



## LATE HOLOCENE ENVIRONMENT OF THE SOUTHERN NORTH SEA FROM THE STABLE ISOTOPIC COMPOSITION OF QUEEN SCALLOP SHELLS

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### ABSTRACT

Six carbon-dated late Holocene Queen Scallop (*Aequipecten opercularis*) shells from the southern North Sea, ranging in age from 2,535 to 965 years BP, were serially sampled and analysed for oxygen and carbon stable isotopic composition. Oxygen isotope profiles show substantial cyclical variation and reflect seawater temperature fluctuation, whose full seasonal range was recorded. Considered in relation to the dates of the shells, the temperature information does not support previous notions of late Holocene climatic change in the European area. Specifically, shells from allegedly warm periods provide evidence of relatively cool conditions; those from allegedly cool periods indicate relatively warm conditions. The data must, however, be treated with great circumspection because of the small number of shells analysed. Carbon isotope profiles exhibit relatively little variation, no consistent pattern, and are difficult to interpret in terms of environmental variables. There is, however, a statistically significant difference between the means of late Holocene and modern carbon isotopic compositions; this probably reflects changes in the anthropogenic supply of CO<sub>2</sub> to the atmosphere. Late Holocene *A. opercularis* rarely exhibit the winter growth interruptions observed in modern shells from the North Sea, and are more abundant. This may reflect the absence of pollution.

KEYWORDS: Queen Scallop, stable isotopes, seasonal temperature, Holocene

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### INTRODUCTION

Information on Holocene climatic variation derives largely from terrestrial evidence, whether

direct human records or indications from a variety of archaeological and geological sources (**Lamb 1995**). With the exception of some evidence from the trace-elemental (**Beck et al. 1992**) and stable-

**Table 1.** Specimen identification and collection details for shells used in study.

Specimen (BGS collection number)	Locality	BGS Core ID	Latitude /Longitude	Depth (m)
SP1 (Zt 9952)	Inner Silver Pit	53/+00/2134	53° 35.65' N 0° 48.41' E	2.06
PB1 (Zt 9957)	Sole Pit	53/+01/210	53° 41.15' N 01° 31.75' E	Not known
PB2 (Zt 9956)	Sole Pit	53/+01/212	53° 41.19' N 01° 30.75' E	1.72
PB3 (Zt 9955)	Sole Pit	53/+01/1552	53° 43.33' N 01° 28.65' E	3.71
PB4 (Zt 9954)	Sole Pit	53/+01/1552	53° 43.33' N 01° 28.65' E	2.15
PB5 (Zt 9953)	Sole Pit	53/+01/327	53° 34.00' N 01° 33.25' E	3.78

isotopic (e.g., **Swart et al. 1996**) composition of tropical corals, comparatively little information has been derived from the marine realm. Relevant data are potentially obtainable and of value to corroborate (or otherwise test) terrestrial evidence and to investigate the linkage between marine environmental conditions and climate. One source of evidence of Holocene marine conditions in extra-tropical areas is the oxygen and carbon stable isotopic composition of mollusc-shell calcium carbonate (e.g., **Eisma et al. 1981; Cohen and Tyson 1995; Hong et al. 1995; Aguirre et al. 1998; Jones and Kennett 1999**). Stable isotope data obtained by ontogenetic sampling of mollusc shell can yield accurate estimates of seasonal marine temperature variation, together with indications of the timing of freshwater influxes, upwelling events, phytoplankton blooms, and the season of death of the animal investigated (e.g., **Krantz et al. 1984, 1987, 1988; Krantz 1990; Jones and Allmon 1995; Hickson et al. 1999; Johnson et al. 2000**). Thus, while providing high-quality temperature information for comparison with terrestrial records, stable isotope data also yield information concerning other climate-related variables. Brief, large-scale freshwater influxes are, for instance, likely to be the result of storms, for which there exists independent evidence of variation in intensity during the Holocene (**Lamb 1995**). Because carbon stable isotopic composition of marine shells also appears to reflect that of the atmosphere, which varies with atmospheric CO<sub>2</sub> concentration (**Beveridge and Shackleton 1994; Böhm et al. 1996**), there is scope in addition for investigating the role of this last factor as a **cause** of climatic variation.

