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Intracolony variation in zooid size in cheilostome bryozoans as a new technique for investigating palaeoseasonality

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Abstract

Variation in zooid size within colonies of fossil cheilostome bryozoans is presented as a potential source of information on palaeoseasonality. We base our approach on the inverse relationship between temperature and zooid size in bryozoans, and analyse the mean intracolony coefficient of variation (CV) in zooid length, zooid width and zooid area (length × width) in a number of Recent bryozoan species collected from many seasonally different environments. A highly significant, positive correlation was obtained between the mean annual range of temperature (MART) experienced by the colonies and the mean intracolony CVs in zooid lengths ($R^2 = 74.7\%$), zooid widths ($R^2 = 58.9\%$) and zooid areas ($R^2 = 80.0\%$). An algebraic equation derived from regression analysis of mean intracolony CV of zooid area and MART is proposed as a new method of investigating the MART of ancient seas by assessing variation in zooid area within fossil cheilostome colonies. This technique is then applied to bryozoan colonies from two Neogene shallow-water deposits in Western Europe. Results from the Coralline Crag in south-eastern England reveal a moderate level of seasonality, in keeping with previous estimates of seasonality for British seas during the Pliocene. Results from the middle Miocene 'faluns' in north-west France suggest less seasonal variation in temperature than occurs in comparable seas today. We conclude that the technique represents a useful new approach that offers some benefits over other techniques of assessing seasonality in marine palaeoenvironments. © 2000 Elsevier Science B.V. All rights reserved.

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1. Introduction

A full understanding of any climate requires an appreciation of the amount of seasonal variation in temperature. This is important not only for present-day climatology but also for investigation

of ancient environments. Describing the thermal characteristics of a palaeoenvironment entirely on the basis of a single estimate of the mean annual temperature (MAT), as is often done, generates only limited palaeoclimatological information. Estimation of seasonality, or the mean annual range of temperature (MART), is considerably more comprehensive and can provide much greater insights into the biology, ecology and climatology of a palaeoenvironment. In this paper, we review current approaches and their limitations in assess-

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ing palaeoseasonality. We then introduce and apply a new technique that uses bryozoan morphology as an indicator of the MART.

1.1. Seasonal temperature regimes in modern marine environments

Seasonal temperature regimes in modern marine environments show a considerable geographic variation. Pronounced seasonal variation in temperature is characteristic of mid-latitude temperate seas in which the MART can often exceed 20°C. Such thermal fluctuations are chiefly driven by seasonal changes in surface water heating as a result of the obliquity of the ecliptic of the earth away from the sun. However, seasonal stratification, water column mixing, and surface water cooling from cold continental winds during the winter can influence local temperature regimes. Where coastal waters are shallow and restricted from the moderating effect of the open ocean, continental atmospheric temperature regimes can result in thermal characteristics akin to a large lake rather than the open ocean (Prandle and Lane, 1995).

Marine environments with low levels of seasonal variation in temperature include the abyssal depths, very-high-latitude seas, and many tropical regions. Deep abyssal waters are buffered against extremes of temperature, while constant, low temperatures, minor surface to bottom thermal gradients, and the absence of a permanent thermocline typify polar waters. Seasonal variation in temperature in Antarctic coastal waters can be as little as 1.5°C (Clarke et al., 1988). In tropical regions, surface-water heating is relatively constant, waters are typically permanently stratified, and seasonal variation in temperature is low. However, this pattern does not pertain to tropical coastal waters subject to periodic upwelling. For instance, the Panamanian Caribbean coast remains a stable 28–30°C, while just 100 km to the south, strong seasonal upwelling in the Gulf of Panama (eastern Pacific) results in a MART of around 11°C (D'Croz and Robertson, 1997).

1.2. Importance of studying palaeoseasonality

Information on seasonal temperature regime of an ancient sea can provide insight on environmen-

tal factors such as latitude and depth of the sea, the local, regional and global oceanography and climate (e.g. Andreasson and Schmitz, 1996), water-column stratification (e.g. Purton and Brasier, 1997), and upwelling (e.g. Teranes et al., 1996). In addition, seasonality data will increase the understanding of the palaeobiology of fossil organisms. The life cycles, growth habits, behaviour, reproduction, physiology and ecology of most organisms are greatly influenced by their seasonal environments. Furthermore, because physiological tolerances often determine the geographical ranges of species (Cox and Moore, 1993), seasonality plays an extremely important role in biogeography. None the less, the incorporation of seasonality data into palaeo-studies is often inadequate, particularly in the marine realm. Quantitative estimates of palaeoseasonality therefore represent an important goal for both palaeobiologists and palaeoclimatologists.

1.3. Previous approaches to assessing palaeoseasonality

Palaeoseasonality is traditionally estimated by analogy with extant organisms. This approach, commonly termed the 'nearest living relative method' or 'taxonomic uniformitarianism', assumes that the environmental parameters that govern the distribution of present-day biota similarly govern the distributions of nearest living relatives within a fossil assemblage. In its simplest form, this approach divides fossil assemblages into 'more' or 'less' seasonal than present. More sophisticated developments involve transfer function techniques and multivariate statistical analysis of Recent assemblages to formulate equations that relate various environmental parameters to species abundance (e.g. Dowsett, 1991). In either case, the reliability of approaches that rest upon the principle of taxonomic uniformitarianism is constrained by a number of assumptions. These include: (1) that we fully understand and are able to isolate the environmental parameters governing the present-day distribution of biota; (2) that the distribution of both present day and fossil biota are in equilibrium with environmental parameters; (3) that the ecological affinities of the organisms

have not changed through time; and (4) that a fossil assemblage is representative of the death assemblage (Lowe and Walker, 1986). In practice, it is unlikely that all of these requirements can ever be fully satisfied. Furthermore, confident application of the nearest living relative method is rarely achieved in pre-Neogene environments, simply because too few extant taxa are available.

An increasingly popular and possibly more promising technique for determining palaeoseasonality is isotope profiling. This technique analyses changes in the isotopic composition of mineralogic material that has been laid down sequentially during seasonal growth of organisms. Variation in the ratio of oxygen isotopes provides information on the seasonal environment in which the organism developed (e.g. Purton and Brasier, 1997), as well as on the growth rates and longevity of fossil animals (Jones, 1998). Isotope profiling can be applied widely, from the enamel of mammalian teeth (Sharp and Cerling, 1998) to the shells of molluscs (Purton and Brasier, 1997) and the tests of long-lived single celled protozoans (Wefer and Berger, 1980). Two preliminary studies have shown potential for the application of this approach to bryozoans (Pätzold et al., 1987; Bader, 2000). With the advent of micro-drilling techniques and small sample analysis, isotope profiling should provide extremely high resolution data on palaeoenvironments (Jones, 1998).

