

The Queen Scallop *Aequipecten opercularis*: a new source of information on late Cenozoic marine environments in Europe

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Abstract: Few data exist on seasonal variation in the temperature (or other aspects of the environment) of late Cenozoic shelf seas in Europe. Ontogenetic records in the shell of *Aequipecten opercularis*, a widespread, fast-growing and typically well-preserved bivalve, are a potential source. Study of modern forms has shown that oxygen stable isotopes are incorporated in equilibrium with surrounding seawater (hence providing a faithful record of temperature) and data from late Holocene *A. opercularis* of the southern North Sea Basin (SNSB) indicate that extreme winter (as well as summer) temperatures are registered. Oxygen isotope data from apparently well-preserved, mid-Pliocene shells of the SNSB indicate seasonal temperatures similar to present, whereas microgrowth increment data suggest substantially warmer conditions, in accordance with other evidence. The balance of evidence thus implies cryptic diagenetic corruption of the isotopic temperature signature in mid-Pliocene shells. However, it would be premature to discount the possibility of cooler mid-Pliocene conditions than currently recognized. Ontogenetic variation in carbon isotopic composition within shells is minor and apparently unrelated to environment, but differences between mid-Pliocene, late Holocene and modern shells probably relate to changes in atmospheric CO₂ concentration. Unlike certain taxa, seasonal variation is not evident in the strontium or magnesium contents of the *A. opercularis* shell, but may be displayed by other trace elements, hence affording (together with seasonal increment width variation) a means of independent temporal calibration of isotope profiles. Ontogenetic records of environment from *A. opercularis* can be complete (and, in the case of increment data, easily recovered) but are of short duration. They must be complemented by (less complete) records from longer lived taxa to obtain the fullest possible environmental history. Seasonal cycles in ontogenetic records afford a means of establishing age and growth rate, and can therefore provide information of value for evolutionary studies and management of living populations.

Concerns over the possible effect on climate of anthropogenic CO₂ emissions to the atmosphere have promoted interest in the extent and cause of recent natural climatic fluctuation, and have hence directed attention to the late Cenozoic interval. Variations in atmospheric CO₂ content have, with little doubt, contributed to changes in global mean temperature during the late Cenozoic, e.g. in the mid-Pliocene when atmospheric CO₂ was apparently 30–35% above the pre-industrial modern level (Kürschner *et al.* 1996; Raymo *et al.* 1996) and the global mean temperature an estimated 3.6°C higher (Sloan *et al.* 1996). However, locally and, in particular, in the northeastern North Atlantic area, climatic variation may well have

been determined more by changes in the supply of heat through ocean currents than by alterations in atmospheric retention of reflected solar radiation as a result of shifts in CO₂ level. Thus, reduced Gulf Stream heat supply has been plausibly invoked to explain intervals of relative cold during the Pleistocene in the European area (Broecker 1997), while during the mid-Pliocene, Gulf Stream heat supply was apparently substantially enhanced (Dowsett *et al.* 1992) and presumably, at least in part, the cause of warmer conditions on land in Europe (Thompson & Fleming 1996).

Although the geographic pattern of mid-Pliocene warming in the North Atlantic favours enhanced Gulf Stream heat supply, the reduced overall

latitudinal temperature gradient in the oceans (Dowsett *et al.* 1996) makes this a theoretical improbability (Crowley 1996). The evidence of temperature in the mid-Pliocene North Atlantic (and of ocean temperatures generally) derives from the distribution of various elements of the microbiota and is not immune from question, being based on analogy with the temperature associations of modern representatives of taxa. The same applies to almost all estimates of sea temperature on the European continental shelf in the Pliocene (e.g. Raffi *et al.* 1985; Wood *et al.* 1993; Head 1997, 1998) and Pleistocene (e.g. Funnell *et al.* 1979; Gibbard *et al.* 1991; Meijer & Preece 1995); only scant evidence is available from the alternative approach of oxygen isotope thermometry (Buchardt 1978). Lack of secure palaeotemperature estimates for the European continental shelf sea is regrettable because this area, transitional between land and the Atlantic Ocean proper, is surely key to evaluating the influence of variations in Gulf Stream heat supply on climate of the European landmass. From the fact that at present, summer and winter sea temperatures on the Atlantic seaboard of Europe are approximately equally elevated above those (uninfluenced by the Gulf Stream) at the same latitude off North America (National Oceanic and Atmospheric Administration of the United States 1999), it can be expected that enhanced Gulf Stream heat supply would be manifested in shelf temperature increases of about the same magnitude in summer and winter (and likewise diminished supply by approximately equal decreases). It has been predicted, by contrast, that, at the latitude of Europe, markedly discrepant increases in summer and winter atmospheric (and by inference oceanic) temperatures would result from elevated atmospheric CO₂ (Crowley 1991).

It is evident from the above that accurate data on seasonal sea temperature variation in the European area during the late Cenozoic would be of value both to test existing temperature estimates and to investigate the causes of secular change. Such data, together with information on other aspects of environment, are potentially recoverable from chemical and morphological ontogenetic records contained in accretionary skeletons. The Queen Scallop, *Aequipecten opercularis* (L.), has a large, rapidly accreted shell and, as a common component of Miocene–Recent marine faunas in Europe, appears to be a promising subject for research. In this paper the general suitability of *A. opercularis* for provision of environmental information from ontogenetic records is reviewed, and then the quality and implications of data from three specific sources – stable isotopes, micro-growth increments and trace elements – are discussed.

General suitability of *Aequipecten opercularis*

As a scallop, *A. opercularis* (Fig. 1) has a predominantly calcitic shell which, while not guaranteeing faithful preservation of ontogenetic records of environment, is unlikely to suffer the wholesale alteration or dissolution common in aragonitic taxa. Being epibenthic, scallops are more likely to provide a record of general water conditions than infaunal forms, whose carbon isotopic composition, at least, may reflect porewater geochemistry (Krantz *et al.* 1987). Shelf-dwelling scallops are generally fast-growing and *A. opercularis* is no exception, reaching a height of c. 40 mm after one year and 55 mm after two years, with growth occurring during the winter months (Ursin 1956; Hickson 1997). This provides, in principle, for a well-resolved and complete record of seasonal environmental variation.