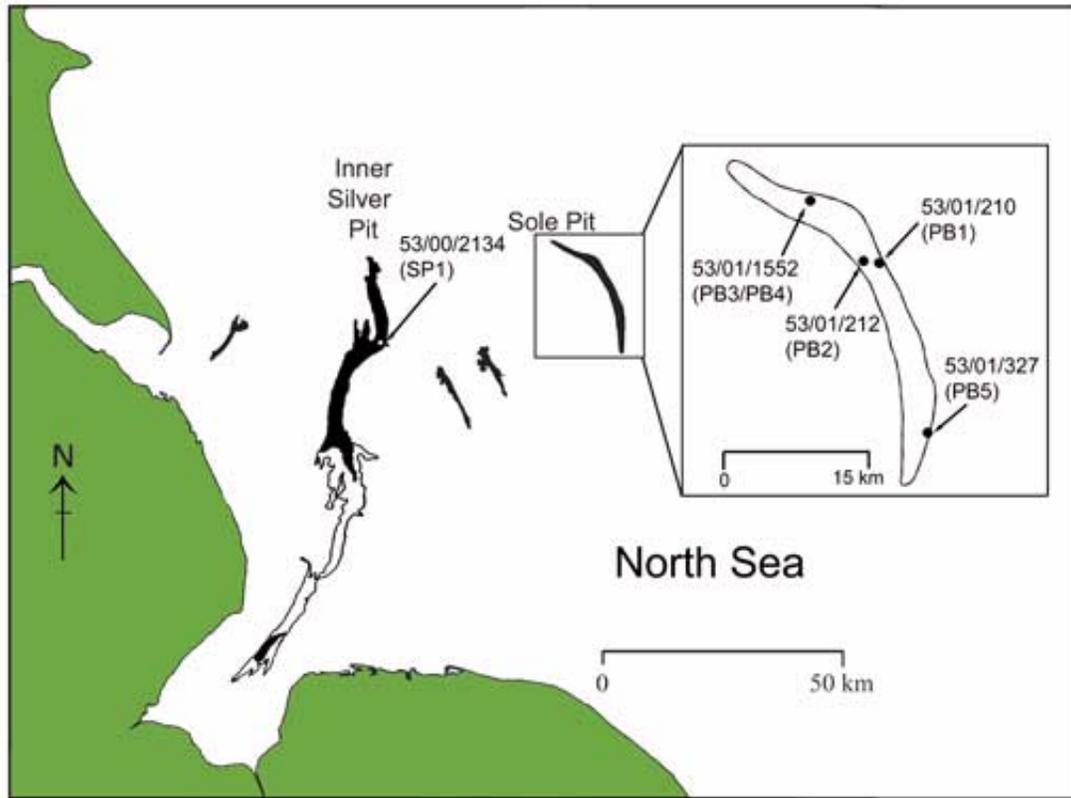
Abundant molluscs are present in cores of North Sea Holocene deposits taken by the British Geological Survey (BGS) as part of the Land-Ocean Evolution Perspective Study (LOEPS), a branch of the Land-Ocean Interaction Study (LOIS). This molluscan fauna (**Balson et al. 1997**)

includes the Queen Scallop, **Aequipecten opercularis**, a benthic bivalve. Study of modern specimens of this species has shown it to be well suited to provision of environmental information through isotopic analysis (**Hickson et al. 1999**). **Aequipecten opercularis** deposits calcite of the outer shell layer at or near isotopic equilibrium with ambient waters and has the potential for growth throughout the year (at least in young specimens); hence it affords a full record of seasonal environmental variation.

In this paper we report the results of analysis of six <sup>14</sup>C-dated Holocene shells and confirm that detailed environmental information can be obtained from ancient material. We discuss estimates of marine temperature in the light of indications of atmospheric temperature from terrestrial sources, present evidence of the level of atmospheric CO<sub>2</sub> in the Holocene relative to the present day, and consider the cause of differences in occurrence and growth pattern between Holocene and modern **A. opercularis** in the southern North Sea.

## METHODOLOGY

The six **A. opercularis** shells were obtained from five BGS cores taken in the Inner Silver and Sole Pits, two of a series of elongated troughs on the bed of the southern North Sea. Full locality details, specimen depths in the cores, and specimen identification numbers are given in Table 1; a location map and simplified core logs are provided in Figures 1 and 2, respectively. All specimens used in this study are held at the BGS, Keyworth. Material from each shell was converted to graphite by Fe/Zn reduction at the NERC Radiocarbon Laboratory, East Kilbride, and <sup>14</sup>C AMS-dated at the NSF Arizona Radiocarbon Laboratory. The uncorrected results are given in Table 2, together with values that have been corrected for the marine reservoir effect (**Sutherland 1986**). Two specimens