However, despite its great potential, the following considerations indicate that an independent approach to isotopic profiling is highly desirable. First, a number of investigations suggest serious limitations. For example, variation in the oxygen isotope composition of gastropod, brachiopod and bivalve material from an environmentally stable locality was found to be too great to have been purely the result of seasonal temperature changes (Marshall et al., 1996). In addition, seasonal variation in the oxygen and carbon isotope composition in long-lived, Recent reef corals revealed significant and unexplained differences between coral colonies within the same climatic locality (Guzman and Tudhope, 1998). These studies suggest that isotope profiling may provide inaccurate palaeoclimatic information.

In addition, isotope profiling requires a few

assumptions that, in practice, may not always be met. One is that the material is original and has not been diagenetically altered. Also, if absolute palaeotemperature data are desired, the ratio of isotopes must have been fractionated in equilibrium with the isotopic composition of the ambient water at the time. If only relative trends in palaeotemperature are sought, this is not such a problem. However, if the material was fractionated out of equilibrium, it must be assumed that the degree of disequilibrium did not change on a seasonal basis.

1.4. *Bryozoan zooid size and temperature*

Cheilostome bryozoans are colonial, benthic invertebrates that are common in a wide variety of marine habitats around the world. The fossil record shows that cheilostomes have been abundant and diverse since the late Cretaceous. Colonies are generally sessile and are composed of asexually budded modules, termed zooids (Fig. 1), which are calcified to varying degrees. Once a zooid is budded, it remains a fixed size since the external lateral walls do not undergo subsequent outward expansion. Cheilostome bryozoans generally form encrusting or erect colonies that are epilithic or epibiotic.

The size of normal feeding zooids in cheilostome bryozoans is consistently found to be a function of the ambient water temperature, with smaller

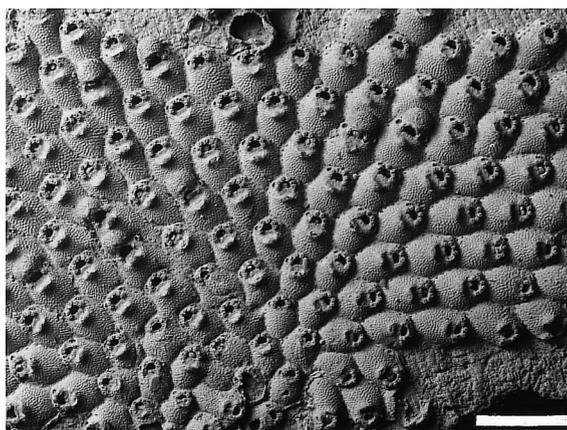


Fig. 1. *Escharina dutertrei*: a cheilostome bryozoan colony from the Pliocene Coralline Crag. The colony is composed of iterated, box-like zooids. Scale bar: 1 mm.

zooids being produced in warmer waters. This occurs both within species over geographical ranges (Ryland, 1963; Morris, 1976), within species over time (Okamura, 1987; Okamura and Bishop, 1988) and within genotypes (individual colonies) over seasonally derived changes in temperature (O'Dea and Okamura, 1999) and laboratory culture (Menon, 1972; Hunter and Hughes, 1994). Such a decrease in body size at higher temperatures is observed in many taxa, ranging from vertebrates to plants, and thus has been termed the 'temperature-size rule' (see Atkinson, 1994). In the Bryozoa, the temperature-size response occurs irrespective of the food levels (Hunter and Hughes, 1994; O'Dea and Okamura, 1999), the reproductive state of colonies, and the rate of growth within colonies (O'Dea and Okamura, 1999).

Conformation of zooids to the temperature-size rule has led to the suggestion that temporal trends in zooid size within bryozoan species could be used to infer relative trends in palaeotemperature (Okamura and Bishop, 1988; Hunter and Hughes, 1994; O'Dea and Okamura, 1999). Although a similar technique has previously been used with bivalves (Strauch, 1968), a foraminiferan (Malmgren and Kennett, 1978) and a mammal (Tchernov, 1984), bryozoans present unique advantages such as iteration of zooids (see also Section 4) that make them particularly suitable.

1.5. *Aims of study*

Here, we develop a novel application of the temperature–size rule to investigate seasonal variations in palaeotemperature. Given that zooid size is temperature-dependent, our study aims to estimate how variation in zooid size within colonies of cheilostome bryozoans is related to the seasonal variation in temperature that a colony experiences. This is achieved by evaluating the sizes of zooids in replicate colonies of a number of Recent species that were collected from a variety of seasonally different environments. Predictions, based on the relationship between within-colony variation in zooid size and seasonal variation in temperature for these Recent species, are then applied, in retrospect, to fossil bryozoans to investigate sea-

sonal variations in temperature in ancient seas. Although seasonal changes in zooid size have been documented within species (Okamura, 1987) and within colonies (O'Dea and Okamura, 1999), this is the first study to use intracolony zooid-size variations in fossil bryozoans to infer palaeoseasonal climates.

2. **Developing the technique: seasonal zooid-size variation in Recent bryozoans**

2.1. *Material, methods and criteria of data collection*

Twenty-nine cheilostome species from 16 localities were found to be suitable for analysis. These species, along with information on the number of colonies sampled, locality, and the associated MART typical of each locality, are listed in Table 1. The identification of suitable species entailed detailed and often extensive inspection of material collected by ourselves and housed in museum and private collections. Species from various localities were chosen only if sufficient replicate material was available (see below) and if climatological data allowed accurate estimates of the MART experienced by the colonies.

The MARTs of the localities ranged from 2.1 to 11.0°C (Table 1). These data were derived from a variety of sources (Table 1) and were calculated as the range between mean summer and mean winter temperatures over a number of years. All data relate to the depth at which the bryozoans were collected except the four Antarctic species from the Discovery Stations, for which surface water data were used. Since Antarctic water temperatures change little with depth, the use of surface water data provides a close approximation of the actual temperatures experienced by benthic colonies.

