Proceedings of the International Bryozoology Association Conference, 2000, pp. 316-320

Cheilostome Bryozoans As Indicators Of Seasonality In Two Neogene Epicontinental Seas Of Western Europe

Aaron O'Dea
School of Biological Sciences, University of Bristol, Woodland Road, Bristol. BS8 1UG, U.K. email: a.odea@bristol.ac.uk

Beth Okamura
School of Animal and Microbial Sciences, The University of Reading, Whiteknights, PO Box 228, Reading. RG6 6AJ, U.K. email: b.okamura@reading.ac.uk

Abstract

The amount of variation in zooid length within colonies of Recent cheilostome bryozoans has been shown to be a function of the seasonal temperature regime prevailing during a colony's growth, and has been formulated in a regression equation which may be used to estimate absolute values of palaeoseasonality. Using this technique, data on intracolony zooid lengths from colonies from the lower Pliocene Coralline Crag in southern England and the Middle Miocene 'Falun' in Northwest France reveal changes in the seasonal regimes of western European epicontinental seas through the Neogene. An estimated mean annual range of temperature of 5.8ºC (±2.2ºC) during the Pliocene indicates a seasonal regime less pronounced than the seas around western Europe today. This result is supported by independent estimates of palaeoseasonality and is inferred here to be a consequence of an enhanced Gulf Stream and a warmer winter atmosphere. A low mean annual range of temperature of only 2.8ºC (±0.1ºC) estimated for the Middle Miocene implies that a much more 'equable' climate existed on land than at present.

Introduction

Zooid size in cheilostome bryozoans is consistently found to be inversely proportional to the temperature of the ambient water under both field and controlled laboratory conditions (Ryland, 1963; Menon, 1972; Morris, 1976; Okamura, 1987; Okamura, and Bishop, 1988;

Hunter and Hughes, 1994). In general, zooid length shows much greater sensitivity to temperature than zooid width and other width-dependent measures such as area and shape. While the explanations for these phenotypic changes are still debated (see Atkinson and Sibly, 1997), an inverse temperature-size relationship is found in numerous invertebrate and vertebrate taxa (see Van Voorhies, 1995 and references therein)

By assessing variation in module size during seasonal growth of colonial organisms this ecophenotypic response may also prove to be useful for studying palaeoseasonality. Indeed, although a seasonal change in zooid size was inferred in a Recent bryozoan species (Okamura 1987), the implications for assessing palaeoseasonality have not previously been pursued. Recently, we have taken this approach to investigate differences in zooid length within colonies of Recent encrusting cheilostome bryozoans from well-characterised and varying seasonal climates (O'Dea and Okamura, in prep.). This study has revealed that the mean coefficient of variation (CV) of zooid length within colonies is a function of the mean annual range of temperature (MART) prevailing in the area in which the colonies occurred. This relationship is quantified by the exponential regression:

$$\textbf{MART (ºC)} = \mathbf{1.025e}^{\mathbf{0.212(mean\ CV\ of\ intracolony\ zooid\ length)}}$$

Assuming that zooid responses to temperature variation have not changed, this regression equation provides a means of estimating an absolute degree of palaeoseasonality through interpolation of intracolony zooid length data from fossil assemblages. Here we use this technique to investigate the seasonal regimes of two epicontinental seas of Western Europe

during the Neogene. In particular we assess the MART during the Lower Pliocene in southern England and during the Middle Miocene in Northwest France.

Background information on systems of study

The Coralline Crag (Figure 1) comprises a 12m thick suite of cross-bedded, bioclastic calcareous sands in Southern England and has been convincingly aged at around 3.55 - 3.75 Ma; i.e. 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. The Coralline Crag was deposited in a sea considerably warmer than occurs around the British Isles at present, receiving warm waters predominantly from the south through the then wider straits of Dover (see Jenkins and Houghton, 1987; Funnel, 1996 and references therein).