Against these favourable growth characteristics must be set the relatively short lifespan of *A. opercularis* (rarely more than six years; Broom 1976) and the sharp decline in growth rate with age, such that if an animal reaches six years old its growth is almost zero (Taylor & Venn 1978). This precludes recovery of a long continuous history of environment. However, such limited data as exist provide no indication that any other species with an accretionary skeleton, found widely in the late Cenozoic deposits of Europe, combines sub-

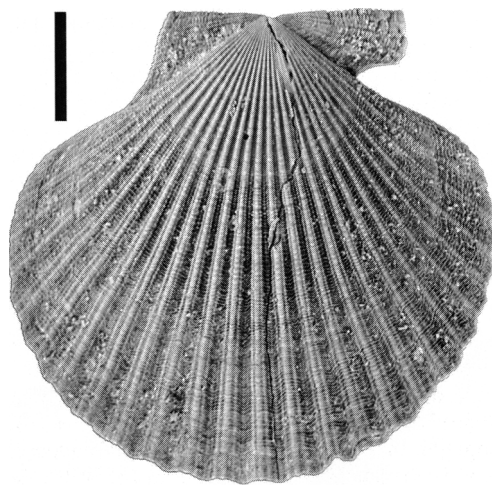


Fig. 1. Right valve of the Queen Scallop, *Aequipecten opercularis* (L.), from the Coralline Crag (mid-Pliocene) of Suffolk, eastern England. Specimen: University of Derby, Division of Earth Sciences (UD) 52795. Scale bar, 10 mm.

stantially greater longevity with significant growth at all times of year. *Mytilus edulis* is quite widespread from early Pleistocene times onward and, according to Seed (1976), lives for up to 16 years. However, winter growth is only c. 5 mm in the first year and even less in the second; in view of a decline in annual growth rate, winter growth must be negligible in older animals [see also Jones (1983)]. *Pinna nobilis*, locally common at present in the Mediterranean Sea, reaches 13 years and is still growing rapidly (probably in winter as well as summer) at eight years (Richardson *et al.* 1999). Unfortunately, however, this species appears to be restricted to warm waters, not extending into northern Europe even in the Pliocene (Raffi *et al.* 1985). The infaunal bivalve *Arctica islandica* reaches very much greater ages (200+ years; Jones 1983) but ceases growing in winter (Weidman *et al.* 1994). Evidence from North American species suggests that seasonal growth interruptions may be characteristic of relatively long-lived infaunal bivalves (Jones 1980; Jones *et al.* 1989; Jones & Quitmyer 1996).

A. opercularis is a common and widespread species at present, breeding populations extending from northern Norway around the Atlantic coast of Europe and as far east into the Mediterranean as the Adriatic (Waller 1991; Margus 1991). It thus occupies waters ranging in temperature from an average winter minimum of c. 5°C to an average summer maximum of c. 24°C (National Oceanic and Atmospheric Administration of the United States 1999). This tolerance predisposes *A. opercularis* to be useful as a tool for documenting temperature in that its own occurrence is unlikely to be affected by this variable, something borne out by the presence of the species in, for instance, cold-water deposits of the Pleistocene in eastern England (Funnell *et al.* 1979) and warm-water deposits of the Pliocene in southern Spain (Aguirre *et al.* 1996). *A. opercularis* also occurs over a substantial depth range (from low water to 183 m) and is tolerant of a wide variety of substrates, being abundant at present on sediments ranging from sandy mud to sandy gravel and shell hash (Tebble 1976).

Although eurytopic in the above respects, *A. opercularis* requires some current flow (Ursin 1956) and is tolerant only of quite small, short-term departures from normal marine salinity (Paul 1980). As a result of the latter, while it may be common in fully marine late Cenozoic sequences [e.g. in the southern North Sea Basin (SNSB), the Pliocene Coralline and Red Crag formations of eastern England, and the Oosterhout Formation of the Netherlands], the species is absent from sequences deposited under strong fluvial influence (e.g. much of the Pleistocene of the Netherlands;

Gibbard *et al.* 1991). This feature at least ensures that salinity-related variation in the isotopic composition of ambient water can be largely ruled out as a factor influencing shell isotopic composition, hence simplifying interpretation of isotopic data (see below).

The frequency with which *A. opercularis* occurs in British Geological Survey cores of late Holocene deposits beneath the southern North Sea is in marked contrast to its rarity in surface grab samples from the same area (A. Weller, pers. comm.). Indigenous modern individuals also exhibit more interrupted growth (see below). Given that conditions of temperature, salinity, tides and substrate in modern and late Holocene times were almost identical (Cameron *et al.* 1992), it seems likely that present-day occurrence and growth characteristics in the southern North Sea reflect some form of pollution rather than a natural control.

Although affected by some natural and, apparently, anthropogenic factors, *A. opercularis* exhibits remarkable short-term hardiness which makes it highly suitable for *in vivo* experimental studies. Thus, animals used in the North Sea culture referred to below suffered no ill effects in a 12 h car journey from their source (western Scotland) merely enveloped in wet seaweed and ice. Moreover, growth occurs at a healthy rate even in specimens tightly packed within onion nets, a method of culture used experimentally off western Scotland (J. P. Mikolajunas, pers. comm.). Such tolerance suggests that experiments involving artificial manipulation of conditions to assess the fidelity of ontogenetic records (e.g. temperature control of oxygen isotopic composition and microgrowth increment width; control of shell trace element content by environmental concentration – see discussions below) could be conducted without risk of mortality.

Data from modern, late Holocene and mid-Pliocene shells

Stable isotope data

Although investigations of ontogenetic variation in the stable isotopic composition of the *A. opercularis* shell were initiated only recently (Hickson 1997; Hickson *et al.* 1999), studies of scallop species occurring outside Europe started some time ago (e.g. Krantz *et al.* 1984), and stable isotope data have been used as a source of information on seasonal variation in temperature (including water-column stratification) and the timing of upwelling events, phytoplankton blooms and freshwater influxes (e.g. Krantz *et al.* 1987, 1988; Krantz 1990; Jones & Allmon 1995). All such inferences are based on the assumption of

something close to equilibrium incorporation of elemental isotopes into shell carbonate; i.e. incorporation in accordance with their relative abundance in the immediate environment and a fractionation factor which, in the case of oxygen, varies strongly with temperature. At the smallest spatial and temporal scale equilibrium is probably unavoidable, but at larger scales, e.g. where seawater surrounding a shell is taken to be the immediate environment rather than the extrapallial fluid from which it is actually precipitated, the condition does not necessarily hold. Thus, in the scallop *Pecten maximus* (Mitchell *et al.* 1994; C. A. Richardson, pers. comm.) the interposition of some effect relating to the biology of the organism, perhaps slow replenishment from seawater of ions in the extrapallial fluid (resulting in significant 'pollution' by, or reequilibration with, mantle-derived ions; cf. Hickson *et al.* 1999), results in disequilibrium between shell and seawater.