Because the magnitude of variation in size of any population is often dependent upon the mean size of the individuals, the coefficient of variation (CV) was chosen to examine variation of zooid size within colonies. Since the CV is a measure of the variation as a percentage of the population

Table 1
Recent cheilostome species used to assess the effect of seasonality on intracolony zooid size variation^a

Species	Number of colonies	Location	Depth	MART (°C)
<i>Fenestrulina rugula</i> Hayward & Ryland	5	Signy Island, Ant.	Subtidal	2.1 ⁶
<i>Inversiula nutrix</i> Jullien	5	Signy Island, Ant.	Subtidal	2.1 ⁶
<i>Aspidostoma giganteum</i> (Busk)	5	Disc. St: WS 85, Ant.	79 m	2.1 ^{5, 7}
<i>Cellaria diversa</i> Livingstone	5	Disc. St: 42, Ant.	120 m	2.1 ^{5, 7}
<i>Smittipora levinseni</i> (Canu & Bassler)	5	Mochina Bay, Ven.	Subtidal	2.4 ¹
<i>Watersipora subtorquata</i> d'Orbigny	8	Mochina Bay, Ven.	Subtidal	2.4 ¹
<i>Membranipora tenuis</i> Desor	6	Mochina Bay, Ven.	Subtidal	2.4 ¹
<i>Hippoporella gorgonensis</i> Hasting	5	Mochina Bay, Ven.	Subtidal	2.4 ¹
<i>Reptadeonella</i> cf. <i>plagiopora</i> (Busk)	5	Mochina Bay, Ven.	Subtidal	2.4 ¹
<i>Akatopora</i> sp. Davis	5	El Moreno, Ven.	Subtidal	2.5 ¹
<i>Cosciniopsis incisa</i> (Busk)	5	Disc. St: WS 124, Ant.	40 m	2.5 ^{5, 7}
<i>Melicerita obliqua</i> (Thornely)	5	Disc. St: 175, Ant.	> 20 m	2.5 ^{5, 7}
<i>Electra verticillata</i> Norman	5	Cape Blanco, Maur.	Subtidal	2.9 ^{5, 7}
New species new genus	5	Otago Shelf, NZ	115 m	3.8 ³
<i>Schizosmittina cinctipora</i> (Hincks)	5	Otago Shelf, NZ	83 m	4.0 ³
<i>Calloporina angustipora</i> (Hincks)	5	Otago Shelf, NZ	83 m	4.0 ³
<i>Chiastosella enigma</i> Brown	5	Otago Shelf, NZ	83 m	4.0 ³
<i>Carbasea solanderi</i> Norman	5	Shetland Isles, UK	Subtidal	5.5 ²
<i>Securiflustra securifrons</i> (Pallas)	5	Firth of Forth, UK	64 m	6.5 ²
<i>Aimulosia marsupium</i> MacGillivray	5	Wellington, NZ	Subtidal	6.5 ³
<i>Electra verticillata</i> Norman	6	Sitges, Spain	Subtidal	8.0 ⁴
<i>Parasmittina trispinosa</i> (Johnston)	5	Plymouth, UK	30 m	9.0 ²
<i>Schizoporella errata</i> (Waters)	5	Porlock Bay, UK	Subtidal	10.5 ²
<i>Escharella immersa</i> (Fleming)	7	Porlock Bay, UK	Subtidal	10.5 ²
<i>Escharella labiosa</i> (Busk)	5	Porlock Bay, UK	Subtidal	10.5 ²
<i>Callopora lineata</i> (Linnaeus)	5	Porlock Bay, UK	Subtidal	10.5 ²
<i>Phaeostachys spinifera</i> (Johnston)	5	Porlock Bay, UK	Subtidal	10.5 ²
<i>Escharina vulgaris</i> (Moll)	5	Monaco, France	34 m	10.5 ⁴
<i>Microporella ciliata</i> (Pallas)	5	Monaco, France	34 m	10.5 ⁴
<i>Schizoporella longirostris</i> Hincks	5	Marseilles, France	15 m	11.0 ⁴

^a Also listed: the growth habit of species, number of colonies utilized for each species, the locality, depth and the mean annual range of temperature (MART) typical for the locality of collection. Material from Porlock (UK) was collected in 1997, material from France was donated by J.G. Harmelin (Centre d'Océanologie de Marseille), and *Fenestrulina rugula* colonies were borrowed from British Antarctic Survey collections. All other material is housed in the Department of Zoology at the Natural History Museum, London. Data on MART are from various sources; (1) Hastenrath and Lamb (1977), (2) Lee and Ramster (1981), (3) Jillet (1969), (4) Mars (1963), (5) Shea et al. (1990), (6) Clarke et al. (1988), (7) Levitus (1982). Ven. = Venezuela; Maur. = Mauritania; Ant. = Antarctica; Op. Tab. = Operation Tabarin; Disc. St. = Discovery Station.

mean, comparisons can be made between populations with differing means.

We used a minimum of five colonies per species for analysis. Within each colony, 20 normal feeding zooids (autozooids) were randomly selected using a transparent grid over the colony and random numbers as co-ordinates. For each zooid, the maximum length and maximum width were measured using a micrometer eyepiece fitted to a stereomicroscope. The length and width were combined to derive an index of zooid frontal area

(length × width). The CVs for zooid lengths, widths and areas for each colony were generated and then averaged for each species at each locality, thereby providing a mean intracolony CV for each measure of zooid size for each species at a single locality.

The selection of species and colonies was rigorously standardized and a number of rules adhered to. This approach reduces variation in the data due to factors known to affect zooid size, including; substratum irregularities, biotic interactions (e.g.

competition for space; see Poluzzi and Coppa, 1991), physical damage to colonies, and water-flow regime (Okamura and Partridge, 1999).

Species were utilized only if: (1) zooid margins were clearly distinguishable throughout ontogeny; (2) colonies were sufficiently calcified that zooid distortion as a result of desiccation was not significant; (3) colonies could potentially reach a fairly large size [i.e. were not determinately growing small spot colonies; Bishop (1989)]; and (4) at least five replicate colonies were available from a single locality.

Colonies were selected for analysis only if: (1) they comprised at least 30 ontogenetically complete autozooids; (2) substratum irregularities were minimal at both the zooid and colony level (not relevant for erect species); (3) no part of the colony was restricted from the ambient environment (e.g. by an overhang); and (4) levels of competition from neighbours were low, and epibionts did not restrict growth.

Although the selection of zooids within colonies was randomized, some subjective sampling was exercised. A randomly selected zooid was only measured if: (1) it was a normal autozooid (e.g. it was not an ovicellular zooid, kenozooid, avicularium or a vibraculum); (2) it was not frontally budded from the original linear series; (3) it was outside the zone of astogenetic change [a region of a colony that is characterized by a successive increase in zooid size; Boardman et al. (1969)]; or (4) it was not 'abnormal' in size or shape as a result of physical damage or biotic interactions.

For each species, the mean intracolony CVs of zooid length, width and frontal area were plotted against the MART for the respective localities from which colonies were collected. The relationships between the MART and mean CV of zooid length, width and area were analysed using a Model I linear regression (MINITAB).