The Middle Miocene in Northwest France is represented by the 'Faluns' (Figure 1), a set of unconsolidated bioclastic marine sands that have become preserved and exposed by regional metamorphic events. These calcareous sediments were deposited under a shallow (50m) sea (Lécuyer et al., 1996). Oblique and cross bedding structures indicate deposition under rather high energy conditions. The 'Faluns' are highly fossiliferous, yielding around 1000 species of marine invertebrates, fossil fish, terrestrial crocodiles, and mammals (Cavelier, 1989 and references therein). Precise dating of the 'Faluns' has been difficult due to the lack of well-preserved micro and nano-fossils. Lécuyer et al. (1996), using an unusually preserved assemblage of foraminifers, suggest a Langhian to early Serravallian age of approximately 16-14 Ma, i.e. early Middle Miocene.

The presence of a thermophilic faunal assemblage places the 'Faluns' within the sub-tropical marine realm (Lécuyer et al., 1996),

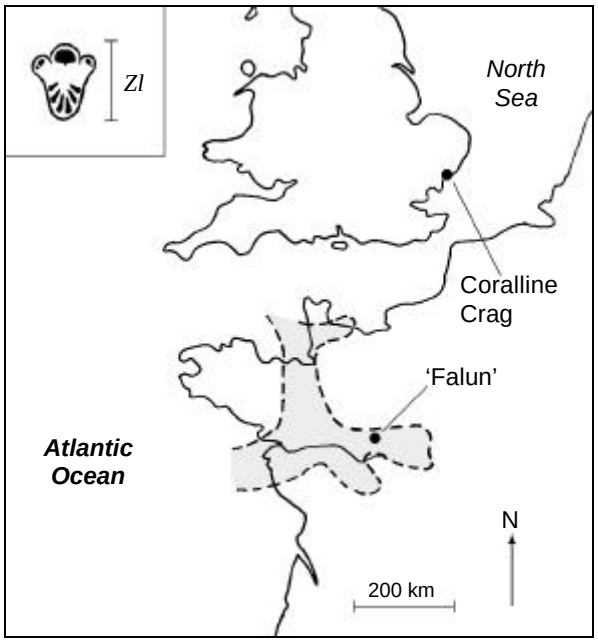

Figure 1. The Neogene fossil localities of western Europe used in this study: The Pliocene Coralline Crag, in Southeast England and the Middle Miocene 'Falun' at Channay-Sur-Lathan in Northwest France. Shaded area represents the shallow sea covering Northwest France during the Middle Miocene (from Alvineries et al., 1992). Inset: Zooid of a cheilostome bryozoan showing measurement of maximum zooid length (*Zl*)

although absolute palaeotemperature estimates from these deposits are limited. Lécuyer et al. (1996) used the oxygen isotopic composition of phosphates in vertebrate teeth and bone to indicate a water temperature of 20ºC (SD ±2ºC) but noted that fluctuations in salinity could easily have caused interpretative problems. Nevertheless, this value agrees with the palaeotemperature estimates of 20-25ºC deduced from the oxygen isotope composition of planktonic Foraminifera from the North Pacific during this time (Savin et al., 1985).

Materials and Methods

Bryozoans encrusting smooth pebbles or bivalves were collected from a single stratigraphic horizon in the 'Falun' at Channay-Sur-Lathan, Northwest France (Figure 1. See also; Buge, 1957; p.20). Material studied from the Pliocene Coralline Crag (Figure 1) is held

in the collections of the British Museum (Natural History).

When using the regression equation to estimate palaeoseasonality we require that several strict rules are adhered to. These include standardising the selection of species and colonies within species to minimise noise due to factors such as variation in colony growth rate between species and microenvironmental effects within colonies (e.g. competition and substrate irregularities). The details are too lengthy to be published here but will be outlined at a later date (O'Dea and Okamura, in prep.)

Five species were identified from the Middle Miocene that were appropriate for this study: *Biflustra savartii* (Savigny-Audouin), *Thalamoporella neogenica* Buge, *Callopora* cf. *lineata* Linnaeus, *Steginoporella rhomboidalis* (Canu and Lecointre) and *Escharoides coccinea* (Abildgaard). Five replicate colonies were available for measurement of each species.

Nine species from the Lower Pliocene were appropriate for study: *Cribrilina cryptooecium* Norman, *Cribrilina watersi* Andersson, *Membranipora oblonga* Busk, *Escharella immersa* (Fleming), *Escharella labiosa* (Busk), *Fenestrulina malusii* (Audouin), *Escharina dutertrei* (Audouin), *Amphiblestrum trifolium* (Wood) and *Schizomavella auriculata* (Hassall). Five colonies of each species were analysed except *C. cryptooecium*, *E. immersa* and *E. labiosa* for which six colonies were available.