Equilibrium between shell and external environment has been demonstrated convincingly for the scallops *Placopecten magellanicus* (Krantz *et al.* 1984) and *Adamussium colbecki* (Barrera *et al.* 1990) but, given the evidence from *Pecten maximus*, cannot be assumed for other species. Indeed, the whole issue of the detailed mechanisms by which carbonate precipitates, and their effects on its isotopic composition, is a subject of active debate (Spero *et al.* 1997; Zeebe 1999). It was for these reasons that, preparatory to analysis of ancient *A. opercularis*, an investigation of the occurrence of isotopic equilibrium was conducted on modern examples. This involved analysis of shells which had grown under known environmental conditions, the animals concerned either having been maintained in monitored cultures over an autumn–winter period in the southern North Sea or collected live from sites for which environmental data were available from general monitoring programmes. The results have been published elsewhere (Hickson *et al.* 1999) and are only summarized below, attention being concentrated on the implications of data from late Holocene and mid-Pliocene shells.

Oxygen isotopes. Isotopic ratios are expressed in the δ notation, in per mil (‰), where $\delta^{18}\text{O}$ (or $\delta^{13}\text{C}$) = $[(R_{\text{sample}}/R_{\text{standard}}) - 1] \times 10^3$. R is the $^{18}\text{O}/^{16}\text{O}$ (or $^{13}\text{C}/^{12}\text{C}$) ratio, and the standards are Vienna Pee Dee Belemnite (VPDB) for carbonates and Vienna Standard Mean Ocean Water (VSMOW) for water (Coplen 1994). Under conditions of isotopic equilibrium the difference between the $\delta^{18}\text{O}$ value of calcite and the $\delta^{18}\text{O}$ value of the water from which it precipitates is dependent on temperature, and for water with a

seasonally constant isotopic composition (as is usually the case for fully marine waters) the change in $\delta^{18}\text{O}_{\text{calcite}}$ as a function of temperature is c. $-0.24\text{‰ }^{\circ}\text{C}^{-1}$ (O'Neil *et al.* 1969).

For the investigation of modern shells (Hickson *et al.* 1999), seawater temperatures and $\delta^{18}\text{O}$ were either measured (for cultured animals) or derived from other records (for indigenous animals). Solutions of the equation of O'Neil *et al.* (1969), relating the difference between $\delta^{18}\text{O}_{\text{calcite}}$ and $\delta^{18}\text{O}_{\text{water}}$ as a function of temperature, then yielded predictions of $\delta^{18}\text{O}$ for shells growing in isotopic equilibrium. The range of $\delta^{18}\text{O}_{\text{shell}}$ values from both cultured and indigenous animals (according quite closely with the predicted values), and the pattern of change in the former (increasing $\delta^{18}\text{O}_{\text{shell}}$ with decreasing temperature), show that something (at least) very near to isotopic equilibrium existed between shells and seawater at the time of precipitation. Indigenous shells (e.g. Fig. 2a) uniformly exhibit $\delta^{18}\text{O}$ maxima (i.e. extreme winter values) slightly less than values corresponding to the minimum temperatures experienced. Rather than disequilibrium, this almost certainly reflects a brief interruption of growth during the coldest months because in each case the $\delta^{18}\text{O}$ maximum corresponds to a marked 'growth ring' (formed of a group of very small microgrowth increments – see below), which is evidently the culmination of a slowdown in growth (shown by the relatively sharp increase in $\delta^{18}\text{O}$ against shell height in Fig. 2a).

Data from a late Holocene shell from the SNSB (Fig. 2b) describe a strikingly different winter record, with an asymptotic approach to the $\delta^{18}\text{O}$ maximum which is greater (reflecting a lower temperature) than in any modern indigenous shell; no growth ring is developed. The same features are observed in isotopic profiles from the first two years of growth of other late Holocene shells, ranging in age from c. 1 to 3 Ka, and only rarely is there a significant growth ring associated with the maximum $\delta^{18}\text{O}$ value (Hickson 1997). This evidence, which is matched by data from cultured shells, shows that, under appropriate circumstances (evidently not abnormally warm winter conditions), *A. opercularis* does not merely exhibit growth in the overall winter period but actually grows significantly in the coldest months. Given that at present in the southern North Sea, where winter growth interruptions are observed, *A. opercularis* is uncommon (presumably as a result of some unfavourable feature of the environment; see above), it may be that, under conditions which support larger populations, growth during the coldest months is the norm, at least in the first year or two of life.