2.2. Results

Fig. 2 displays the mean intracolony CV's of zooid length (Fig. 2a), width (Fig. 2b) and area (Fig. 2c) for each species at each locality plotted against the MART experienced by the colonies. Each single point represents a mean intracolony

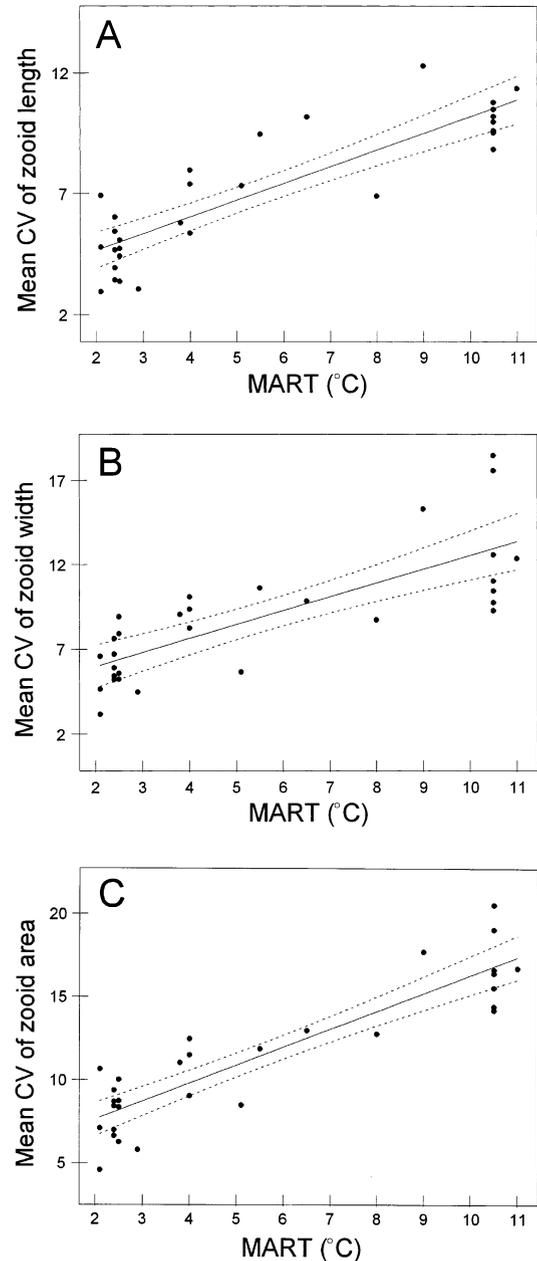


Fig. 2. Plots of the mean coefficient of variation (CV) of intracolony variation in zooid morphology against the mean annual range of temperature (MART) experienced by the colonies (A) Zooid length ($R^2=74.7\%$). (B) Zooid width ($R^2=58.9\%$). (C) Zooid area (length \times width ($R^2=80.0\%$). Each point represents the mean CV of at least five colonies for a single species at a single locality. Plots are fitted with a linear trend line, the 95% confidence limits of which are indicated by dashed lines.

Table 2

Results of regression analysis (ANOVA) on the response of the mean coefficient of variation (CV) of intracolony zooid length, width and area in cheilostome bryozoan colonies with the mean annual range of temperature experienced by the colonies

Response	Regression results			
	R^2 (%)	MS	F	P
Zooid length	74.7	172.11	86.46	<0.001
Zooid width	58.9	240.91	42.61	<0.001
Zooid area	80.0	422.31	117.04	<0.001

CV from a species at a single locality, and each plot is fitted with a trend line derived by the least-squares method and the 95% confidence intervals for the line. Regression analysis revealed that each measure of zooid size shows a highly significant ($P < 0.001$) and positive correlation with the MART (Table 2). The most robust measure of zooid size was zooid frontal area ($R^2 = 80.0\%$) with zooid length showing a similarly strong association ($R^2 = 74.7\%$) and zooid width less so ($R^2 = 58.9\%$).

To ascertain whether these relationships were best represented by a linear regression, the residuals of each were plotted against the MART (Dytham, 1999). No patterns were observed in the plots, thus supporting the interpretation of a linear rather than a curved relationship.

2.3. Algebraic technique for assessing seasonality

It is legitimate to rearrange the algebraic predictor resulting from a regression so that the 'effect' can predict the 'cause', although the confidence intervals of the previous regression cannot be applied to the predicted data (Sokal and Rohlf, 1995). As zooid frontal area demonstrates the strongest relationship with the MART (Table 2), we propose that this measure of zooid size will provide the best estimate of the MART for fossil bryozoan colonies. Thus, by rearranging the linear equation derived from regression analysis, the following is presented as a novel method of determining palaeoseasonality:

$$\text{MART} = -3 + 0.745(b)$$

where MART = mean annual range of temperature experienced by the bryozoan colonies ($^{\circ}\text{C}$), and b = the mean intracolony CV of zooid frontal area (derived as stated previously).

2.4. Sources of error and assumptions of approach

Although rigorous steps were taken to optimize the collection of data from Recent colonies, background noise is apparent in the plotted data (Fig. 2) and the resulting linear equations from regression analysis. Since each equation has a positive constant, a MART of 0°C does not result in zero intracolony variation in zooid size, as would be expected if the measured variations in zooid size were purely the result of temperature variations. Many factors may account for this noise and thus compromise the accuracy of the technique. Such background variation cannot be removed from the analysis and is inherent within bryozoan colonies. While this variation is possibly the most important drawback, we none the less believe that the technique offers a useful and independent means of inferring palaeoseasonality provided that large data sets are used, and the collection of data are rigorously standardized using the criteria described previously.

One of the main sources of noise in the data is likely due to varying growth rates and longevity of the different species used. Although attempts were made to reduce such effects through the careful selection of species and colonies, the life histories of most bryozoan species are poorly understood (McKinney and Jackson, 1989). Growth of some species will clearly be restricted to certain times of the year, and growth rates within a year will vary (e.g. O'Dea and Okamura, 1999), thereby introducing a sampling bias towards smaller or larger zooids within colonies. Another related potential source of error is intracolony variation in secondary thickening of internal walls that occurs in some cheilostomes (Wass, 1991). Lack of recognition of such thickening could result in measurement errors if the external lateral walls are obscured. However, careful inspection of potential material for study should reveal such instances and suggest species to avoid.

Apart from the noise in the data, we must point out the following assumptions on which the approach is based:

1. That the modern climatic data are reliable.
2. That zooid size variations within the colonies selected for measurement are primarily controlled by variations in temperature.
3. That the nature of the zooid size response to temperature does not vary between species and has not changed through geologic time.

Of particular concern is the assumption that zooid size responds primarily to temperature. It is conceivable that temperature could be a correlate of some other seasonally varying environmental factor that influences zooid dimensions. However, many studies have revealed temperature-related changes in zooid size irrespective of other seasonally influenced factors, including food availability (Hunter and Hughes, 1994; O'Dea and Okamura, 1999), salinity (O'Dea and Okamura, 1999), and reproductive state and growth rate (O'Dea and Okamura, 1999). Consideration of responses of the populations of *Electra verticillata* from Mauritania and Spain provides further evidence that zooid size varies directly with temperature as the variation in zooid size is in keeping with the very different seasonal temperature regimes experienced by both populations (Table 1). This example additionally indicates that the relationship between intracolony zooid size variation and seasonal temperature regime occurs within species [as was also shown by Okamura and Bishop (1988)] and is not a taxonomic artifact.

