the southern North Sea (Murray, 1992), the same living species was dominant throughout the year (dominant dead species given in parentheses): sta. 2 at 25 m, *Elphidium excavatum* (*E. excavatum*), and sta. 5 and 4 at 63 and 81 m water depth respectively, *Stainforthia fusiformis* (sta. 5, *S. fusiformis*, *E. excavatum*, *Eggerelloides scaber* depending on the month; sta. 4, *S. fusiformis*). However, sta. 3 at 52 m had dominant *Epistominella vitrea* in April/May 1988, *E. scaber* in September 1988 and

May/June 1989, and *S. fusiformis* in December 1988 (*E. excavatum*). It can be seen that these variations in the living assemblages were not always recorded in the preserved dead assemblages.

5.1.4. Species diversity

There are few published data on this and unless the census data sets are published it is not possible to calculate the values. In the Lim channel (survey conducted over 14 months, Daniels, 1970), species diversity measured by the alpha index showed some variability but no obvious pattern within a single station (seaward, sta. 39, range 12 -17, mean 13.5, SD 1.7; landward, sta. 1, range 9 -14, mean 11.8, SD 1.8). In the Bahrain survey, the information function (H(S)) had a mean value of 0.5 from February 1991 to July 1992 and, in association with the faunal changes, it rose to a mean of 1.4 from August 1992 until February 1993 (Basson and Murray, 1995).

5.1.5. Summary

From the time-series studies carried out so far, it can be seen that there is considerable variability from one season to the next; the pattern of variability is not necessarily repeated precisely from year to year; the variability affects the standing crop, the dominant species, and the species diversity. These data sets provide a fundamental baseline from which to evaluate long-term environmental change.

5.2. Long-term change

Examples of long-term change include one-way and cyclical: progressive environmental changes (one-way); pollution (one-way); and anoxia and flushing of basins (cyclical). In one-way changes there may be differences in the dominant species (previously rare species replacing formerly common ones) and changes in the rate of production and accumulation of tests. This is quite different from the cyclic change from anoxia, which kills off the fauna, to oxygenation, which allows recolonisation initially by opportunistic species.

5.2.1.Progressive environmental changes (one-way)

Such changes could result from an increase or decrease in a variable over a long period of time.

There is some evidence that the deep Skagerrak basin in the northeast North Sea has been the site of progressive faunal change over the past 60 years and especially over the last three decades. In 1937 a detailed survey of the benthic foraminifera focused mainly on the taxonomy (Höglund, 1947) but data were also gathered on the total (live plus dead) assemblages. In 1992/1993, the Norwegian Geological Survey and the University of Bergen, Norway, took a series of cores from the same area that Höglund had sampled. Since Höglund did not distinguish live from dead, the only possible comparison was between the total assemblage results from the upper 2 cm of the new cores with Höglund's total assemblage data (also from the top 2 cm) from the same localities, Alve and Murray (1995) were able to show that since 1937:

- there has been an almost threefold increase in the total abundance of tests in the deep Skagerrak Basin (Fig. 4)
- the 1937 basin fauna was dominanted by calcareous species (*Cassidulina laevigata*, *Pullenia osloensis*) whereas now it is dominated by agglutinated forms (*Haplophragmoides bradyi*)
- *Trochamminopsis pusillus* and *Saccammina* spp. were not recorded in 1937 but now they are common and characteristic basin taxa so they must have migrated into the area
- on the Norwegian slope the dominant species in 1937 was *C. laevigata* but now it is *P. osloensis*; since 1937, the absolute abundance of *C. laevigata* has halved whereas that of *P. osloensis* has tripled
- on the Danish slope there has been a dramatic increase in *Stainforthia fusiformis* since 1937 and a significant reduction in both the absolute and relative abundance of *C. laevigata* and *Hyalinea balthica*.

Comparative studies of the living and dead assemblages in the surface sediments have demonstrated that dissolution of calcareous tests is now active in the deep basin so that the dead assemblages are dominated by agglutinated taxa (Alve and Murray, 1997).