PALAEOENVIRONMENTAL DATA FROM THE QUEEN SCALLOP

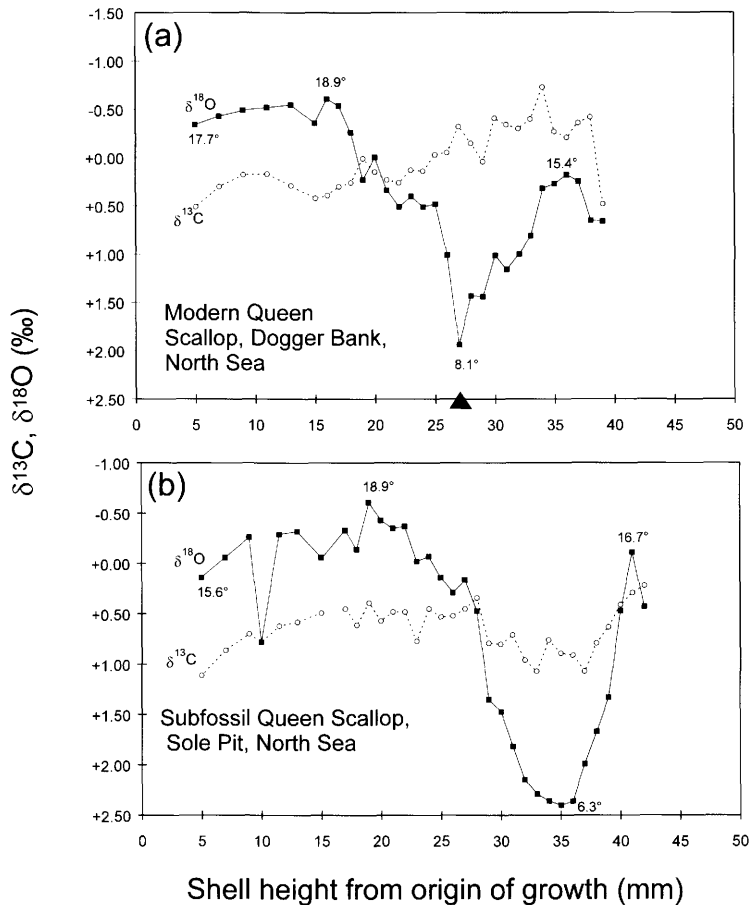


Fig. 2. Examples of oxygen ($\delta^{18}\text{O}$) and carbon ($\delta^{13}\text{C}$) stable isotopic compositions of: (a) indigenous modern; (b) subfossil (late Holocene) Queen Scallops from the southern North Sea. In accordance with convention, δ values are shown decreasing upwards on the y-axis. High $\delta^{18}\text{O}$ at a shell height of 10 mm in (b) almost certainly reflects an instrumental aberration. Temperatures shown were calculated from $\delta^{18}\text{O}$ values using the equation of O'Neil *et al.* (1969) and $\delta^{18}\text{O}_{\text{water}} = +0.1\text{‰}$ (v. VSMOW). \blacktriangle , Position of growth ring (growth cessation). Uncorrected ^{14}C AMS date of late Holocene specimen: 2760 ± 50 years BP (Lab. Code AA-27134). Specimens: (a) Naturmuseum Senckenberg DOGD 25; (b) British Geological Survey Zt 9954 [PB4 of Hickson (1997)].

Data (Fig. 3) from two apparently well-preserved mid-Pliocene specimens of *A. opercularis* from the SNSB exhibit a cyclicity similar to that seen in data from younger shells, indicating a primary (temperature) control. However, whilst assemblage analysis and the few existing isotopic data (see above) suggest that mid-Pliocene temperatures were substantially higher than now, the temperatures represented by both $\delta^{18}\text{O}$ maxima and minima in Fig. 3 are not significantly greater than typical winter (5.5–7.5°C) and summer (16–18°C) extremes in the current southern North Sea (Lane & Prandle 1996). Shell UD 52797 (Fig. 3b) provides evidence of slightly warmer extreme winter temperatures (8.8°C) but the summer extreme is

indistinguishable from present, and that indicated by shell UD 52796 (Fig. 3a) is, at 13.0°C, substantially below typical modern extreme summer temperatures.

These last two findings could be explained by the existence of a summer growth halt (resulting in failure to register the highest temperatures experienced), as in warm water populations of the bivalve *Mercenaria* (Jones & Quitmyer 1996). However, while the 'peaks' (in fact, relatively low $\delta^{18}\text{O}$ values) in the isotope profiles are rather narrower than those from late Holocene and modern shells (Fig. 2), such growth rings as exist are conspicuously not coincident with them (Fig. 3a). Other than the rather remote possibility that previous

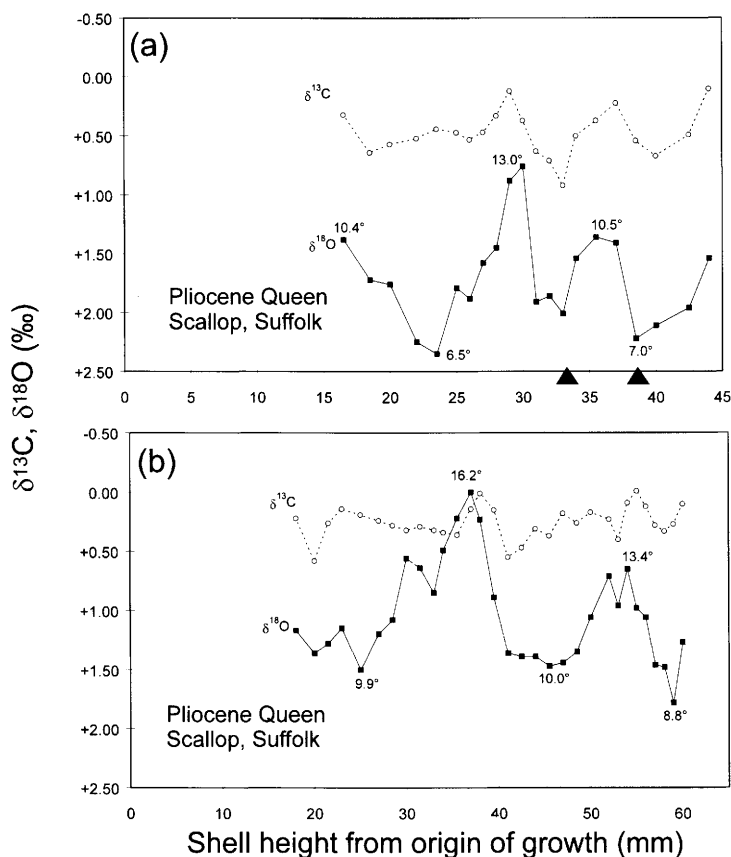


Fig. 3. Isotopic profiles from mid-Pliocene (Coralline Crag) Queen Scallop shells from eastern England. Format as in Fig. 2. In calculating temperatures, no correction was made for possible ice-volume effects due to a lack of consensus over the most appropriate value (cf. Jones & Allmon 1995). All suggested corrections would result in a lowering of calculated temperatures. Specimens: (a) UD 52796; (b) UD 52797.

temperature estimates are all markedly in error, two potential explanations remain: that the analysed shells lived during anomalously cool years or that they underwent cryptic diagenetic alteration, resulting in corruption of the isotopic signature. The latter possibility is supported by evidence from microgrowth increment widths (see below) which indicate warmer conditions than present.