Evidence that the relationship between temperature and intracolony variation in zooid size does not vary between species is provided by the wide variety of environments from which Recent colonies were collected, and conformation to the trend by multiple, diverse species. In the study, low MART localities included warm equatorial coastal seas (the Caribbean), cold high-latitude seas (Antarctica) and a deep temperate sea below the seasonal thermocline (Otago Shelf). Although each environment is fundamentally different in many respects, the low level of seasonal variation in temperature was none the less associated with low levels of variation in zooid size. This result strongly suggests that the changes in zooid size

largely represent common responses to temperature fluctuations by all bryozoans. Conformation to the trend by multiple species is in keeping with the apparently universal response of body size to temperature. The ubiquity of this response suggests that it may represent an unavoidable biological phenomenon (e.g. Atkinson, 1994; van Voorhies, 1996; Atkinson and Sibly 1997; O'Dea and Okamura, 1999), and its wide documentation has resulted in reference to the relationship as 'the temperature–size rule' (Atkinson, 1994). We are therefore confident that the relationship between zooid size and temperature is similar amongst species and, furthermore, that it has not changed through geologic time. This latter assumption gains support from our subsequent analysis (see below) of seasonality from Coralline Crag bryozoans, which is in agreement with previous estimates of seasonality during the Pliocene.

3. Application of technique to investigate palaeoseasonality in two case studies

In this section, our technique is applied to investigate the seasonality in the Pliocene Coralline Crag in Britain and the Miocene 'faluns' in France. Presentation of these two case studies aims not only to further understand the palaeoclimate during these two periods but also to test the strength and validity of the technique when applied to fossils. The Coralline Crag was chosen because a great deal is known about the temperature regime of the time, and it thus serves as a 'test' of our approach. The 'faluns' were studied because seasonality has not previously been estimated from this deposit, previous seasonality data from Miocene terrestrial localities has provided conflicting results, and the abundance and preservation of bryozoan material provided colonies that were adequate for our analysis.

3.1. Depositional environment of the Coralline Crag

The Coralline Crag is a 12 m thick deposit of cross-bedded, bioclastic calcareous sand that outcrops in Suffolk, southern England (Fig. 3).

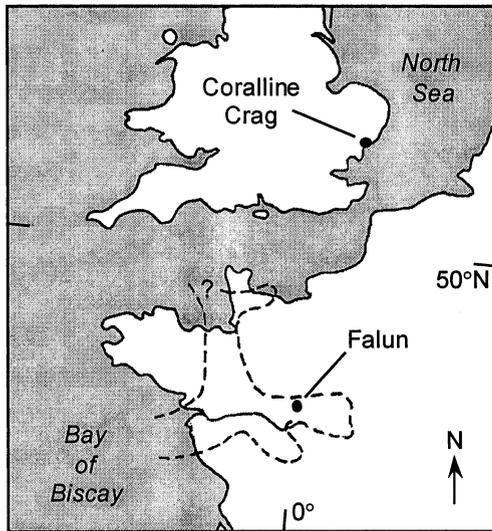


Fig. 3. Neogene fossil localities used in this study: the Pliocene Coralline Crag in south-east England and the middle Miocene 'faluns' at Channay-Sur-Lathan in north-west France. The dashed area represents the inferred limits of the shallow sea covering north-west France during the deposition of the 'faluns' (from Alvinerie et al., 1992).

Thorough analysis of the Coralline Crag fauna has dated the deposits at 3.55–3.75 Ma; Lower Pliocene (see Funnel, 1996). The succession is rich in well-preserved micro- and macrofossils and yields an abundant and diverse assemblage of erect and encrusting bryozoans. It has long been recognised that the Coralline Crag was deposited in a sea that was considerably warmer than occurs around the British Isles at present (Wood, 1848–1882). Waters entering the sea of the Coralline Crag were predominantly from the south through the then wider straits of Dover (see Funnel, 1996 and references therein), and seasonal water-temperature estimates range from 10 to 24°C (see Wilkinson, 1980 and references therein). Coccolith assemblages in the Crag suggest that the sediments were deposited in waters with weak tidal currents that had a pronounced Atlantic influence (Jenkins and Houghton, 1987).

Previous palaeoenvironmental analysis of the Coralline Crag suggests that the sea underwent less seasonal variation in temperature than occurs at present. By assessing the extant bryozoan fauna of the Crag, Cheetham (1967) estimated a maxi-

imum summer temperature of no more than 21°C, and Lagaaij (1963) estimated that the minimum winter temperature did not fall below 14°C. Thus, these two studies suggest a maximum annual range of temperature of 7°C. Using the presence of extant species of Foraminifera, Jenkins and Houghton (1987) suggested a maximum annual range of temperature of 8°C. The analysis of Foraminifera assemblages from Deep Sea Drilling Program site 552 indicates that the north-east Atlantic surface water underwent a MART of 4.9°C at the time of deposition of the Coralline Crag (Cronin and Dowsett, 1996), which is less than the seas at a similar locality experience today (Lee and Ramster, 1981).

3.2. *Palaeoseasonality of the Coralline Crag: material and methods*

Coralline Crag bryozoans were obtained from collections of the Natural History Museum, London. Eleven species were appropriate for study (see Table 3) using the methods and criteria of data collection employed for the Recent species (see Section 2.1). Substitution of the mean intracolony CV of zooid area in the regression equation obtained for Recent species allowed us to infer the associated MART experienced by each species sampled from the Coralline Crag.

3.3. *Palaeoseasonality of the Coralline Crag: results and conclusions*

The overall mean obtained from the individual mean intracolony CVs for the 11 species studied provides an estimated MART of 6.6°C (Table 3). The MART estimated individually by the 11 species ranged from 4.6 to 8.9°C, and the standard deviation of the mean was 1.3°C. Today, there is a more seasonal environment in the southern North Sea, with a benthic MART of around 11.5°C (Lee and Ramster, 1981). Our result corroborates previous estimates of seasonality for the Coralline Crag (see previously) and thus provides evidence for the validity of our technique.