In a related study, Alve (1996) studied down-core distributions. Subsurface levels were dated using ^{210}Pb so it is possible to relate the changes in faunal composition to a timescale. Alve presented faunal assemblage data and calculated the accumulation rates of tests for successive time increments. Core 56 from the deep basin (652 m) spans the time period from around 1870 to 1993 and the sea floor at the time Höglund collected his samples is now represented by the 16-18 cm interval (1935-1943). To provide an objective analysis of the whole data set, multivariate analysis has been undertaken. Both cluster analysis and MDS ordination produce two well-defined groups of samples, pre- and post-1971 (Fig. 5) supporting Alve's conclusion that there has been a change up-core particularly since about 1970.

There was a major change in the accumulation rates of agglutinated tests at around 1970-71 (Fig. 6: 1935-1970 mean 92 tests/10cm^2/yr; 1971-1993: mean 205 tests/10cm^2/yr). However, the overall accumulation rate decreased during this time (1935-1970: mean 419 tests/10cm^2/yr; 1971-1993: mean 325 tests/10cm^2/yr). Whereas agglutinated tests formed 22% of the accumulating assemblages in 1933-1970, they increased to 63% in 1971-1993. These accumulation rates could be interpreted as evidence that there was:

- an up-core increase in the production of agglutinated tests
- a down-core increase in destruction of agglutinated tests
- an up-core decrease in the production of calcareous tests
- an up-core increase in the dissolution of calcareous tests

Alve considered that although there may have been some destruction of agglutinated tests, overall their preservation is good. The preserved agglutinated fauna at a core depth equivalent to 1937 is very similar to that recorded by Höglund. Furthermore, the upward increase is in part due to the re-introduction of species (*Trochamminopsis pusillus* and *Saccammina* spp.) which were not recorded by Höglund at these sites but are occasionally present in pre-1940 sediments in core 56. A similar upward abundance increase was recorded by Haas (1997) from cores taken between 245 and 450 m. The increase in the dissolution of calcareous tests already noted by Alve and Murray (1995) is confirmed by the core 56 data. *Pullenia osloensis* was one of the commonest living species in the 1991-93 survey, but rare in surface dead assemblage although very abundant in pre-1970 assemblages. The following conclusions can be drawn: no amount of dissolution of calcareous tests from the post-1970 samples could lead to an *increase* in the absolute numbers of agglutinated tests or their rate of accumulation; the upward increase in agglutinated tests could arise if there was a downward increase in the destruction of these tests but the arguments presented above make this unlikely; if there was no downcore increase in the destruction of agglutinated tests, it follows that there must also have been a decline in the production of calcareous tests in the post-1970 period.

How might these results be interpreted? Are there parallel changes in the macrofauna? Biologists report that there has been an increase in the supply of organic matter and this has led to a recent increase in the biomass and standing crop of the macrofauna (Rosenberg, *et al*., 1987; Josefson, 1990). However, they do not have the same historical data base that has been worked out for the foraminifera. Nevertheless, long-term changes in the North Sea benthos have been attributed to anthropogenic rather than natural causes since there have been no significant changes in water temperature or salinity but there has been a marked increase in eutrophication, pollution, and fisheries impact on the sea floor (Kröncke, 1995). Plankton biomass increased by three to four times and its effects on the benthic biomass on muddy sediments in the German Bight peaked in the 1970s.

Furthermore, in a comparable study of the foraminifera from the northeastern rim of the Skagerrak and from the Kattegat, Moodley, *et al*. (1993) considered that there was a *decrease* in foraminiferal densities due to eutrophication which favoured the macrofauna. Alve and Murray (1995) and Alve (1996) concluded that the faunal changes (especially the increased production of agglutinated tests in the deep part of the basin) are likely to be linked to an environmental change (an increase in nutrients and the flux of organic matter) which might be natural but is more likely to be caused by anthropogenic activity. The changes in the Skagerrak parallel those described as due to anthropogenic causes in adjacent areas of the North Sea and the Kattegat.

On a smaller time scale, prior to 1991 *Amphistegina gibbosa* was abundant and healthy in the shallow waters of the Florida Keys, USA, but in 1991 these forms started to undergo symbiont-loss. This has led to a slow-down in reproduction and an increase in shell breakage. This trend has continued and as a consequence the numbers of individuals have fallen dramatically. The cause is as yet undetermined but might be related to increased solar radiation (Williams, *et al*., 1997).