Carbon isotopes. Isotope mass balance equations relating to ^{13}C and ^{12}C , and incorporating appropriate fractionation factors, indicate that, unlike other marine bivalve species, a maximum of 20% of carbon in the shell carbonate of *A. opercularis* is derived from metabolic sources (Hickson *et al.* 1999). This, in turn, suggests that something close to isotopic equilibrium exists at the time of precipitation between shell carbon and dissolved inorganic carbon (DIC) in seawater. There is no

measurable temperature effect on $^{13}\text{C}/^{12}\text{C}$ fractionation between DIC and carbonate (Romanek *et al.* 1992), hence, given isotopic equilibrium, variations in $\delta^{13}\text{C}_{\text{shell}}$ will reflect changes in $\delta^{13}\text{C}_{\text{DIC}}$. Short-term variations of $\delta^{13}\text{C}_{\text{DIC}}$ in shelf seas relate to factors such as local phytoplankton blooms (causing increased $\delta^{13}\text{C}_{\text{DIC}}$ by removal into tissue of a relatively high proportion of ^{12}C) and influxes of freshwater or deep-marine waters (typically causing reduced $\delta^{13}\text{C}_{\text{DIC}}$ by introduction of water relatively rich in ^{12}C from the decay of organic matter). Over the longer term, changes in $\delta^{13}\text{C}$ of atmospheric CO_2 (caused partly by variations in the rate of oxidation of organic matter and hence related to the atmospheric concentration of CO_2) might be expected to influence $\delta^{13}\text{C}_{\text{DIC}}$ by air-sea exchange (Charles *et al.* 1993), although the relatively large size of the oceanic carbon reservoir would tend to damp fluctuations. That changes in

atmospheric CO₂ content are indeed reflected in $\delta^{13}\text{C}_{\text{DIC}}$, and recorded in skeletal calcium carbonate, is shown by the reduction in $\delta^{13}\text{C}$ of shallow-depth foraminiferal and sponge material over the period of significant anthropogenic addition to atmospheric CO₂; apparently, preservation of the atmospheric signal is due to incomplete mixing of shallow and deeper waters (Beveridge & Shackleton 1994; Böhm *et al.* 1996).

Unlike records from modern scallops of the US Atlantic Coast (Krantz *et al.* 1988), $\delta^{13}\text{C}$ data from modern to mid-Pliocene *A. opercularis* of the SNSB exhibit little within shell variation, rarely > 1‰ over the lifespan (or period of North Sea growth) of the organism (Figs 2 and 3; Hickson 1997; Hickson *et al.* 1999). This is consistent with evidence (from direct measurement or the composition of biotic assemblages) of relatively invariant salinities at the locations of the shells concerned and the considerable distance of the southern North Sea (depth generally < 40 m) from any substantial area of significantly deeper water (hence eliminating the possibility of major upwelling effects). A spring phytoplankton proliferation occurs, but unlike many other areas (including the northern North Sea) is not immediately followed by a depletion of resources and population crash (Tett & Walne 1995). It is possible that this protracted 'bloom' causes little perturbation of $\delta^{13}\text{C}_{\text{DIC}}$ and consequently of $\delta^{13}\text{C}_{\text{shell}}$.

With respect to longer term changes, the modern shell represented in Fig. 2a and the mid-Pliocene shells represented in Fig. 3 all exhibit $\delta^{13}\text{C}$ values which are generally less than those of the late Holocene shell represented in Fig. 2b. This pattern is confirmed by comparison of mean values for all data available from modern and late Holocene (Hickson 1997) and mid-Pliocene (Fig. 3) shells, [−0.04 ($n = 197$), +0.79 ($n = 209$) and +0.34 ($n = 43$), respectively]. It is in accordance with, for the present time, evidence from direct measurement and, for the Pliocene, consistent proxy evidence (Kürschner *et al.* 1996; Raymo *et al.* 1996) of relatively high atmospheric CO₂ concentrations. In view of rather limited ontogenetic variation it appears, therefore, that $\delta^{13}\text{C}$ values of *A. opercularis* shell could be used to chart late Cenozoic changes in atmospheric CO₂ content, although independent evidence of phytoplankton levels (e.g. from trace element data; see below) and the extent of upwelling would be necessary to obtain an accurate picture.

Microgrowth increment data

Except in cases of extreme abrasion, the shell exterior of *A. opercularis* displays a conspicuous record of the pattern of fine-scale accretion in the



Fig. 4. Enlarged view of the ventral part of the shell illustrated in Fig. 1, showing microgrowth increments of varying width but no growth ring (i.e. group of very small microgrowth increments marking a growth cessation). Area outlined is enlarged further and analysed in Fig. 6. Scale bar, 4 mm.

form of microgrowth increments of varying width (Fig. 4). Regular examination of animals grown under semi-natural conditions has revealed that, at certain times of year (May–July), the number of increments deposited approaches, but does not exceed, the number of days elapsed (Broom & Mason 1978). Therefore, it may be that each increment corresponds to one day's growth. Even if this is so (a contrasting interpretation has been made in the case of similar increments in *Pecten maximus*; Gruffydd 1981), it cannot be the case that growth occurs every day because at other times of year there is a marked discrepancy between the number of days and increments. Broom & Mason (1978) also recorded a marked seasonal variation in the width of microgrowth increments. They suggested that this is determined by food supply as

much as temperature, but their data (Broom & Mason 1978, fig. 5), which show increasing increment widths during May and June whilst the phytoplankton standing crop underwent a major

reduction, suggest that temperature is the primary control, at least when food supply is above the minimum for body maintenance.