The shift in the seasonal regime in the seas around the British Isles since Pliocene times is likely to be a function of myriad environmental

Table 3

Cheilostome species from the Pliocene Coralline Crag, the number of colonies used to determine the mean coefficient of variation (CV) of intracolony zooid areas of each species, together with derived estimates of mean annual range of temperature (MART)

Species	Number of colonies	Mean CV	Estimated MART (°C)
<i>Cribrilina cryptoecium</i>	6	13.42	7.00
<i>Membranipora oblonga</i>	5	12.44	6.26
<i>Escharella immersa</i>	6	13.39	6.97
<i>Escharella labiosa</i>	6	10.25	4.63
<i>Fenestrulina malusii</i>	5	14.70	7.95
<i>Escharina dutertrei</i>	5	12.40	6.23
<i>Cribrilina watersi</i>	5	12.56	6.36
<i>Amphiblestrum trifolium</i>	5	11.06	5.24
<i>Schizomavella auriculata</i>	5	16.05	8.96
<i>Chorizopora brongniartii</i>	5	11.31	5.43
<i>Cellaria sinuosa</i>	5	13.84	7.31
Overall mean		12.85	6.58
Overall standard deviation		1.68	1.25

factors. During deposition of the Coralline Crag, the waters entering the British Isles from the Atlantic were much warmer than at present, the North Atlantic warm water gyre was displaced northwards (Cifelli, 1976), and the Gulf Stream and North Atlantic Drift were likely to have been enhanced (Cronin and Dowsett, 1996). Continental regions were also generally warmer (see Shabalova and Konnen, 1995). Thus, winter-time cooling of surface waters through contact with continental air may have been less intense and the associated seasonal variation in temperature reduced.

An additional explanation is that the sea of the Crag may have been deep enough to allow a well-developed thermocline to persist (Jenkins and Houghton, 1987), thus buffering the benthic environment from marked seasonal shifts in temperature. Today, the southern North Sea is generally too shallow and well mixed to allow prominent seasonal thermal stratification to develop (Lee and Ramster 1981). Bathymetric estimates for the Coralline Crag have ranged from 10 to 305 m. Wilkinson (1980) believed the depth to be near 20 m, in which case, the entire water column was probably well mixed, particularly if there was a tidal influence, as has been suggested (Jenkins and Houghton, 1987). However, the sediments of the Crag suggest that deposition occurred within a water body with a well-developed thermocline

(Jenkins and Houghton, 1987). To resolve the question of thermal stratification in this sea, an estimate of seasonality from surface waters is required. If the level of seasonality in surface waters greatly exceeds that in benthic waters, there would be a strong case for thermal stratification.

3.4. *Depositional environment of the Miocene 'faluns'*

In north-west France, a few disused quarries outcrop parts of highly fossiliferous, marine deposits, known locally as the 'faluns' (Fig. 3). At Channay-sur-Lathan, the 'faluns' are represented by a set of unconsolidated bioclastic sands that have become preserved and exposed by regional metamorphic events. The presence of oblique and cross-bedded sedimentary structures suggests that the sediments were deposited in a shallow (<50 m) sea under high-energy conditions (Lécuyer et al., 1996). Around 1000 fossil species of marine invertebrates, fish, terrestrial crocodiles, and mammals are present (Cavelier, 1989). The assemblage of foraminiferans indicates a Langhian to early Serravallian age of approximately 16–14 Ma, i.e. early middle Miocene (Lécuyer et al., 1996).

The thermophilic faunal assemblage of the 'faluns' indicates mean annual water temperatures much warmer than the present day and analogous to the sub-tropical marine realm (Lécuyer et al.,

1996). Oxygen isotopic composition of phosphates in vertebrate teeth and bone indicates a mean annual water temperature of 20°C (Lécuyer et al., 1996). There are no estimates of seasonal variation in temperature for the 'faluns' or for any other mid-latitude marine environment of similar age.

3.5. *Palaeoseasonality of the Miocene 'faluns': material and methods*

Bryozoans encrusting smooth pebbles or bivalves were collected from a single stratigraphic horizon in the 'faluns' deposit at Channay-Sur-Lathan, north-west France (Fig. 3; see also Buge, 1957; p. 20). Five species were identified as suitable for study (see Table 4) using the methods and criteria of data collection employed for Recent species.

3.6. *Palaeoseasonality of the Miocene 'faluns': results and conclusions*

The overall mean obtained from the individual mean CVs of the five species studied provided an estimated MART of 5.4°C (Table 4) and a standard deviation of 1.1°C. The range in the MART indicated by the individual species was between 4.2 and 6.9°C (Table 4). Today, the northern part of the Bay of Biscay averages a MART of 8°C (Shea et al., 1990).

The sea of the 'faluns' was not exposed to fully oceanic conditions as it was connected to the

Atlantic Ocean only via a shallow strait to the west (Fig. 3). Estimates of high salinities (Lécuyer et al., 1996) and the presence of gypsum in some localities (Durand, 1960) substantiate this view by indicating that during deposition of the 'faluns', evaporation probably exceeded precipitation. Today, enclosed epicontinental seas of similar latitudes undergo seasonal fluctuations in temperature more in accord with the atmospheric continental climate than with the oceanic temperature regime (Prandle and Lane, 1995). Thus, our estimate of a relatively low MART for the 'faluns' suggests that the prevailing continental climate in north-west France during the Middle Miocene was more 'equable' than today [defined by Sloan and Barron (1990)] as a 'substantially reduced annual cycle of temperature'.

Faunal and floral evidence suggests that pre-mid Miocene continental regions experienced greater 'equability' compared to subsequent periods (e.g. Markwick, 1994; Smith and Patterson, 1994), although the evidence is fragmentary and frequently contested (e.g. Andreasson and Schmitz, 1996). None the less, our results provide independent evidence that continental Europe may have been more 'equable' at this time.

4. Conclusions

We have shown that a highly significant linear relationship exists between the mean annual range of temperature and variation in zooid size within colonies of cheilostome bryozoans. Application of this relationship allows us retrospectively to derive absolute estimates of the MART of an ancient sea by interpolation of zooid size variation in fossil bryozoan colonies. This approach has provided a reasonable estimate of the MART for the Pliocene sea of the Coralline Crag and the first estimate of seasonality for the middle Miocene sea of the 'faluns' in north-west France.

Our technique may be particularly useful for application in shallow-water marine environments for the following reasons: (1) being sessile organisms, bryozoans provide an estimate of seasonality that is relevant to a single locality, unlike organisms which may migrate seasonally through water

Table 4

Cheilostome species from the Miocene 'faluns', the number of colonies used to determine the mean coefficient of variation (CV) of intracolony zooid areas of each species, together with derived estimates of mean annual range of temperature (MART)

Species	Number of colonies	Mean CV	Estimated MART (°C)
' <i>Biflustra</i> ' <i>savartii</i>	5	10.91	5.13
<i>Thalamoporella neogenica</i>	5	9.63	4.17
<i>Callopora</i> cf. <i>lineata</i>	5	10.11	4.53
<i>Steginoporella rhomboidalis</i>	5	12.41	6.24
<i>Escharoides coccinea</i>	5	13.26	6.88
Overall mean		11.26	5.39
Overall standard deviation		1.53	1.14

bodies (e.g. foraminiferans, ammonites, fish); (2) cheilostome bryozoans are common fossils in Cretaceous, Paleogene, Neogene and Quaternary marine sediments; (3) cheilostome bryozoans often tolerate broad thermal ranges; (4) cheilostome colonies are generally small, thereby facilitating collection of large amounts of material; (5) colonies comprise many zooids, thus providing ample replicate data; and (6) the technique is easily applied and inexpensive. We conclude that, provided appropriate data are collected with care, bryozoans offer a unique and valuable source of information for palaeoenvironmental inference. Our technique provides an independent means of estimating palaeoseasonality that does not suffer from the assumptions and errors inherent in other techniques currently used to estimate palaeoseasonal temperature regimes. Thus, provided sufficient bryozoan material is present for investigation, our technique should be highly complementary to existing approaches.