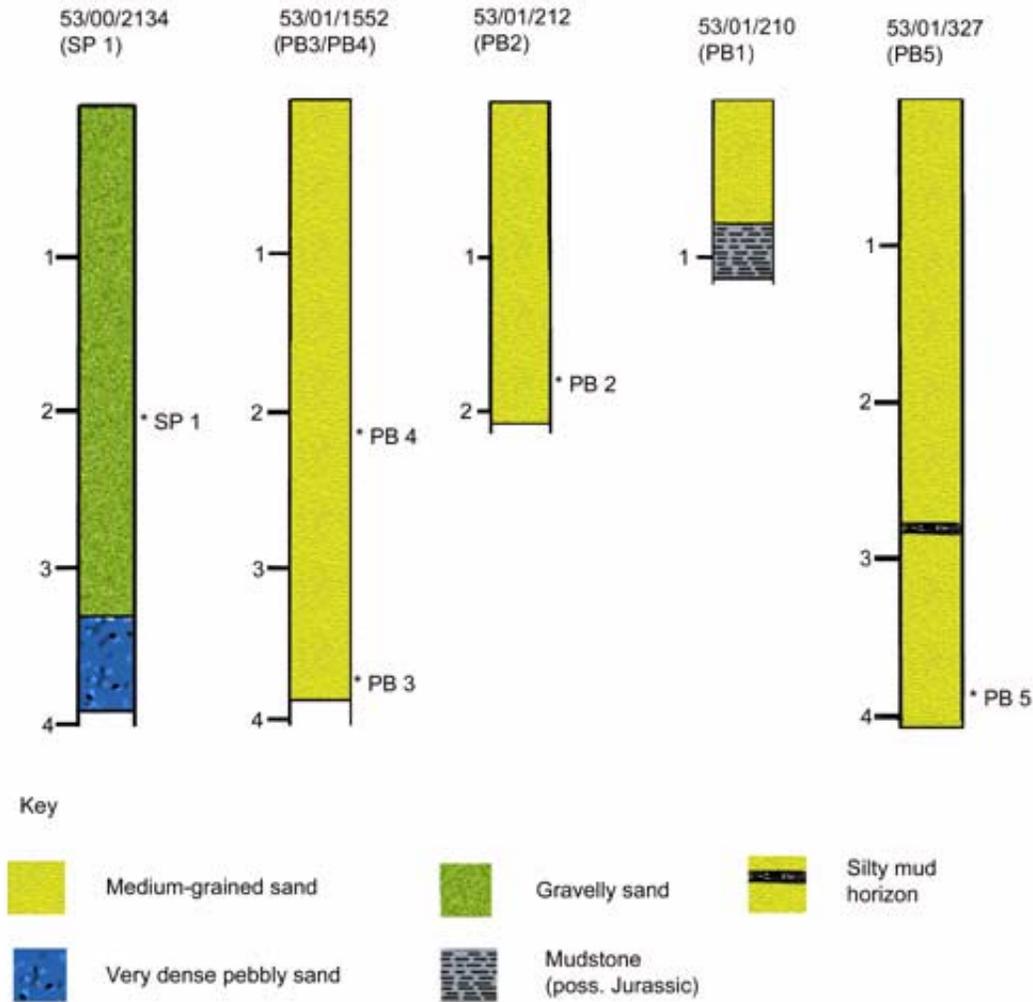
**Figure 1.** Location map showing part of eastern England and adjacent North Sea. The positions of Inner Silver Pit and Sole Pit, referred to in text, are shown. British Geological Survey (BGS) coring stations, from which *Aequipecten opercularis* shells were obtained, are indicated in each pit. Reference numbers are the BGS core numbers; references in parentheses indicate the specimen (as referred to in text) obtained from that core.

from the same core (PB3 and PB4) yield absolute dates in accordance with their relative stratigraphic position. The remaining specimens, all from different cores, do not yield dates that relate closely to their respective depths below the sediment surface (for instance PB5, the youngest shell of all, is from the greatest depth). This is, however, far from surprising given the significant local variation in the overall rate of Holocene sedimentation in the southern North Sea (e.g., **Caston 1979**; figure 7.14). Indeed, the variable thickness and indeterminate age of the sediment fill within southern North Sea “pits” were the principal reasons for the coring and carbon-dating programme, in order accurately to determine depositional history (Land-Ocean Interaction Study 1994; p. 23).

All specimens exhibited excellent preservation of shell structure and showed little evidence of abrasion or long exposure on the sea floor (e.g., encrustation by epibionts on the inner surface), although the corer had damaged some shells. Two specimens (SP1 and PB5) had some pigmentation preserved (Figure 3). Five specimens were

obtained as single valves only; the other (SP1 from the Inner Silver Pit) was found articulated and in life position (i.e., left valve uppermost), implying rapid post-mortem burial or death in conjunction with sediment deposition.

Specimens were scrubbed, then cleaned using an air-abrasive tool. The outer surface of cleaned specimens was then sequentially sampled along the dorso-ventral axis (average sample separation 1-1.5 mm) using a small drill, producing samples of approximately 0.5 mg weight. Isotopic analyses were performed at the NERC Isotope Geosciences Laboratory (NIGL), Keyworth, using a VG Isocarb + Optima system. Approximately 0.1 mg of sample was used in each analysis. Isotopic compositions were calculated by comparison with concurrently analyzed laboratory-standard carbonate, calibrated against the international standards NBS-19 and NBS-18. Analytical precision, expressed as 1 S.D. and based on laboratory standards and replicate sample analysis, was typically <0.12‰ for  $\delta^{18}\text{O}$  and  $\delta^{13}\text{C}$ ; in the case of the



**Figure 2.** Simplified logs for BGS cores from which shells were obtained. Reference numbers as for Figure 1. Depth in core is given in metres. Specimen PB1 was derived from sands above ?Jurassic sediments, but its exact depth is unknown.