Measurement of increment widths in North Sea

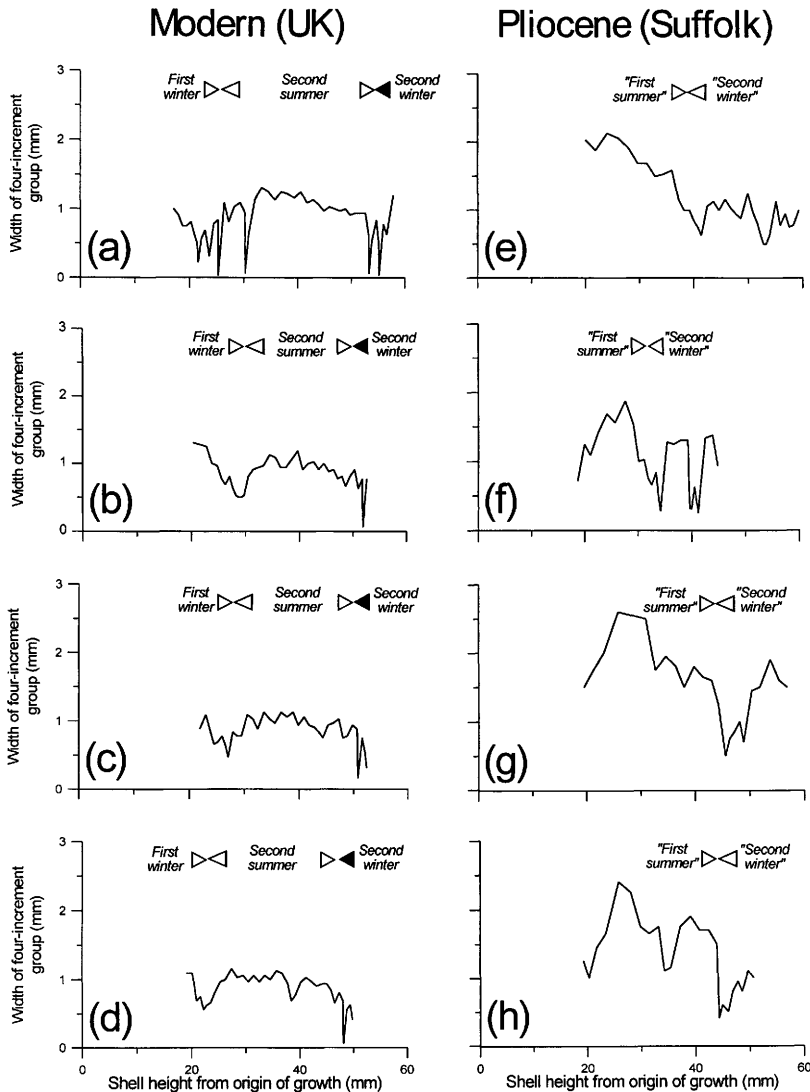


Fig. 5. Profiles of microgrowth increment width in modern [(a)–(d)] and mid-Pliocene [(e)–(h)] Queen Scallop shells, measured using a microscope fitted with an eyepiece graticule. Modern animals had been spawned in spring–summer 1993 and cultured on the west coast of Scotland until October 1994, when they were transferred to nets in the southern North Sea until February 1995, alongside animals spawned in spring–summer 1994. The pattern of growth in the latter, together with published information on growth rates (e.g. Broom & Mason 1978; Paul 1981), confirms identification of seasons represented in former prior (open symbol) to second winter (solid symbol) growth. Interpretation of seasons in mid-Pliocene shells assumes autumn spawning. Specimens (all UD): (a) 52791; (b) 52792; (c) 52793; (d) 52794; (e) 52796; (f) 52797; (g) 52798; (h) 52799. Profiles in (e) and (f) cannot be precisely compared with isotopic profiles from the same specimens (Fig. 3) because ‘shell height’ in increment plots is derived by addition of increment widths; hence, even a slight systematic error in measurement of the latter will result in a significant departure from true shell height at large sizes.

cultured shells (see above) confirms the existence of a seasonal cycle of variation; a similar pattern is evident amongst mid-Pliocene shells from eastern England (Fig. 5), including the two (Fig. 5e and f) for which isotope data are available. The mid-Pliocene shells, however, show markedly higher increment width maxima and minima (presumably corresponding to extreme summer and winter temperatures) and, in association, higher average increment widths (range of means for four-increment groups: 1.00–1.55 for Pliocene shells and 0.82–0.86 for modern shells). On the basis of the increment width–temperature relationship, this indicates substantially warmer conditions in the mid-Pliocene, a finding in agreement with all previous views (see above) and at variance with isotopic evidence (Fig. 3) from the shells represented in Fig. 5e and f.

While these results suggest that growth increment data from *A. opercularis* might provide an independent means of determining secular temperature change through the late Cenozoic, the approach requires testing by analysis of modern forms from different temperature regimes. The specific matter of the accuracy of increment-based temperature estimates for the mid-Pliocene could be investigated with data from Mediterranean populations, which experience temperatures similar to those generally inferred for the SNSB in the mid-Pliocene. Even if it should prove unjustifiable to attach absolute temperatures to increment width values, it seems very likely that increment widths will supply a reliable indication of season and hence provide the basis for an independent temporal scale to calibrate isotope profiles. Such calibration is of considerable value for isotope profiles from fossil shells, where it is never entirely possible to exclude the possibility of cryptic diagenesis and the existence of spurious peaks and troughs (providing misleading indications of seasonal temperature variation). Increment width data might also be used to distinguish between growth rings resulting from traumatic causes (e.g. storms or attempted predation, both of which are likely to be represented by an abrupt reduction in the width of microgrowth increments) and those growth rings due to cessations of growth associated with summer or winter extremes of temperature (likely to be preceded by gradual reduction of increment widths).

Not only are microgrowth increments in *A. opercularis* generally well preserved, width data can be recovered easily and quite quickly by direct measurement under the microscope. Even more rapid data acquisition can be envisaged by application of image-analysis software. Figure 6 shows a 'brightness' trace for the area of shell outlined in Fig. 4. The edges of increments are faithfully

identified as major peaks and it is a simple matter to translate the positions of these into a plot depicting increment width variation (Fig. 7). Use of this technology [see Chavaud *et al.* (1998) and Diou *et al.* (1999) for similar approaches] offers the opportunity to obtain really large data sets, a boon for investigations of palaeotemperature where substantial variation about the mean is to be expected and a small body of data might give a

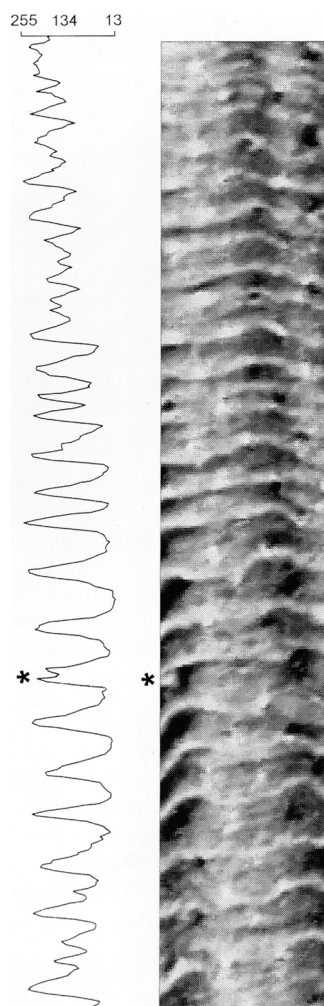


Fig. 6. Enlargement of area outlined in Fig. 4 with plot of 'brightness' (arbitrary scale) measured along left edge of display. Major peaks, in general, correspond precisely with edges of microgrowth increments. Double peak at * is caused by presence of adherent sediment particle; such 'noise' might be removed by use of an appropriate wavelength filter. Image analysis using Wit Version 5.2 (Logical Vision).