5.2.2. Pollution (one-way)

Where there is a build up of pollutant concentration through time, such environments provide an example of change in one direction (although if the input of pollutants declines, the pre-pollution fauna may be re-established). The effects of pollution can be monitored by studying the consequent faunal changes through time although in some cases there has not been a baseline study of the area prior to the onset of pollution.

In a review of the effects of pollution on foraminifera, Alve (1995a) noted that the effects of pollution are complex but that a few generalisations can be made: in cases of severe organic pollution, an abiotic zone or an area with extremely reduced abundance is present in the immediate vicinity of point sources; increased abundance (hypertrophic) relative to the natural background level, close or at some distance from the outfall; reduced number of species close to the outfall, compared to the surrounding sea floor and, in some cases, increased compound diversity (i.e., measures such as the information function, which take into account species proportions) at some distance from the outfall; modification of the original assemblage composition. Some tolerant or opportunistic species benefit from organic pollution, and through reduced competition and predation if these groups are reduced or excluded. These consequences of pollution are all long-term changes beyond the range of normal environmental variability.

With increased awareness of the need to minimize pollution, many countries have introduced legislation to reduce the discharge of pollutants. Former badly polluted areas are now less polluted and foraminifera can be used to monitor this recovery (see Alve, 1995a, b, Chapter x this volume, and below).

Where baseline studies have not been carried out prior to the onset of pollution or where it is desired to study the historical development of pollution (and recovery) the analysis of core data which extend back into the pre-pollution time period is invaluable. A schematic diagram shows the possible sequence of events in a heavily organically polluted area (Fig.7). Alve (1995a) divided the foraminifera into ‘natural’ N (i.e, the normal pre-pollution fauna), ‘transitional’ T and ‘opportunistic’ O groups according to their tolerance to pollution disturbance. When the hypertrophic conditions are reached, species diversity falls, faunal dominance increases, and the number of tests reaches a peak; then abiotic conditions develop when pollution is at a maximum. The order of events is reversed as the area recovers following the cessation of pollution. In such studies, particular attention must be paid to any taphonomic loss of information. Good examples of this approach using the preserved foraminiferal record are the reconstructions of past bottom water oxygen conditions in Drammensfjord, Norway (discussed below) and Frierfjord, Norway (Alve, chapter x this volume). This is a very powerful technique for documenting environmental change.

5.2.3. Flushing of basins (cyclical)

Certain enclosed basins have restricted communication with the open sea due to lack of tidal influence, salinity contrasts and usually the presence of a sill which restricts the ingress of more saline deep waters. Under these conditions, the deep waters in the basin become depleted in oxygen because renewal is too slow to compensate for the biological and chemical consumption. Classic examples are fjords, the Baltic Sea, and basins on the California borderland.

Periodic flushing has been documented in Drammensfjord, southern Norway (Alve, 1991). The combination of a well-developed halocline and a sill at 10 m restricts deep water exchange to the inner basin of the fjord and this takes place only every three to five years. Although from about 1500-900 years ago the basin was flushed, oxygenated and had calcareous foraminiferal assemblages, from 900 until about 170 years ago, changes in climatic conditions increased the inflow of freshwater, reduced the exchange with the open sea, and led to assemblages which were dominantly agglutinated. Beginning about 170 years ago there have been additional pressures from organic, oxygen-consuming pollution which caused anoxia.

From ~1830 to 1970 the basin received waste from pulp mills and sewage but after this the pulp mill closed and the input of sewage was reduced so the environment started to recover. In 1982 anoxia was present at water depths >30-35 m but between 1984 and 1988 the redox boundary was lowered to around >50-55 m. Alve (1995b) took samples in 1984 and 1988 to document these improvements. She found that:

- living forms were present on substrates only from 0 to 30 m water depth in 1984 but by 1988 they extended down to 50 m
- the sediments which had previously been anoxic for >5 years did not become suitable for foraminiferal colonisation until more than one year after they had been exposed to oxic bottom waters (a good example of a lag effect)
- in areas at 10-35 m (bathed by the transitional water layer), the standing crop doubled between 1984 and 1988 as conditions improved
- the first important coloniser of the formerly anoxic sediments, *Stainforthia fusiformis*, is a highly opportunistic species (Alve, 1994); it is naturally small and thin-walled and its juveniles are easily transported

- although there was a diversity increase as the fauna became established, diversity remained low as would be expected in a marginal marine environment.