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References

- Alvinerie, J., Antunes, M.T., Cahuzac, B., Lauriat-Rage, A., Montenat, C., Pujol, C., 1992. Synthetic data on the paleogeographic history of northeastern Atlantic and Betic-Rifian basin, during the Neogene (from Brittany, France, to Morocco). *Palaeogeogr., Palaeoclimatol., Palaeoecol.* 95, 263–286.
- Andreasson, F.P., Schmitz, B., 1996. Winter and summer temperatures of the early middle Eocene of France from *Turritella* $\delta^{18}\text{O}$ profiles. *Geology* 24, 1067–1070.
- Atkinson, D., 1994. Temperature and organism size—a biological law for ectotherms? *Adv. Ecol. Res.* 25, 1–58.
- Atkinson, D., Sibly, R.M., 1997. Why are organisms usually bigger in colder environments? Making sense of a life history puzzle. *Trends Ecol. Evol.* 12, 235–239.
- Bader, B., 2000. Life cycle, growth rate and carbonate production of *Cellaria sinuosa*. In: Herrera, A., Jackson, J.C.B. (Eds.), Proc. 11th Int. Bryozoology Association Conf.. Allen Press, Panama.
- Bishop, J.D.D., 1989. Colony form and the exploitation of spatial refuges by encrusting Bryozoa. *Biol. Rev. Camb. Phil. Soc.* 64, 197–218.
- Boardman, R.S., Cheetham, A.H., Cook, P.L., 1969. Intracolony variation and the genus concept in Bryozoa. In: Proc. North American Paleontological Convention, 294–320.
- Buge, E., 1957. Les bryozoaires du Néogène de l'ouest de la France. *Mem. Mus. Natl. d'Hist. Nat.* C6, 1–436.
- Cavelier, C., 1989. Le bassin Parisien au Néogène. In: Actes 114e Congr. Natl. Soc. Savantes, Paris 1989, sect. Sci. Géol. Bassin Parisien. Com. Trav. Hist. Sci. Paris, 41–54.
- Cheetham, A.H., 1967. Palaeoclimatic significance of the Bryozoan *Metarabdotos*. *Trans. Gulf Coast Assoc. Geol. Soc.* 17, 400–407.
- Cifelli, R., 1976. Evolution of ocean climate and the record of planktonic foraminifera. *Nature* 264, 431–432.
- Clarke, A., Holmes, L.J., White, M.G., 1988. The annual cycle of temperature, chlorophyll and major nutrients at Signy Island, South Orkney Islands, 1969–1982. *Br. Antarct. Surv. Bull.* 88, 65–86.
- Cox, C.B., Moore, P.D., 1993. *Biogeography. An Ecological and Evolutionary Approach*. Blackwell, Oxford.
- Cronin, T.M., Dowsett, H.J., 1996. Biotic and oceanographic response to the Pliocene closing of the central American isthmus. In: Jackson, J.C.B., Budd, A.F., Coates, A.G. (Eds.), *Evolution and Environment in Tropical America*. University Press of Chicago, Chicago, IL, pp. 21–56.
- D'Croz, L., Robertson, D.R., 1997. Coastal oceanographic conditions affecting coral reefs on both sides of the Isthmus of Panama. In: Proc. 8th Int. Coral Reef Symp. 2. Smithsonian Tropical Research Institute, Balboa, Republic of Panama, pp. 2053–2058.
- Dowsett, H.J., 1991. The development of a long-range foraminifer transfer function and application to late Pleistocene North Atlantic climatic extremes. *Paleoceanography* 6, 259–273.
- Durand, S., 1960. Le Tertiaire de Bretagne. *Mém. Soc. Géol. Minéral. Bretagne* 13, 23–35.
- Dytham, C., 1999. *Choosing and Using Statistics: A Biologist's Guide*. Blackwell, Oxford.
- Funnel, B.M., 1996. Plio-Pleistocene palaeogeography of the southern North Sea basin (3.75–0.60 Ma). *Quat. Sci. Rev.* 15, 391–405.
- Guzman, H.M., Tudhope, A.W., 1998. Seasonal variation in skeletal extension rate and stable isotopic ($^{13}\text{C}/^{12}\text{C}$ and $^{18}\text{O}/^{16}\text{O}$) composition in response to several environmental