For each colony 20 randomly selected zooids were measured for maximum length (Figure 1). A mean CV of intracolony zooid length for each species could then be used to estimate an absolute value of palaeoseasonality by interpolation from the regression presented earlier.

Results

An estimated MART of 5.8ºC (±2.2ºC) was obtained by interpolating the overall mean CV of the nine species from the Coralline Crag using the regression for MART vs. mean CV in intracolony zooid length (Table 1). The MART estimated individually by the nine species ranged from 3.8 - 11.1ºC (Table 1). Similar data from five species of bryozoans from the Miocene 'Falun' estimate a low seasonal regime with an overall MART of 2.8ºC (± 0.1ºC) (Table 2). The range in the MART indicated by the individual species was between 2.7 and 3.0ºC (Table 2).

Today, the seas of Western Europe are considerably more seasonal. A MART of 11.5ºC is recorded in the southern North sea (from Lee and Ramster, 1981) while in the Northern part of the Bay of Biscay the MART is on average around 8ºC (from Shea et al., 1990).

Table 1.
Mean Coefficient of Variation (CV) of intracolony zooid lengths of cheilostome colonies from the Pliocene Coralline Crag, together with derived estimates of mean annual range of temperature (MART). SD = standard deviation.

Species	Mean CV	MART (ºC)
Cribrilina cryptooecium	9.05	6.99
Membranipora oblonga	7.24	4.76
Escharella immersa	6.14	3.77
Escharella labiosa	6.37	3.96
Fenestrulina malusii	8.18	5.81
Escharina dutertrei	7.50	5.03
Cribrilina watersi	7.93	5.51
Amphiblestrum trifolium	7.40	4.92
Schizomavella auriculata	11.21	11.05
Mean	**7.89**	**5.75**
(SD)	(1.53)	(2.21)

Table 2.
Mean Coefficient of Variation (CV) of intracolony zooid lengths of cheilostome colonies from the Middle Miocene 'Falun', together with derived estimates mean annual range of temperature (MART). SD = standard deviation.

Species	Mean CV	MART (ºC)
Biflustra savartii	4.87	2.88
Thalamoporella neogenica	4.59	2.72
Callopora cf. *lineata*	5.09	3.02
Steginoporella rhomboidalis	4.74	2.80
Escharoides coccinea	4.59	2.71
Mean	**4.78**	**2.82**
(SD)	(0.21)	(0.13)

Discussion

The Lower Pliocene

The results of this study indicate that during deposition of the Pliocene Coralline Crag the southern North Sea was comparable in its MART to present day sub-tropical shallow seas as far south as the Canary Islands (Shea et al., 1990). This result corroborates previous estimates of seasonality for seas around the British Isles during this time [i.e: a maximum annual range of 7ºC (from Cheetham, 1967 and Lagaaij 1963), a maximum annual range of 8ºC (Jenkins and Houghton, 1987) and a mean annual range of 4.9ºC (from Cronin and Dowsett, 1996)]. This shift in the seasonal regime in the seas around the British Isles since Pliocene times is likely to be a function of myriad environmental factors. It is known, however, that 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 known to have been generally warmer than at present (see Shabalova and Konnen, 1995), and therefore the cooling of surface waters through contact with continental air during the winter may not have been so intense as it is today. We can therefore attribute the moderately seasonal result obtained here and in previous studies to an enhanced Gulf Stream bringing consistently warm waters into western Europe, and a lack of surface water cooling during winter periods.

The Middle Miocene

During the early Middle Miocene a shallow warm sea covered areas of Western France. This study suggests that this sea experienced very minor seasonal fluctuations in temperature (Table 2), comparable to seas in tropical regions today (Hastenrath and Lamb, 1977). Unfortunately, there are at present no palaeoseasonal estimates for moderate latitude seas at this time with which to compare this result.