The Santa Barbara Basin off California, USA, has a maximum depth of 625 m and a sill depth of around 475 m. Episodic ventilation of the bottom waters leads to oxygen depletion of bottom waters below the sill depth inbetween periods of flushing. When oxygen levels in the deep basin are less than 23 µM O_2 (~0.5 ml 0_2/l), macrofaunal predators are excluded and even much of the meiofauna is affected. Nevertheless, certain foraminifera tolerate these low oxygen levels and standing crop values are very high (up to 1197 individuals cm^3, Bernhard and Reimers, 1991; up to 2176 individuals cm^3, Bernhard, *et al*., 1997). Some foraminifera survive short periods of anoxia but following weeks/months of anoxia, the foraminiferal fauna is entirely wiped out (Bernhard and Reimers, 1991). There is a sequential tolerance to progressively lower oxygen concentrations: (lowest tolerance) *Uvigerina juncea*, *Suggrundina ekkisi*, *Loxostomum pseudobeyrichi*, *Bolivina argentea*, *Trochammina pacifica*, *Bolivina seminuda*, *Buliminella tenuata*, *Chilostomella ovoidea*, *Spiroplectammina earlandi*, and *Nonionella stella* (highest tolerance, dominant when oxygen levels fell to <2µM O_2, Bernhard, *et al*., 1997). It should be noted, however, that all these species also live in environments having an ample supply of oxygen and that there are no species confined entirely to very low-oxygen settings.

5.2.4. Summary

A progressive change, such as that described from the Skagerrak, is in some ways similar to a build-up of pollution in that the change is in one direction. The consequences are that there may be a change in the dominant species (rarer species replacing formerly common ones). There may also be changes in the rate of production and accumulation of tests. This is quite different from the cyclicity which goes from anoxia, which kills off the fauna, to oxygenation, which allows recolonisation initially by opportunistic species.

5.3. Rapid non-cyclic change

These may be single events (like making a new harbour channel and thereby changing the water circulation pattern, or the introduction of a new species) or they may be irregular in occurrence (volcanic eruptions, earthquakes).

5.3.1. Change in water circulation

The lagoons along the coast of the United Arab Emirates had remained largely unaffected by human activity until the late 1960s. The foraminiferal assemblages of the Abu Dhabi lagoon were studied in 1965 (Murray, 1970a) and again in 1969 (Murray, 1970b). In 1965 the tidal flow into the lagoon was restricted by the tidal oolith delta. Seagrass in the lagoon was sparse. By 1969 the channel across the oolith delta had been dredged deeper and a new channel at the landward end of Abu Dhabi island allowed water exchange with the adjacent lagoon. The tidal range within the Abu Dhabi lagoon seemed to be greater, the seagrass was healthy and luxurious, and the fivefold increase in human population was presumably matched by a similar increase in organic matter as the sewage was discharged into the sea.

In the 1965 survey, living foraminifera were found to be confined largely to plant substrates (especially seagrasses) with few on the sediment substrates but no quantitative measurements were made. By 1969 the numbers of live forms must have increased because it was possible to obtain standing crop data from all subenvironments. These changes, together with the greater amount of seagrass, may have been the consequence of improved water circulation with the open gulf, thus reducing the hypersalinity, and with higher levels of organic matter (from the sewage)

The total assemblages collected in 1964-65 from Miramichi River estuary, Canada, were used to define two biofacies: river with dominant *Miliammina fusca* and bay with dominant *Elphidium* spp. (Bartlett, 1966; Tapley, 1969). A decade later the area was sampled again and three assemblage zones defined: upper estuarine (= river) with *M. fusca*, transition with *Ammotium cassis*, and open bay (= bay) with *Elphidium excavatum clavatum* (Scott, *et al*., 1977). The transition zone fauna occurs in an area which was previously occupied by a calcareous assemblage and this change was attributed to alterations in water circulation due to changes in the barrier islands and increased river discharge.

5.3.2. Introduction of new species

The re-introduction of two species into the Skagerrak basin between 1937 and around 1970 has already been mentioned in connection with inferred environmental changes. The mechanism of introduction is unknown but is presumably natural. The introduction of *Ammotium cassis* into the Baltic Sea probably took place between 1936 and 1952 (Lutze, 1965) and this species is now common beneath the transition water layer in the southern part of the Sea.