**Table 2.** Radiocarbon ages of specimens analyzed (all in years BP; i.e., before 1950 AD); correction for ocean reservoir effect from **Sutherland (1986)**.

Specimen	Publication Code	Uncorrected age	Corrected age
SP1	AA-34288	1835±45	1430
PB1	AA-12370	2250±50	1845
PB2	AA-12371	1835±50	1430
PB3	AA-27135	2940±50	2535
PB4	AA-27134	2760±50	2355
PB5	AA-27136	1370±50	965

former, this equates to an error of <0.5°C in temperature estimates.

Palaeotemperatures were calculated using the equation of **O'Neil et al. (1969)** for a calcite system:

$$T = 16.9 - 4.38 (\delta^{18}O_c - \delta^{18}O_w) + 0.10 (\delta^{18}O_c - \delta^{18}O_w)^2$$

where T is water temperature (in °C),  $\delta^{18}O_c$  is the  $\delta^{18}O$  value of shell carbonate (vs. Vienna Pee Dee Belemnite [VPDB]) and  $\delta^{18}O_w$  is the  $\delta^{18}O$  value of ambient seawater (vs. Vienna Standard Mean Ocean Water [VSMOW]) (minus 0.26‰ to convert to VPDB; **Coplen et al. 1983**). The value of  $\delta^{18}O_w$  used was 0.1‰, similar to modern North Sea values (cf. **Hickson et al. 1999**); use of this value is justified by the fact that fully marine conditions, like



**Figure 3.** Left valve of *Aequipecten opercularis* specimen SP1 (BGS collection number Zt9952) showing (i) preservation of original colour, especially near the umbonal area, (ii) growth interruption ('growth ring') formed during second winter of life (marked by arrow), and (iii) sampling grooves for stable isotope analysis. Material for  $^{14}\text{C}$  dating was removed from the anterior auricle (upper left). Scale bar = 10 mm.

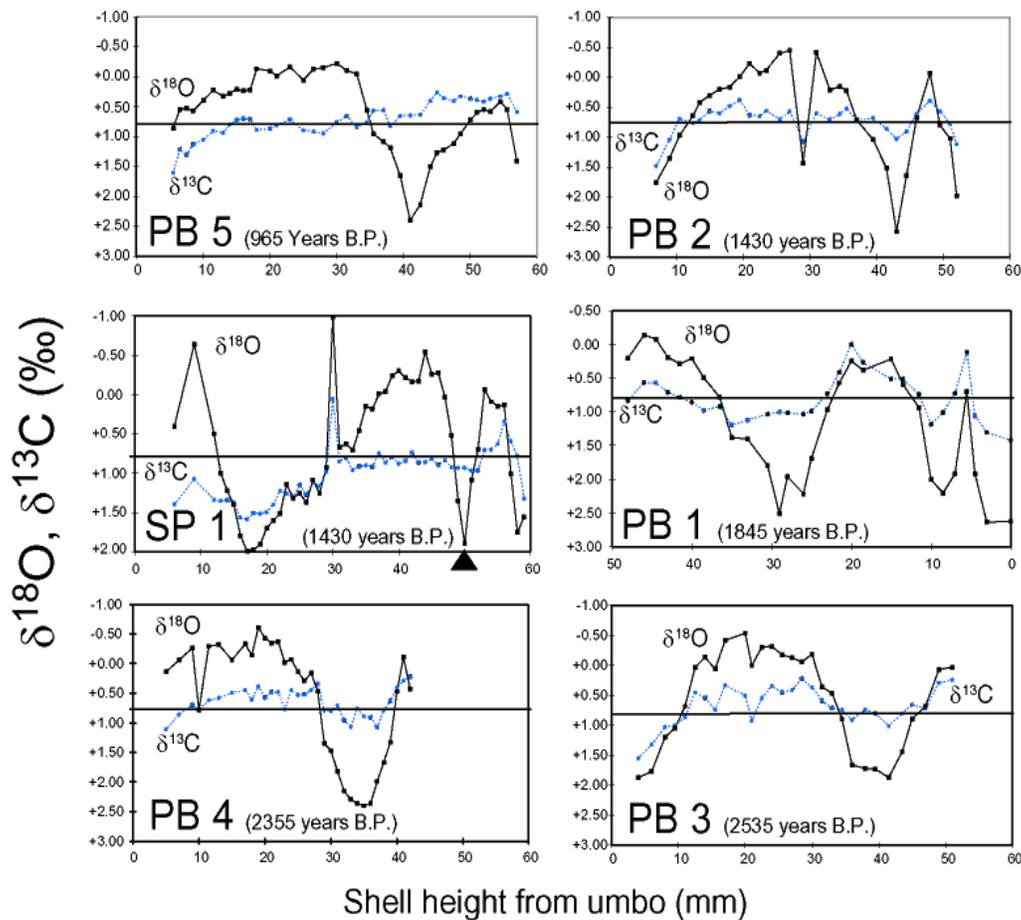
those of the present day, were established some 6,000 years BP, long prior to the date of the oldest shell investigated (Cameron et al. 1992). Given fully marine conditions, it is unlikely that  $\delta^{18}\text{O}_w$  underwent anything more than the negligible seasonal variation observed at present.