However, the sea of the 'Faluns' is likely to have been restricted from fully oceanic conditions, only being connected to the Atlantic Ocean via a shallow strait to the west (Figure 1). Estimates of high salinities by Lécuyer et al. (1996) and the observation of gypsum in some localities by Durand (1960) substantiates this conclusion by implying that during deposition of the 'faluns' evaporation probably exceeded precipitation. The seasonal temperature regime of such a restricted sea would therefore have almost certainly been determined by local climatic fluctuations.

These considerations suggest that the prevailing climate in Northwest France during the Middle Miocene was more 'equable' [defined by Sloan & Barron (1990) as 'a substantially reduced annual cycle of temperature]. This is in marked contrast to the highly seasonal climate in Northern France today where the MART is approximately 15 ºC (Rudloff 1981).

Globally, there is both faunal and floral evidence to suggest that from the Eocene to the Middle Miocene many continental regions experienced greater 'equability' as compared to subsequent periods. Nonetheless, this evidence is fragmentary and has often been contested (e.g. Andreasson and Scmitz, 1996).

Summary and Conclusions

Data for intracolony zooid lengths of encrusting bryozoans from the Lower Pliocene Coralline Crag reveal a seasonal regime less pronounced than the seas around the British Isles today. This result is supported by independent estimations of palaeoclimate during deposition of the Crag. The surprisingly unpronounced seasonal regime indicated by encrusting bryozoans from the Middle Miocene 'Falun' provides evidence that a much more 'equable' continental climate existed in Northwest Europe during this time as compared to today.

Previous approaches to estimating palaeoseasonality have used the nearest living relative method, factor analytic transfer functions (e.g. Dowsett, 1991) or variations in the isotopic composition of shell secreting organisms (e.g. Purton and Brasier 1997). Here we show for the first time how iterative growth of modules within bryozoan colonies can be exploited to reveal comparably accurate information on seasonality in palaeoenvironments.

Acknowledgements

We wish to thank Ken McKinney for his generous help with locating the 'Faluns', Jo Harmelin for lending Recent bryozoan material and Mary Spencer-Jones and Paul Taylor for their help and enthusiasm for the project and in providing access to museum collections. The manuscript was very kindly commented upon by Helen Coxall. A. O'Dea would also like to thank Bristol Alumni Foundation, The John Ray Trust and Reading University for financial assistance to attend the 11th meeting of the IBA.

References

Alvineries, J., M. T. Antunes, B. Cahuzac, A. Lauriat-Rage, C. Montenat, C. Pujol.
1992. Synthetic data on the Paleogeographic History of Northeastern Atlantic and Betic-Rifian Basin, During the Neogene (from Brittany, France, to Morocco). *Palaeogeography, Palaeoclimatology, Palaeoecology*, 95:263-286.

Atkinson, D. and R. M. Sibly.
1997. Why are Organisms usually bigger in Colder Environments? Making Sense of a Life History Puzzle. *Trends in Ecology and Evolution*, 12(6):235-239.

Buge, E.
1957. *Les Bryozoaires du Néogène de l'ouest de la France*. Mémoires du Muséum National d'Histoire Naturelle. Série *C*, 6:1-436.

Cavelier, C.
1989. Le Bassin Parisien au Néogène, Progrès Récents. *In*, Actes 114e Congr. Natl. Soc. Savantes, Paris 1989, sect. *Sci. Géol. Bassin Parisien. Com. Trav. Hist. Sci*. Paris, pages 41-54.

Cheetham, A. H.
1967. Palaeoclimatic Significance of the Bryozoan *Meterabdotos. Transactions of the Gulf Coast Association Geological Society*, 17:400-407.

Cifelli, R.
1976. Evolution of Ocean Climate and the Record of Planktonic Foramifera. *Nature*, 264:431-432.

Cronin, T. M. and H. J. Dowsett.
1996. Biotic and Oceanographic Response to the Pliocene Closing of the Central American Isthmus. *In*, J. B. C. Jackson, A. F. Budd, and A. G. Coates (Editors), *Evolution and Environment in Tropical America.* 21-56. Chicago University.

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. *Mémoire du Societé Géologie Minéral*. Bretagne, 13:23-35

Funnel, B. M.
1996. Plio-Pleistocene Palaeogeogrpahy of the Southern North Sea Basin (3.75-0.60 Ma). *Quaternary Science Reviews*, 15:391-405.