The introduction of *Trochammina hadai* into San Francisco Bay, USA, is thought to have taken place during the 1980s and it is possible, though not proven, that it might be as a result of man's activity. McGann and Sloan (1996) report that it already forms between 8 and 56 % of core top total assemblages suggesting that it is a strong competitor which may have important long-term consequences for the meiofaunas of the area.

5.3.3. Volcanic eruptions

Volcanic eruptions occurred on Deception Island, Antarctica, in 1967-1970 and these killed off much of the fauna. Samples were taken each summer from 1971-1975 to investigate recolonisation of the area. The aim was to make census studies based on counts of 300 individuals per sample (Finger and Lipps, 1981). Within the caldera (Port Foster), only one of the samples yielded 300 living individuals and many were barren but by 1973 nine of the eleven samples had a rich fauna. The 1971 assemblage was dominated by *Trochammina malovensis, Miliammina arenacea, Globocassidulina crassa* and *Nonionella bradii* but by 1975 the dominant forms were *M. arenacea*, *Stainforthia fusiformis* and *N. bradii*. On the flank slope of the volcano it was not until 1974 that the faunas had become rich enough to yield 300 stained individuals per sample. The dominant species was *Globocassidulina crassa*. Both within the caldera and on the flanks the living forms were patchy in occurrence even in 1975 and it is doubtful whether the fauna was fully re-established.

The pre-eruption fauna collected in 1927 and documented by Earland (1934) was dominated by *M. arenacea*. It is interesting that, once again, *S. fusiformis* was an early recolonising species even though it is not normally a component of the assemblages (no calcareous forms were recorded by Earland). Finger and Lipps concluded that the post-eruption assemblages in the caldera are sufficiently different from those recognised by Earland in 1934 to suggest that the foraminiferal fauna 'may have undergone significant reorganization in this century'.

A more recent example is the 1991 eruption of Mount Pinatubo in the South China Sea. The deep sea floor down-wind at the time of the eruption became blanketed in volcanic ash which buried the fauna to a depth of 2-6 cm. Hess and Kuhnt (1996) sampled the area three years after the eruption. The dead assemblages from beneath the volcanic ash are dominated by tubular agglutinated foraminifera such as *Saccorhiza ramosa* and *Rhabdammina abyssorum*. The living assemblages from the thin layer of mixed hemipelagic sediment and volcanic ash above the ashfall deposits are dominated by *Reophax dentaliniformis* and *Quinqueloculina seminula* (Fig. 8, April 1994). The dead assemblage in this surface layer includes numerous small *Textularia* sp. rarely found living. Hess and Kuhnt speculated that *Textularia* sp. were the earliest recolonisers which had been replaced by *Reophax* and *Quinqueloculina* by the time the samples were taken. There was a major decrease in diversity between the pre- and post-ash assemblages. The presence of *Reophax* as an early recolonising species conforms with observations made in experiments on recolonisation at 3912 m in the Panama Basin of the Pacific (Kaminski, *et al*.,1988). Further sampling in 1996 (Fig. 8 June 1996) showed that suspension feeding tubular agglutinating foraminifera had re-established themselves (Kuhnt, pers. comm. 1998).

In summary, deposition of ash was a catastrophic event which caused mass mortality of the foraminifera. In each case, there was a new assemblage of opportunistic taxa starting the process of recolonisation and in these two examples even 3-5 years after the eruption the recovery process was clearly only in its early stages.

6. EXPERIMENTS

Experimental studies can help to determine the causes and responses to change but few have been carried out (Moodley and Hess, 1992; Alve and Bernhard, 1995; Moodley, *et al*., 1997).

The response of foraminifera to declining oxygen levels was tested by Alve and Bernhard (1995). They placed a piece of virtually undisturbed sea floor sediment in each of two tanks. One was maintained as a control with normal oxygenated conditions. In the other the oxygen level was reduced incrementally every month over a period of four months to a minimum level of 0.2 ml/l. At this low oxygen level, virtually all the macrofauna died. However, the effect on the foraminifera was to cause previously infaunal species to move out of the sediment and become epifaunal on polychaete tubes extending above the sediment surface. Following re-oxygenation of the water, the foraminifera started to return into the sediment. The dominant species were *Stainforthia fusiformis* and *Bulimina marginata*. *Stainforthia fusiformis* is an opportunist and the first species to recolonise previously anoxic sediments in fjords, as noted above. This experiment shows that foraminifera are able to tolerate very low levels of oxygen for extended periods and that infaunal organisms may become epifaunal in order to track oxygen and survive.