### RESULTS AND INTERPRETATION

The results of isotopic analysis are shown in Figure 4.  $\delta^{18}\text{O}$  and  $\delta^{13}\text{C}$  values are plotted on the y-axis (values decreasing upward, as conventional) against shell height from the origin of growth (except for specimen PB1, where the early part of

the shell had been destroyed; in this specimen height is expressed relative to the ventral margin). A tabulated version of the full dataset, together with calculated temperatures, can be obtained as a downloadable Excel (v.5/95) file from <http://www-odp.tamu.edu/paleo/>

All shells analyzed show cyclical patterns of  $\delta^{18}\text{O}$ , with values mostly ranging between approximately  $-0.5$  and  $+2.5$ ‰. This range, together with the shell-height separation of minima and maxima, is similar to that observed in modern indigenous *A. opercularis* from the southern North Sea (Figure 5), and, as in these, can be interpreted as the result of seasonal temperature variation (given

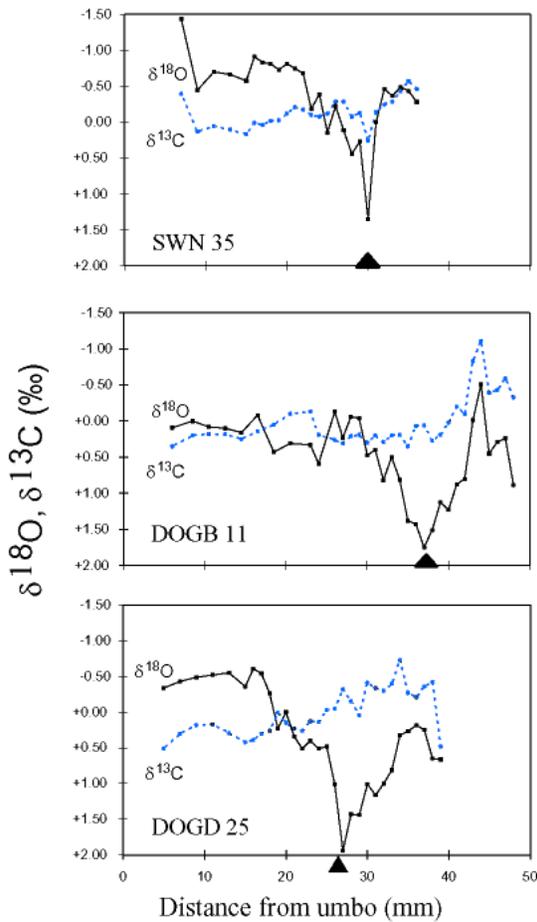


**Figure 4.** Carbon and oxygen isotopic profiles from late Holocene specimens of *Aequipecten opercularis*. Specimen name is indicated in the lower left hand corner of each plot, together with the corrected radiocarbon date for that shell. Specimen SP1 is from the Inner Silver Pit; other specimens are from the Sole Pit. Oxygen isotope profiles are represented by solid black lines; carbon by dashed blue lines. The umbonal area was broken off in specimen PB1; shell height is therefore related to the ventral margin in this specimen. Solid triangle in SP1 indicates position of prominent growth ring as shown in Figure 3. The horizontal line on each profile indicates an arbitrary boundary between “summer” and “winter” (using  $\delta^{18}\text{O} = 0.79\text{‰}$ , equivalent to a temperature of  $13^{\circ}\text{C}$ , as the transition), as referred to in the text.

equilibrium deposition, demonstrated in modern *A. opercularis*, shell isotopic composition is determined only by temperature and the isotopic composition of ambient water; the latter can be assumed to be constant—see above). Single-point large interruptions (in  $\delta^{18}\text{O}$  and  $\delta^{13}\text{C}$ ) to the cyclical pattern -- at 29 mm from the umbo in PB2, 10 mm in PB4 and 30 mm in SP1 -- probably constitute a “transient spike” (Krantz et al. 1988), or analytical artifact, rather than an environmental effect. Minor peaks and troughs in the profiles are almost certainly related to environmental influences; similar small fluctuations, greater than levels of analytical precision, were noted in modern shells and explained by reference to measured temperature fluctuations that probably relate to movements of