- variables in the Caribbean reef coral *Siderastrea siderea*. *Mar. Ecol.-Prog. Ser.* 166, 109–118.
- Hastenrath, S., Lamb, P.J., 1977. *Climatic Atlas of the Tropical Atlantic and Eastern Pacific oceans*. Wisconsin Press, WI, 100 pp.
- Hunter, E., Hughes, R.N., 1994. The influence of temperature, food ration and genotype on zooid size in *Celleporella hyalina* (L.). In: Hayward, P.J., Ryland, J.S., Taylor, P.D. (Eds.), *Biology & Palaeobiology of Bryozoans*. Olsen & Olsen, Fredensborg, Denmark.
- Jenkins, D.G., Houghton, S.D., 1987. Age, correlation and palaeoecology of the St. Erth beds and the Coralline Crag of England. *Mededelingen van de Werkgroep voor Tertiaire en Kwartaire Geologie* 24, 147–156.
- Jillet, J.B., 1969. Seasonal hydrology of waters off the Otago peninsula south-eastern New Zealand. *NZ. J. Mar. Freshwat. Res.* 3, 349–375.
- Jones, D.S., 1998. Isotopic determination of growth and longevity in fossil and modern invertebrates. In: *Isotope Paleobiology and Paleoecology*. Norris, R.D., Corfield, R.M. (Eds.), *Paleontological Society Papers Vol. 4*, 37–67.
- Lagaaij, R., 1963. *Cupuladria canariensis* (Busk)—Portrait of a bryozoan. *Palaeontology* 6, 172–217.
- Lécuyer, C., Grandjean, P., Paris, F., Robardet, M., Robineau, D., 1996. Deciphering 'temperature' and 'salinity' from biogenic phosphates: The $\delta^{18}\text{O}$ of coexisting fishes and mammals of the middle Miocene sea of western France. *Palaeogeogr., Palaeoclimatol., Palaeoecol.* 126, 61–74.
- Lee, A.J., Ramster, J.W., 1981. *Atlas of the Seas Around the British Isles*. Ministry of Agriculture Fisheries and Food, Lowestoft, UK, 140 pp.
- Levitus, S., 1982. *Climatological Atlas of the World Ocean*. National Oceanic and Atmospheric Administration Professional Paper 13. Department of Commerce, Washington, DC., 173 pp.
- Lowe, J.J., Walker, M.J.C., 1986. *Reconstructing Quaternary Environments*. Longman, Harlow, UK.
- McKinney, F.K., Jackson, J.B.C., 1989. *Bryozoan Evolution*. Unwin Hyman, Boston, MA.
- Malmgren, B.A., Kennet, J.P., 1978. Late quaternary palaeoclimatic applications of mean size variations in *Globigerina bulloides* d'Orbigny in the southern Indian Ocean. *J. Paleontol.* 52, 845–854.
- Markwick, P.J., 1994. Equability, continentality and Tertiary climate—The Crocodilian Perspective. *Geology* 22, 613–616.
- Mars, P., 1963. Les faunes et la stratigraphie du quaternaire méditerranéen. In: *Recueil des Travaux de la station marine de l'Endoume*, Marseille 43 (bull. 28), 61–97.
- Marshall, J.D., Pirrie, D., Clarke, A., Nolan, C.P., Sharman, J., 1996. Stable-isotopic composition of skeletal carbonates from living Antarctic marine invertebrates. *Lethai* 29, 203–212.
- Menon, N.R., 1972. Heat tolerance, growth and regeneration in three North Sea bryozoans exposed to different constant temperatures. *Mar. Biol.* 15, 1–11.
- Morris, P.A., 1976. Middle Pliocene temperature implications based on the Bryozoa *Hippothoa* (Cheilostomata—Asphora). *J. Paleontol.* 50, 1143–1149.
- O'Dea, A., Okamura, B., 1999. Influence of seasonal variation in temperature, salinity, and food availability on module size and colony growth in the estuarine bryozoan, *Conopeum seurati*. *Mar. Biol.* 135, 581–588.
- Okamura, B., 1987. Seasonal changes in zooid size and feeding activity in epifaunal colonies of *Electra pilosa*. In: Ross, J.R.P. (Ed.), *Bryozoa: Present and Past*. Western Washington University, Bellingham, Washington, pp. 197–203.
- Okamura, B., Bishop, J.D.D., 1988. Zooid size in cheilostome bryozoans as an indicator of relative palaeotemperature. *Palaeogeogr., Palaeoclimatol., Palaeoecol.* 66, 145–152.
- Okamura, B., Partridge, J.C., 1999. Suspension feeding adaptations to extreme flow environments in a marine bryozoan. *Biol. Bull.* 196, 205–215.
- Pätzold, J., Ristedt, H., Wefer, G., 1987. Rate of growth and longevity of a large colony of *Pentapora foliaceae* (Bryozoa) recorded in their oxygen isotope profiles. *Mar. Biol.* 96, 535–538.
- Poluzzi, A., Coppa, M.G., 1991. Zoarial strategies to win substratum space in *Calpensia nobilis* (Esper). In: Bigey, F.P., d'Hondt, J. (Eds.), *Bryozoaires Actuels et Fossiles: Bryozoa Living and Fossil*. 337–360 *Bulletin de la Société des Sciences Naturelles de l'Ouest de la France Mémoire HS 1*. Société des Sciences Naturelles de l'Ouest de la France, Nantes, France.
- Prandle, D., Lane, A., 1995. Stability of the annual temperature cycle in shelf seas. *J. Therm. Biol.* 20, 111–120.
- Purton, L., Brasier, M., 1997. Gastropod carbonate $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ values record strong seasonal productivity and stratification shifts during the late Eocene in England. *Geology* 25, 871–874.
- Ryland, J.S., 1963. The species of *Haplopoma* (Polyzoa). *Sarsia* 10, 9–18.
- Shabalova, M.V., Konnen, G.P., 1995. Climate-change scenarios—comparison of paleoreconstructions with Recent temperature changes. *Climate Change* 29, 409–428.
- Sharp, Z.D., Cerling, T.E., 1998. Fossil isotope records of seasonal climate and ecology: Straight from the horse's mouth. *Geology* 26, 219–222.
- Shea, D.J., Trenberth, K.E., Reynolds, R.W., 1990. *A Global Monthly Sea Surface Climatology*. National Centre for Atmospheric Research, Washington, DC.
- Sloan, L.C., Barron, E.J., 1990. 'Equable' climates during the earth's history? *Geology* 18, 489–492.
- Smith, G.R., Patterson, W.P., 1994. Mio-Pliocene seasonality on the Snake river plain—Comparison of faunal and oxygen isotopic evidence. *Palaeogeogr., Palaeoclimatol., Palaeoecol.* 107, 291–302.
- Sokal, R.R., Rohlf, F.J., 1995. *Biometry*. W.H. Freeman, San Francisco, CA.
- Strauch, F., 1968. Determination of Cenozoic sea-temperatures using *Hiattella arctica* (Linné). *Palaeogeogr., Palaeoclimatol., Palaeoecol.* 5, 213–233.
- Tchernov, E., 1984. Fauna turnover and extinction rate in the Levant. In: Martin, P.S., Klein, R.G. (Eds.), *Pleistocene*

- Extinction. University of Arizona Press, Tucson, AZ, pp. 528–552.
- Teranes, J.L., Geary, D.H., Bemis, B.E., 1996. The oxygen isotopic record of seasonality in Neogene bivalves from the Central American isthmus. In: Jackson, J.B.C., Budd, A.F., Coates, A.G. (Eds.), *Evolution and Environment in Tropical America*. University Press of Chicago, Chicago, IL, pp. 21–56.
- van Voorhies, W.A., 1996. Bergmann size clines: A simple explanation for their occurrence in ectotherms. *Evolution* 50, 1259–1264.
- Wass, R.E., 1991. Intracolony variation in the cheilostome genera, *Adeona* and *Adeonellopsis*. In: Bigey, F.P. (Ed.), *Bryozoaires Actuels et Fossiles: Bryozoa Living and Fossil* 337–360. Bulletin de la Société des Sciences Naturelles de l'Ouest de la France Mémoire HS 1. Société des Sciences Naturelles de l'Ouest de la France, Nantes, France, pp. 523–529.
- Wefer, G., Berger, W.H., 1980. Stable isotopes in benthic foraminifera: Seasonal variation in large tropical species. *Science* 209, 803–805.
- Wilkinson, I.P., 1980. Coralline Crag Ostracoda and their environmental and stratigraphical significance. *Proc. Geol. Assoc* 91, 291–306.
- Wood, S.V., 1848–1882. *The Crag Mollusca*. Part 1 (1848), 1–208; Part 2 (1851–1857), 1–342; Suppl. (1872–1874), 1–231; 2nd Suppl. (1879), 1–58; 3rd Suppl. (1882), 1–24. *Palaeontogr. Soc. Monogr.*