Moodley and Hess (1992) pointed out that, since infaunal foraminifera live close to the redox boundary, it is essential for survival that they are able to tolerate short periods of anoxia (facultative anaerobiosis). This was tested in experiments and it was reported that those taxa with hard tests survived anoxia for a period of 78 days (the duration of the experiment, Moodley, *et al*., 1997).

7. RATE OF RESPONSE

The response of organisms to environmental variability/change will depend on a number of factors including: whether they have a short or long turnover time in relation to the period of change; whether they are euryhaline/stenohaline, eurythermal/stenothermal; opportunists/generalists/equilibrium, etc.; whether the change is potentially favourable (increase in food; decrease in stress) or unfavourable (increase in stress; development of limiting conditions such as severe oxygen depletion)

It appears that for many benthic foraminifera, the generation time is less than three to four months. Therefore, there can be a fairly rapid response to an increase of food but there may be a short time lag between the two. For example, Altenbach (1992) reported that *Cribrostomoides subglobosum* from the Norwegian Sea doubled its bodymass within three days of being given abundant food although this was mainly due to storage of food in vacuoles. After a further seven days the vacuoles had been reduced and the bodymass had increased by 17% compared with the original weight. In the experiments noted above, foraminifera survived anoxia for 78 days but presumably would ultimately be killed by the absence of oxygen.

In considering the response of organisms to environmental variables, some ecological factors are limiting in the sense that there is a threshold beyond which the effects on the organism are either to inhibit reproduction or, at the extreme, to cause death. Perhaps environmental variability does not matter too much as long as it stays within the non-limiting range. However, once one parameter goes close to the limits of tolerance for any given species, the stress level for that species will increase dramatically.

The term niche is used to describe the place of an organism in the ecosystem. The niche embraces the effects of all the ecological factors, both biotic and abiotic. The *fundamental niche* is where a species could in theory exist and the *realised niche* is where it actually does because, in practice, environmental variables interact. For instance, a species may be able to tolerate low salinity as long as the temperature is close to the optimum. However, if both variables are close to the limits of tolerance, their combined effects might be to cause death before the true limit of tolerance of either is reached. Because there are so many variables affecting organisms, in practise the realised niche of any given species will differ from one place to another. In other words, different combinations of factors may be limiting distributions in different areas.

Where an environment deteriorates (for instance, by becoming severely oxygen-depleted), it is the more specialised equilibrium species which disappear first. The generalists and opportunists survive longest. Recovery seems to be a slow process and, in the single example of recovery from anoxia, initiation of colonisation took more than one year. In all cases, the fauna had not reached former species diversity and composition even after several years. Likewise, recovery from a volcanic ash fall is slow (on a human timescale). For further details of the process of colonisation see Alve (in press).

Buzas and Culver (1994) argue that under natural conditions there is a pool of species available to occupy new environments and from this pool more-or-less random subgroups of these establish themselves in any new space. Therefore, it should not be expected that newly created similar environments will have exactly the same mature fauna or that disturbed environments will re-establish their previous faunas.

8. IS IT POSSIBLE TO PREDICT THE CONSEQUENCES OF CHANGE?

This is a ‘what if . . . ‘ question. What will happen if x changes by so much? The United Nations Environment Program commissioned a group of scientists to address the question: what would happen to the coastal areas of the Caribbean if there was a global rise of 1.5 °C and a sea level rise of 20 cm by the year 2025? (Maul, 1993). One conclusion was that beaches and deltas would be much affected by the sea level rise but scarcely affected by the temperature change. On the other hand, estuaries and seagrass beds were considered to be equally at risk from both changes. Corals suffer increased disease with higher temperatures. The important point is that different ecosystems and organisms respond to changes in different ways.