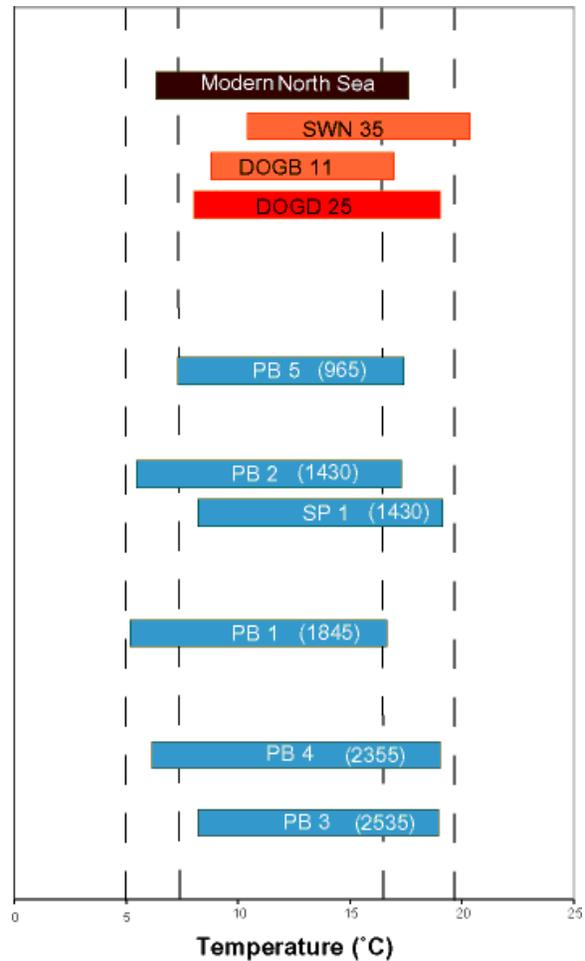
fronts separating water bodies of differing compositions and temperatures (Hickson et al. 1999).

In detail, results from the Holocene shells differ from modern shells. If a  $\delta^{18}\text{O}$  value of 0.79 (corresponding to a temperature of  $13^{\circ}$ , roughly halfway between typical extreme summer and winter temperatures for the southern North Sea; Figure 6) is taken to mark the transition between the warmest (“summer”) and coolest (“winter”) halves of the year, then the “summer” sectors ( $\delta^{18}\text{O}$  values  $<0.79$ ;  $T >13^{\circ}$ ) are shorter in the Holocene shells than in the modern shells; the “winter” sectors ( $\delta^{18}\text{O}$  values  $>0.79$ ;  $T <13^{\circ}$ ) are markedly longer in terms of shell height for the Holocene shells (Figures 4 and 5; Hickson 1997). As well as exhibiting more extensive winter growth in compar-



**Figure 5.** Oxygen isotope profiles from modern *A. opercularis* specimens SWN 35, DOGB 11, and DOGD 25 (Naturmuseum Senckenberg). Solid triangles represent prominent growth rings visible on the shell (cf. Fig. 3; these growth interruptions represent the *first* winter). Oxygen isotope profiles are represented by solid black lines; carbon by dashed blue lines. Reprinted with permission from Elsevier Science from **Hickson et al. (1999)**, copyright (1999).

ison to modern shells, Holocene shells generally lack winter growth rings (marking growth interruptions) and yield larger extreme winter  $\delta^{18}\text{O}$  values, corresponding to lower temperatures (Figures 4 and 6). The temperatures represented by the largest positive  $\delta^{18}\text{O}$  values of modern shells are several degrees above the coldest temperatures that the animals experienced (Figures 5 and 6). Given the presence of strong growth rings in modern shells at positions corresponding to the largest positive  $\delta^{18}\text{O}$  values (Figure 5; **Hickson et al. 1999**), this undoubtedly reflects growth cessation during the period of lowest temperatures. Greater overall winter growth and the general absence of growth rings suggest, by contrast, that the Holocene shells deposited shell material through-



**Figure 6.** Temperature ranges calculated from oxygen isotopic compositions of late Holocene *A. opercularis* shells from the southern North Sea (shown as solid blue bars), compared with ranges calculated from modern shells (**Hickson et al. 1999**; red bars) and values from instrumental records of sea-surface temperature (**Lane and Prandle 1996**, figure 2b). The specimen name is shown on the bar, together with (for subfossil specimens) the corrected radiocarbon date for that shell. The data from instrumental records are for the  $\pm 3$  s ranges about the 10-year means of extreme summer and winter temperatures (vertical broken lines) and for the span between the medians of these ranges (horizontal black bar).

out the winter and that the (lower) minimum temperatures registered are representative of the coldest experienced. The slightly less extensive summer growth of Holocene shells is not matched by the presence of growth rings; hence, as in modern shells, it can be assumed that growth continued uninterrupted during the summer and that the highest temperatures registered are indicative of the warmest temperatures experienced.