Hastenrath, S. and P. J. Lamb.
1977. *Climatic Atlas of the Tropical Atlantic and Eastern Pacific Oceans.* 97 figures. University of Wisconsin.

Hunter, E. and Hughes, R.
1994. The Influence of Temperature, Food Ration and Genotype on Zooid Size in *Celleporella hyalina* (L.). *In*, P. J. Hayward, J. S. Ryland, and P. D. Taylor, *Biology & Palaeobiology of Bryozoans.* Olsen & Olsen, Fredensburg.

Jenkins, D. G. and S. D. Houghton.
1987. Age, Correlation and Plaleocology of the St. Erth Beds and the Coralline Crag of England. *Mededelingen van de Werrkgroep voor Tertiaire en Kwartaire Geologie*, 24:147-156.

Lagaaij, R.
1963. *Cupuladria canariensis* (Busk) - Portrait of a Bryozoan. *Palaeontology*, 6;172-217.

Lécuyer, C., P. Grandjean, F. Paris, M. Robardet and D. Robineau.
1996. Deciphering 'Temperature' and 'Salinity' from Biogenic Phosphates: The $\delta^{18}O$ of Coexisting Fishes and Mammals of the Middle Miocene Sea of Western France. *Palaeogeography, Palaeoclimatology, Palaeoecology, 126:61-74.*

Lee, A. J. and J. W. Ramster.
1981. *Atlas of the Seas Around the British Isles*. Lowestoff: Ministry of Agriculture, Fisheries and Foods., 140 pages.

Menon, N. R.
1972. Heat Tolerance, Growth and Regeneration in Three North Sea Bryozoans Exposed to Different Constant Temperatures. *Marine Biology*, 15:1-11.

Morris, P. A.
1976. Middle Pliocene Temperature Implications Based on the Bryozoa *Hippothoa* (Cheilostomata-Ascophora). *Journal of Paleontology*, 50:1143-1149.

O'Dea, A. and B. Okamura.
In prep. Using Intracolony Variation in Cheilostome Bryozoans as a Novel Technique of Investigating Palaeoseasonality.

Okamura, B.
1987. Seasonal Changes in Zooid Size and Feeding Activity in Epifaunal Colonies of *Electra pilosa*. *In*, J.R.P. Ross (Editor), *Bryozoa: Present and Past*. Western Washington Univ., pages 197-203.

Okamura, B. and J. D. D. Bishop.
1988. Zooid Size in Cheilostome Bryozoans as an Indicator of Relative Palaeotemperture. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 66:145-152.

Purton, L. and M. Brasier.
1997. Gastropod Carbonate $\delta^{18}O$ and $\delta^{13}C$ Values Record Strong Seasonal Productivity and Stratification Shifts During the Late Eocene in England. *Geology*, 25(10):871-874.

Rudloff, W.
1981. *World-Climates With Tables of Climatic Data and Practical Suggestions.* Stuttgart, Germany, Wissenschaftliche Verlagsgesellschaft, 632 pages.

Ryland, J. S.
1963. The Species of *Haplopoma* (Polyzoa). *Sarsia*, 10:9-18.

Savin, S. M., L. Abel, E. Barrera, D. Hodell, D. Keller, J. P. Kennett, J. Killingley, M. Murphy and E. Vincent.
1985. The evolution of Miocene Surface and Near Surface Marine Temperatures: Oxygen Isotope Evidence. *In*, J. P. Kennett (Editor), *The Miocene Ocean: Paleoceanography and Biogeography*. Geological Society of America, Memoir 163:49-82.

Shabalova, M. V. and G. P. Konnen.
1995. Climate-Change Scenarios - Comparison of Paleoreconstructions with Recent Temperature Changes. *Climate Change*, 29(4):409-428.

Shea, D. J., K. E. Trenberth and R. W. Reynolds.
1990. *A Global Monthly Sea Surface Climatology*. National Centre for Atmospheric Research Technical Note, Washington.

Sloan, L. C. and Barron, E. J.
1990. "Equable" Climates During the Earths History?. *Geology*, 18:489-492.

Van Voorhies, W. A.
1996. Bergmann Size Clines: A Simple Explanation for their Occurrence in Ectotherms. *Evolution*, 50(3):1259-1264