At present no-one has attempted to model the effects of a given environmental change on the distribution and abundance of foraminifera although Culver and Buzas (1995) speculated upon the consequences of global warming. In their opinion, the environments at greatest risk are marshes (including those dominated by mangroves), perhaps more through the associated rise in sea level than the global increase in temperature. However, marsh faunas managed to withstand the rapid rise of sea level following the last glacial maximum (~125 m) so there is no cause to be too pessimistic about their future. Indeed, the greatest threat to marshes is their destruction through so-called ‘land- reclamation’. Of course, it is easy to see that a 1 m rise in sea level would have serious consequences for a marginal marine environment and little or no effect on those environments deeper than inner shelf. It would be expected that such a transgressive event would lead to the lateral migration of the marsh microfauna so that former marsh became covered by unvegetated tidal flats. For example, in a temperate setting a change from a *Jadammina/Trochammina/Miliammina* marsh fauna to an *Ammonia/Elphidium/Miliammina* mudflat fauna.

It is possible to summarise the main trends seen when there is an environmental change (Fig. 9). If the change is from low to high stress (e.g., increase in pollution, influx of phytodetritus) then dominance will increase, while diversity and mean size of individuals will decrease. The abundance of equilibrium species will decrease and, when a certain threshold is reached, that of opportunists increase. If the change is from high stress to low stress (e.g., recovery from pollution or from an ash fall) then the trends will be reversed.

9. THE IMPORTANCE OF BASELINE STUDIES FOR MONITORING ENVIRONMENTAL CHANGE

In order to monitor contemporary environmental change it is necessary to unravel the signal resulting from natural variability from that caused by the shift in environmental conditions. At the present state of knowledge, it is easy to do this using foraminifera where the change is fast and large (e.g., input of organic pollution, volcanic eruption, major change in estuarine circulation).

In order to attempt to document slow environmental change, it is necessary to have a detailed database of the natural variability of both the environment and the fauna (including the species present, dominance, diversity, abundance). This entails gathering time-series data over periods of years. Replicate samples should be taken in order to determine patchiness and to provide statistical rigour. This type of sampling programme is very time-consuming to undertake and, in a research climate where funding is difficult to obtain, unlikely to be regarded as frontier science. Yet this is a mistaken view on the part of funding bodies because such baseline studies are essential prerequisites for monitoring change. Ideally, each country should be responsible for maintaining such studies for its own coastal areas (which are those environments most likely to experience change, whether natural or induced by man). There is also some urgency to undertake such studies because progressive environmental change is already under way. Through the analysis of changes in abundance of marker species; the introduction of new species or serious loss of previously existing species; and changes in species diversity, dominance and abundance which extend well outside the established limits of variability; it is possible to document the extent of environmental changes that have taken (or are taking) place. Two hypothetical examples show the difference between progressive and rapid change (Fig. 10.A, B respectively). In each case there is no doubt that changes are taking place.

In order to plan a time-series survey the following procedure is recommended. If the site is intertidal, establish a permanent station by placing a marker (e.g., post). If replicates are to be taken, two markers should be used spaced some meters apart. The first requirement is to determine the depth below the sediment surface where the majority of individuals live by taking a pilot core and sectioning it horizontally into slices (most living forms are commonly in the 0-1cm interval). Then take replicate samples using a core tube of known area) preferably on a monthly basis. In order to avoid sampling disturbance from month to month, it is necessary to take successive samples from a slightly different position close to the marker and to avoid walking on areas yet to be sampled. The survey should continue for several years. Environmental parameters should be measured at each time of sampling.

10. SUMMARY AND CONCLUSIONS

- with the notable exceptions of catastrophic events such as volcanic eruptions, most environmental changes are progressive being made up of small incremental shifts
- there is a continuum from variability over periods of less than one year to conditions which go beyond the range of annual variability over a longer time period
- change is the norm and there are cycles with different periodicities
- in general, because of the short generation time, foraminifera respond quickly to seasonal environmental variability
- as with the macrofauna, when adverse conditions develop, the first taxa to disappear are the more specialised ones and the survivors are the generalists with greater tolerance to environmental stress
- likewise, after the destruction of a microfauna, the first colonisers are opportunists, typically very small in size and with short generation times.

Care must be taken to distinguish between an *apparent faunal change* which is within the normal range of variability and true environmental change.