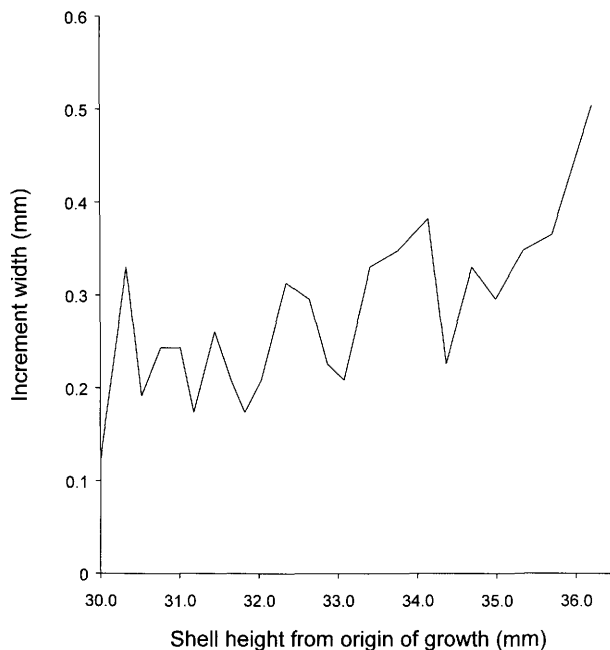


Fig. 7. Plot of increment widths for area of shell analysed in Fig. 6; produced by automatic measurement of distances between major peaks (defined here as those with a brightness value > 200). The plot clearly reflects the overall change in increment widths evident in the display in Fig. 6.

misleading impression (cf. interpretation of oxygen isotope data from mid-Pliocene *A. opercularis*).

At least on the right valve (against the substrate), the record of microgrowth increments is usually obscured by abrasion on the earliest formed c. 15 mm of shell, representing the first 4–8 months of life (Paul 1981). While this shortens the increment record that can be recovered from a shell, the effect is the same on an isotope record obtained (as conventional for scallops) from the outermost part of the outer shell layer. This is because material deposited beneath the shell surface, as sampled on an abraded shell, is not contemporaneous with surface material (marking the advance of the shell edge) and, in any case, may not have been precipitated in isotopic equilibrium with seawater (Hickson *et al.* 1999).

Trace element data

In certain invertebrate taxa, the concentrations in skeletal materials of the trace elements magnesium and strontium show some correlation with temperature (Rosenberg 1980, 1990), although the control is probably metabolic rate (strongly influenced by temperature in invertebrates) rather than temperature itself (Rosenberg & Hughes 1991). For taxa with accretionary skeletons in which the relation-

ship applies there is thus the prospect of identifying seasons, if not absolute temperatures of growth. In the same way as microgrowth increment evidence of season, this would be a valuable complement to stable isotope data.

The magnesium and strontium contents of four North Sea cultured *A. opercularis* shells were investigated using the recently introduced technique of laser ablation inductively coupled plasma mass spectrometry; by reason of the tiny sample sizes involved, this facilitates construction of very detailed ontogenetic profiles (e.g. Fuge *et al.* 1993). Contrary to what had been hoped, profiles of strontium concentration show almost no fluctuation and while magnesium displays some cyclicity this is of much shorter than seasonal period (Fig. 8; cf. Leng & Pearce 1999). Evidently, therefore, strontium and magnesium concentrations in *A. opercularis* shell show no correlation with temperature and cannot provide independent temporal calibration of isotope profiles. (Note: magnesium profiles would be of some use if the cause and/or temporal basis of cyclicity, currently unknown, could be established.)

Other trace elements may yet prove to be useful indicators of the season of shell growth. The concentrations of cobalt, copper, iron, lead, manganese, nickel and zinc all vary seasonally in