Some  $\delta^{13}\text{C}$  profiles show cyclicity (in phase with  $\delta^{18}\text{O}$ ), but this is not represented in every shell investigated, and variation in  $\delta^{13}\text{C}$  (mainly between +0.5 and +1.5‰) is much less than for  $\delta^{18}\text{O}$ . Carbon isotope variations are more difficult to interpret than oxygen; work on non-biogenic carbonates (Romanek et al. 1992) has indicated that temperature is not a primary control. Prior studies of *A. opercularis* have shown that external rather than metabolic sources of carbon are the most important (Hickson et al. 1999); therefore, the likely cause of carbon-isotopic variation in shells is change in the  $\delta^{13}\text{C}$  of dissolved inorganic carbon (DIC), which varies in relation to photosynthesis and decomposition of organic carbon (Arthur et al. 1983). The patterns observed in *A. opercularis* shells (modern as well as Holocene) do not, however, conform to a model (Purton and Brasier 1997; figure 4a) proposed for a hydrographic setting such as that of the southern North Sea: shallow, well-mixed water unaffected by upwelling. Purton and Brasier's model predicts antiphase cyclical variations in  $\delta^{18}\text{O}$  and  $\delta^{13}\text{C}$ , such that when  $\delta^{18}\text{O}$  values are at their highest (in winter/early spring),  $\delta^{13}\text{C}$  values will be at their lowest, due to breakdown of  $^{12}\text{C}$ -rich organic matter; conversely, when  $\delta^{18}\text{O}$  values are low due to higher temperatures,  $\delta^{13}\text{C}$  values should be at their highest, reflecting uptake of  $^{12}\text{C}$  by phytoplankton. In *A. opercularis*, however, fluctuations are either clearly in-phase (e.g., Figure 4e and 4f) or carbon-isotope variation is not cyclical at all (e.g., Figure 4a). Perhaps this in some way relates to the pattern of variation in phytoplankton abundance in the southern North Sea, which differs from that of other temperate shelf seas: at the present time a spring "bloom" does occur, but the population crash that would normally follow this is not as marked as it is, for example, in the northern North Sea (Tett and Walne 1995). In addition, fluctuation in  $\delta^{13}\text{C}_{\text{DIC}}$  might conceivably be dampened by decomposition (particularly in summer) of  $^{12}\text{C}$ -rich organic matter supplied by rivers entering the North Sea or introduced in the form of oil and gas seepages.

Although there appears to be no pattern (or straightforward explanation) of short-term variation in  $\delta^{13}\text{C}$  (i.e., as represented within shells), there is a striking difference in the range and mean of  $\delta^{13}\text{C}$  values from Holocene and modern shells. Most Holocene values are greater than +0.5‰ (mean +0.79;  $n = 209$ ); modern values are nearly always less than +0.5‰ (mean -0.04;  $n = 197$ ; sample consisting of all values given by Hickson 1997).

The difference in means is statistically significant (**F** and **t** tests;  $\alpha = 0.05$ ). Conceivably, this difference could be due to higher year-round productivity in the Holocene (leading to higher  $\delta^{13}\text{C}_{\text{DIC}}$ ). This would be consistent with evidence (see above) of more extensive winter growth in the Holocene (winter growth deceleration in modern *A. opercularis* may be partly due to reduced food supply rather than low temperature [Broom and Mason 1978]) and might also explain slightly less extensive summer growth in that phytoplankton levels above those of the modern North Sea during summer could cause "clogging" of the gills and slower growth (Chavaud et al. 1998). However, there is no independent evidence of higher Holocene productivity and intuitively one would expect modern productivity to be higher, given the vast present-day supply of nutrients to the North Sea from domestic and agricultural sources. By contrast, there is voluminous evidence that, as the result of greater combustion of fossil fuels, modern atmospheric  $\text{CO}_2$  levels are higher than in the pre-industrial Holocene (Friedli et al. 1986), and that associated reductions in atmospheric  $\delta^{13}\text{C}$  have been translated through air-sea  $\text{CO}_2$  exchange into lower modern values of  $\delta^{13}\text{C}$  for DIC and biogenic carbonate (Beveridge and Shackleton 1994; Böhm et al. 1996). Like values of  $\delta^{13}\text{C}$  from modern *A. opercularis*, those from Pliocene examples are also lower than values from Holocene shells (Johnson et al. 2000). Given that independent evidence suggests that Pliocene atmospheric  $\text{CO}_2$  levels were comparable to present (Kürschner et al. 1996), it seems reasonable to conclude that the high  $\delta^{13}\text{C}$  values of Holocene *A. opercularis* shells are a reflection of low atmospheric  $\text{CO}_2$ .