The final conclusion is that: through the analysis of changes in abundance of marker species; the introduction of new species or serious loss of previously existing species; changes in species diversity, dominance and abundance which extend well outside the established limits of variability; it is possible to document the extent of environmental changes that have taken (or are taking) place.

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Table 1. Summary of standing crop data.

Table 2. Analysis of variance (single factor ANOVA, 5% confidence) of standing crop data. *SS* = sum of squares, *df* = degrees of freedom, MS = mean of squares, F = F test, P-value = confidence value, F-crit = critical value of F.

Table 1. Standing crop data for studies of two or more years duration.

AREA	YEAR	STANDING CROP 10 cm^3 Range	Monthly mean	Monthly SD	No. of samples	SOURCE
Bottsand	1965	30-280	135	70	12	Lutze, 1968
Germany	1966	20-65	61	54	12	
	1967	65-200	89	54	6	
Baltic	1973-74	23.5m 47-303	141	64	22	Wefer, 1976
Germany	1974-75	23.5m 36-121	83	46	14	
	1973-74	27m 58-364	198	101	21	
	1974-75	27m 201-1067	536	345	14	
Exe	1979*	7-65	28	20	12	Murray, 1983
England	1980*	9-46	26	13	12	* *Nonion*
	1981*	9-32	19	9	7	*depressulus*
Deseado	1961°	2-13	8	4	8	Boltovskoy, 1964
Argentina	1962°	1-36	11	11	12	° *Elphidium*

	1963°	14-44	36	9	4	*macellum*
Deseado	1964	26-128	61	26	11	Boltovskoy and
Argentina	1965	12-29	21	6	12	Lena, 1969a
	1966	35-51	43	11	4	
Hamana	1987-88	13-493	166	199	5	Matsushita and
Japan	1988-89	9-971	285	285	12	Kitazato, 1990[1]
Bahrain	1991	2-65	18	17	11	Basson and
	1992	11-81	39	27	12	Murray, 1995
	1993	40-42	41	2	2	

[1] Original data supplied by Kitazato.

Fig. 1. Variability and change. A. Variability about a mean: no change. B. Variability about a mean with a progressive change. C. Variability about a mean which has longer-term cyclic variability; segments **a** and **b** may *appear* to indicate change.

Fig. 2. Time-series data on standing crop. A. Bottsand Lagoon, Germany (Data from Lutze, 1968). B. Exe estuary, England (Data from Murray, 1983). C, D. Puerto Deseado, Argentina (Data from Boltovskoy 1964; Boltovskoy and Lena, 1969a);.

Fig. 3. MDS plot of Bahrain standing crop time-series data with no transformation and using the Bray-Curtis similarity index. Stress = 0.04. Dark field for months 1-18, light field for months 19-25 (Month 1 = February). Data from Basson and Murray, 1995.

Fig. 4. Comparison of average relative and absolute abundance of agglutinated tests and total abundance of tests between samples collected in 1937 and 1992/1993 in the Skagerrak (Reproduced from Alve and Murray, 1995).

Fig. 5. MDS plot of Skagerrak core 56 data with no transformation and using the Bray-Curtis similarity index. Stress = 0.03. Dark field = samples from 0-0.5 to 5-6cm, light field for samples from 8-10 to 16-18 cm. Data from Alve, 1996.

Fig. 6. Mean accumulation rate of tests in core 56 from the Skagerrak. Solid line = whole assemblage; broken line = agglutinated component. Data from Alve, 1996.

Fig. 7. Schematic diagram of a core penetrating organically-contaminated deposits. From the base up the generalised faunal changes show the response to increasing pollution and extinction at the pollution maximum. The dotted lines above show the possible path of recovery following improvement in the environment. See text for further discussion. (Reproduced with permission from Alve, 1996).

Fig. 8. Cartoon showing the succession of events from pre-ashfall to post-ashfall in the South China Sea adjacent to Mount Pinatubo (Reproduced with permission, Kuhnt, pers. comm., 1998).

Fig. 9. Summary of trends shown by assemblages responding to environmental change. The y axis values are arbitrary units. See text for discussion.

Fig. 10. Two hypothetical examples of change. Variability in abundance (solid line) and the 10 point moving average (broken line) change from left to right. A. Progressive change, B. Rapid change (time 20/21).