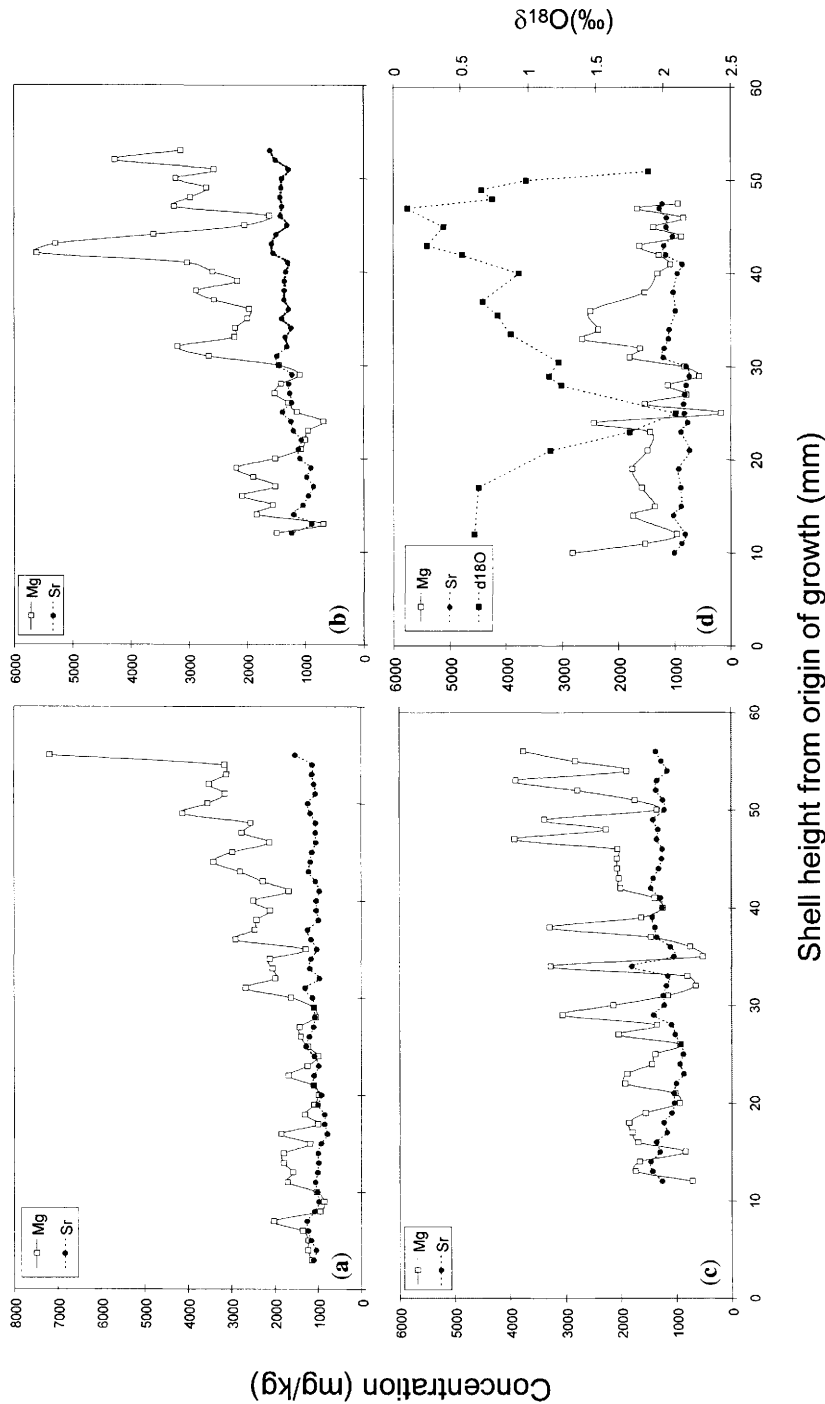


Fig. 8. Profiles of magnesium and strontium concentration for four Queen Scallops initially cultured on the west coast of Scotland and then transferred to the southern North Sea. Oxygen isotope data included in (d), showing summer–winter seasonality, demonstrate that variation in Mg content of this specimen [and those in (a)–(c)] does not have a seasonal basis. Specimens (all UD): (a) 52800 (S2/5); (b) 52801 (N4/A2); (c) 52802 (N4/A28); (d) 52803 (N4/A9). Alphanumeric codes in brackets were used by Hickson (1997) and Hickson *et al.* (1999).

soft tissues of *A. opercularis*, probably in relation to sequestering by phytoplankton (Bryan 1973), and the fact that ontogenetic profiles from shells of other scallop species exhibit seasonal variation in concentration of the trace element cadmium, again probably in relation to phytoplankton uptake (Krantz *et al.* 1988), makes it reasonable to expect that concentrations of elements in the former group would show seasonal variation in the *A. opercularis* shell.

Conclusions and wider applications

A. opercularis is well suited for investigation of late Cenozoic marine environments in Europe. The species has many propitious features, amongst the most important of which are equilibrium (or near) stable isotope incorporation, and the capacity to furnish several detailed and independent ontogenetic records of environment from an individual shell, hence enabling checks for accuracy. It is not, however, a perfect tool: it has the notable defect of a relatively short lifespan which prevents acquisition of long-term records. In this respect, it is distinctly inferior to the bivalve *Arctica islandica* which lives to over 200 years and has been dubbed 'the tree of the North Atlantic' (Thompson & Jones 1977; Weidman *et al.* 1994). However, unlike this species, *A. opercularis* exhibits rapid, year-round growth which enables recovery of well-resolved, complete records of seasonal variation in environment (principally temperature). Combined use of these species represents a means of constructing the fullest possible environmental history.

With respect to the particular major issues identified at the outset, carbon isotope data from mid-Pliocene *A. opercularis* of the SNSB are consistent with the notion of relatively high levels of atmospheric CO₂ and hence of potential 'greenhouse' warming of atmosphere and oceans. Microgrowth increment data appear to indicate higher summer and winter sea temperatures than present but, until the increment width-temperature relationship is calibrated through further research on modern forms, the relative magnitudes of summer and winter temperature increases cannot be determined, and hence the role of greenhouse heating (as v. Gulf Stream heat supply) cannot be fully evaluated. Indeed, further research on modern forms is necessary to confirm that growth increments can provide a reliable indication of differences in general temperature regime. Oxygen isotope data indicate mid-Pliocene sea temperatures little different from now in the SNSB. The balance of evidence suggests that these are erroneous estimates, resulting from cryptic diagenetic alteration of the original isotopic signature. However, there are no more direct indications that this is the

case; hence, pending results from further studies of growth increments in modern forms, it cannot be ruled out that previous notions of relatively high sea temperatures in the SNSB during the mid-Pliocene are significantly in error.

Information on the age and growth rate of organisms is of fundamental importance for management of commercially exploited populations and for investigations of the evolutionary role of heterochrony (changes in the rate and times of onset-cessation of developmental processes). Seasonal cycles in oxygen isotopic composition of skeletal materials have been used as a basis for obtaining such information in both contexts (e.g. Jones 1988; Dare & Deith 1991). However, while seemingly reliable, the oxygen isotope approach demands substantial investment of time and money. Microgrowth increment analysis has been adopted in the management of some scallop fisheries (Dare 1995), but the recent analysis by Jones & Gould (1999) of annual increments in the oyster *Gryphaea* is one of very few instances where any kind of increment size data has been employed in evolutionary studies. At least for scallops, readily obtainable microgrowth increment data offer the prospect of answering many questions concerning the role of heterochrony in evolution (e.g. Johnson 1984).

Stable-isotope analysis was carried out at the NERC Isotope Geosciences Laboratory, Keyworth, under an award of services to ALAJ (IP/417/0994). We thank H. Sloane and C. Arrowsmith for assistance with analysis of carbonates and waters, respectively. The investigation was mainly conducted during tenure by JAH of a NERC studentship (GT/4/94/322). Additional support for trace element analysis (performed at the British Geological Survey, Keyworth) was provided by the University of Derby. We thank J. P. Mikolajunas (formerly at Seafish Industry Authority, Ardtoe) for supply of specimens used in North Sea culture, R. Janssen (Naturmuseum Senckenberg, Frankfurt) for supply of North Sea indigenous specimens and R. Pouwer (Netherlands Institute of Applied Geoscience, Utrecht) for provision of information on the occurrence of Pliocene *A. opercularis* in the Netherlands. We thank A. Weller (British Geological Survey, Keyworth) and C. A. Richardson (University of Wales, Bangor) for permission to quote unpublished findings relating to *A. opercularis* and *Pecten maximus*, respectively.

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