## DISCUSSION

Although the information is limited it is worthwhile to consider the temperature data from *A. opercularis* in the light of what has been inferred from other evidence about late Holocene climate in the European area. Lamb (1995) considered that the last 800 years BC were marked by relatively cool temperatures, succeeded by relatively warm conditions during the first 400 years AD (essentially the period of the Roman empire in western Europe), then followed by a cool interval until 800-900 AD, a warm interval until 1300-1400 AD (essentially spanning the medieval period in Europe), a cool interval until about 1800 AD (the Little Ice Age), and a period of slight overall warming to the present day. The dates of shells PB1 and

PB5 fall within the “Roman” and “Medieval” warm periods, respectively; shells SP1, PB2, PB3, and PB4 derive from allegedly cool intervals. Taking the isotopically-derived temperature ranges from the Holocene shells (Figure 6) to be indicative of the seasonal range experienced (see above), it is noteworthy that PB1 and PB5 record minimum and maximum temperatures almost identical with the median winter and summer extremes of the modern North Sea; the supposed relative warmth of the periods concerned is therefore not borne out by information from these shells, or higher atmospheric temperatures did not cause higher seawater temperatures. Shells SP1, PB2, PB3, and PB4 record somewhat higher maximum temperatures than PB1 and PB5 (outside the range of analytical error) and the minimum temperatures recorded are either very similar (PB2 and PB4) to these two shells or again higher (SP1 and PB3); the supposed relative coolness of the periods concerned is therefore also contradicted by shell-isotope data, or atmospheric coolness was not reflected in seawater temperature. Seawater temperature around northwest Europe is strongly influenced by the North Atlantic Drift, but because the strength of this warm current is related to the strength and persistence of westerly winds, which bring warm air, variation in seawater temperature is likely to mirror atmospheric temperature (**Dawson and O’Hare 2000**; empirical support in **Hickson 1997**, figures 6.6.1, 6.6.2). Because the southern North Sea is a shallow, well-mixed water body, surface temperatures (and hence atmospheric temperatures) should be reflected in bottom temperatures, as supplied herein by the oxygen isotopic composition of a benthic mollusc. It is, of course, entirely possible that the years represented by the small number of shells sampled were uncharacteristic, and the “anomalous” temperatures are in any case not beyond what one might expect as the range of variation under the general climatic conditions inferred by **Lamb (1995)**. However, given the consistency with which the isotope data are somewhat at variance with Lamb’s interpretations of climate, and in the knowledge that these interpretations are themselves based on limited data and have been called into question by other evidence (e.g., **Ogilvie and Farmer 1997**), they represent a useful contribution towards accurate definition of late Cenozoic climatic variation. It is worth noting that shells SP1 and PB2, from locations approximately 40 km apart, yield identical carbon dates (1,430 years BP), and the former was preserved with the valves

articulated. This may reflect a major episode of sedimentation, and consequent shell burial, at this time.

Because five of the six Holocene shells record lower winter temperatures than those from modern indigenous North Sea shells, it is clear that the winter growth interruptions represented by the prominent growth bands in the latter cannot be due to low temperature. Limited food supply is a possible explanation, but has little supporting evidence (see above). Stress resulting from pollution is another candidate: Pollution is undoubtedly greater now in the North Sea than in pre-industrial times (**Middleton and Grant 1990**), and stress so caused has been shown to result in reduced “scope for growth” in marine bivalves (**Widdows and Johnson 1988**; **Widdows et al. 1990**). Pollution might also be the reason for the relative rarity of *A. opercularis* at present in the southern North Sea, to judge from the low frequency of shells in surface “grab” samples taken by the BGS as compared to those in cores of Holocene sediments (A. Weller, personal commun., 1997). It is, however, difficult to reconcile the notion that sparse occurrence and reduced winter growth of modern *A. opercularis* are consequences of pollution with the fact that summer growth is **greater**. Possibly the effects of pollution may be over-ridden in summer by some favourable condition for growth of the modern North Sea (perhaps higher productivity; see above). However, until such a condition is identified it has to be said that pollution is no more than a possible explanation for the modern occurrence and winter-growth characteristics of *A. opercularis* in the North Sea.

## CONCLUSIONS

1. Isotopic signatures of environmental change are as well preserved in Holocene fossil *A. opercularis* shells as in modern examples.
2. Isotopically-based estimates of seawater temperature do not lend support to **Lamb’s (1995)** formulation of Holocene climatic variation, although the data are too limited to refute Lamb’s synthesis.
3. Isotopic evidence supports the notion of lower atmospheric CO<sub>2</sub> levels in the pre-industrial Holocene than at present.
4. The sparse occurrence and interrupted growth of *A. opercularis* in the southern North Sea at present is possibly a reflection of pollution.

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