
Late Pleistocene and Holocene Coastal Palaeoeconomies: A Reconsideration of the Molluscan Evidence from Northern Spain

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The worldwide increase in shell midden deposits on coastlines during the Holocene has been variously explained as the result of human population growth, economic intensification, changes in the visibility of midden deposits with changes in sea level, or climatic and environmental changes. Since coastlines are relatively unstable in geological and ecological terms, and since many archaeological sequences span periods of major climatic change, a critical issue is the ability to disentangle palaeoenvironmental from cultural and anthropogenic effects. We draw on a case study from the cave sequences of northern Spain to illustrate the problems and possibilities of palaeoeconomic and palaeoenvironmental interpretation, using studies of palaeogeographical context and analysis of abundance, taxonomic representation, ecological tolerances, size, growth structures, and other physical and chemical characteristics of the molluscs themselves. We demonstrate that the dominant, but by no means exclusive, factor in archaeologically visible long-term changes in shell-gathering behavior is environmental change rather than cultural change. © 2003 Wiley Periodicals, Inc.

INTRODUCTION

Interpretation of coastal shell midden sequences throughout the world has typically been dominated by two big issues. The first is the apparent explosion in size and number of shell deposits in the mid-Holocene in comparison with preceding periods. An earlier generation of interpretations saw in this large-scale pattern clear evidence for a worldwide process of economic intensification and population growth (Cohen, 1977; Osborn, 1977; Yesner, 1987). More recently there has been increased skepticism about the reality of this pattern as our knowledge of late Pleistocene and early Holocene sea-level change and its local impact on coastal palaeogeography and geomorphology has improved. We now recognize that late Pleistocene and early Holocene coastal shell middens would have existed on shorelines that are now submerged and have therefore been destroyed or obscured by marine transgression.

Several lines of evidence reinforce that view. On many coastlines, the earliest appearance of large and abundant open-air shell mounds coincides with the period

at which sea-level rise approximated the modern level at about 5000 to 6000 yr B.P. Significantly earlier coastal sites or shell deposits are now coming to light on coastlines that have undergone tectonic or isostatic uplift, notably in Norway (Rowley-Conwy, 2001) and the Red Sea basin (Walters et al., 2000). Deep coastal cave sequences in South Africa have produced evidence of substantial shell gathering associated with much earlier periods of high sea level (Deacon and Shuurman, 1992; Henshilwood et al., 2001). Underwater exploration is also beginning to identify coastal sites at least from the early Holocene (Fischer, 1995). Substantial shell mounds comparable to those of mid-Holocene and later have yet to be found in these earlier contexts. However, it is now increasingly accepted that the utilization of intertidal, marine, and aquatic resources was not confined to the Holocene, but may have been a widespread characteristic of much more ancient human palaeoeconomies, albeit of varying extent and intensity (Erlandson, 2001).

Sea-level rise has also almost certainly had a dramatic impact on the physical character and ecology of the coastline, the nature of the available intertidal habitats, and hence the availability and abundance of intertidal molluscs. As sea level stabilized at about the present level, many coastlines would have become more convoluted with more extensive occurrences of sheltered habitats. Shackleton and Van Andel's (1986) attempt to compare changes in species abundance at Franchthi cave with reconstructions of palaeoshorelines and molluscan habitats at different sea-level stands on the adjacent coastline represents a rare attempt to compare independent off-site and on-site evidence in a specific context but is by no means an uncontroversial one (Thomas, 1987).

In northern Australia, rapidly prograding coastlines provide marine sediments that can be mapped and dated to plot changes in the availability of mudflat habitats suitable for extensive beds of bivalve mollusks, a clue to the relatively late appearance of the massive shell mounds that are such a prominent feature there (Chappell, 1982; Chappell and Grindrod, 1984). However, opinion remains divided as to whether the chronology of the shell mounds reflects time lags in the evolution of coastal mudflat habitats suitable for large numbers of mollusks (Bailey, 1983; Bailey et al., 1994; O'Connor, 1999; Bourke, 2000) or time lags in human population growth and social intensification (Beaton, 1985; Lourandos, 1997; Veitch, 1999).

Sorting out the relative influence of palaeoenvironmental, geological and cultural influences on the visibility of coastal evidence and the nature of changes in molluscan quantities in archaeological sequences remains a complex procedure, with results that are often controversial or that cannot be verified by independent data. As Beaton has emphasized:

The impact of the last marine transgression arcs over the Pleistocene–Holocene Transition, and archaeologists working on coastlines everywhere . . . are confronted by similar and challenging issues. Now-familiar themes unite studies of archaeology in such distant places as the Americas, Africa, Asia, Europe and Australia (Beaton, 1995: 804).

A second major issue is the frequently cited evidence for reduction in size of molluscs and changes in taxonomic representation in midden sequences. This too

is often taken to indicate evidence of overexploitation resulting from economic intensification and population growth. Here too, however, climatic and environmental changes may play an equally powerful role through their impact on habitat change and on growth rates and age structure, and alternative hypotheses are rarely explored let alone tested against independent evidence (Claassen, 1998).

In all these examples, the issue that emerges above all others is the critical importance of independent, palaeoenvironmental data as a check on archaeological interpretations. In some cases, geomorphological features showing changes in coastal habitats can provide independent data on environmental change, as in the examples cited earlier. On rocky shorelines with steep offshore gradients like those of northern Spain, where the general trend is towards erosion or submergence of shoreline features, such opportunities are likely to be much rarer. In this case, it is necessary to rely on physical and chemical signals embodied in the shell structure of the exploited molluscs. As we show below, these can offer valuable independent data on palaeoenvironmental and palaeoeconomic trends.

Northern Spain

The Asturian shell middens (*concheros*) of northern Spain epitomize all the issues discussed above. They have been the focus of repeated attention and controversy during the past 30 years (Clark, 1971, 1983; Bailey, 1973, 1978, 1983; Straus, 1979; Clark and Straus, 1983; Clark and Yi, 1983; González Morales, 1982; Straus and Clark, 1983, 1986). They are dated to the period 9000–6500 yr B.P., and are concentrated along a relatively restricted length of coastline in the province of Asturias in northern Spain, where at least 50 such sites have been recorded (Figure 1). They comprise dense masses of edible mollusc shells, principally rocky shore gastropods dominated by limpets, accumulated in the mouths of limestone caves and rockshelters, along with bones of fish and land mammals, and a stone industry characterized by the distinctive Asturian “pic,” a pebble tool roughly flaked to a point. Some of these middens are stratified above Upper Palaeolithic deposits in which marine molluscs are much rarer or completely absent.

The apparent dramatic increase in the rate of shell accumulation represented by the Asturian shell middens can be explained broadly in terms of three hypotheses: (1) removal of earlier shell deposits by sea level rise; (2) economic intensification resulting from population growth; or (3) environmental changes affecting the availability of the molluscs. The data currently available do not allow unequivocal discrimination between these alternatives.

Reduction in size of the limpet shells in the Asturian middens compared to earlier deposits, and the appearance in quantity of the less common and less easily accessible limpet species *Patella depressa*, have both been invoked in support of the hypothesis of increased population pressure on food supplies. However, both could equally well result from environmental changes affecting species availability and growth rates.

We address all these issues through an analysis of species abundance, size and

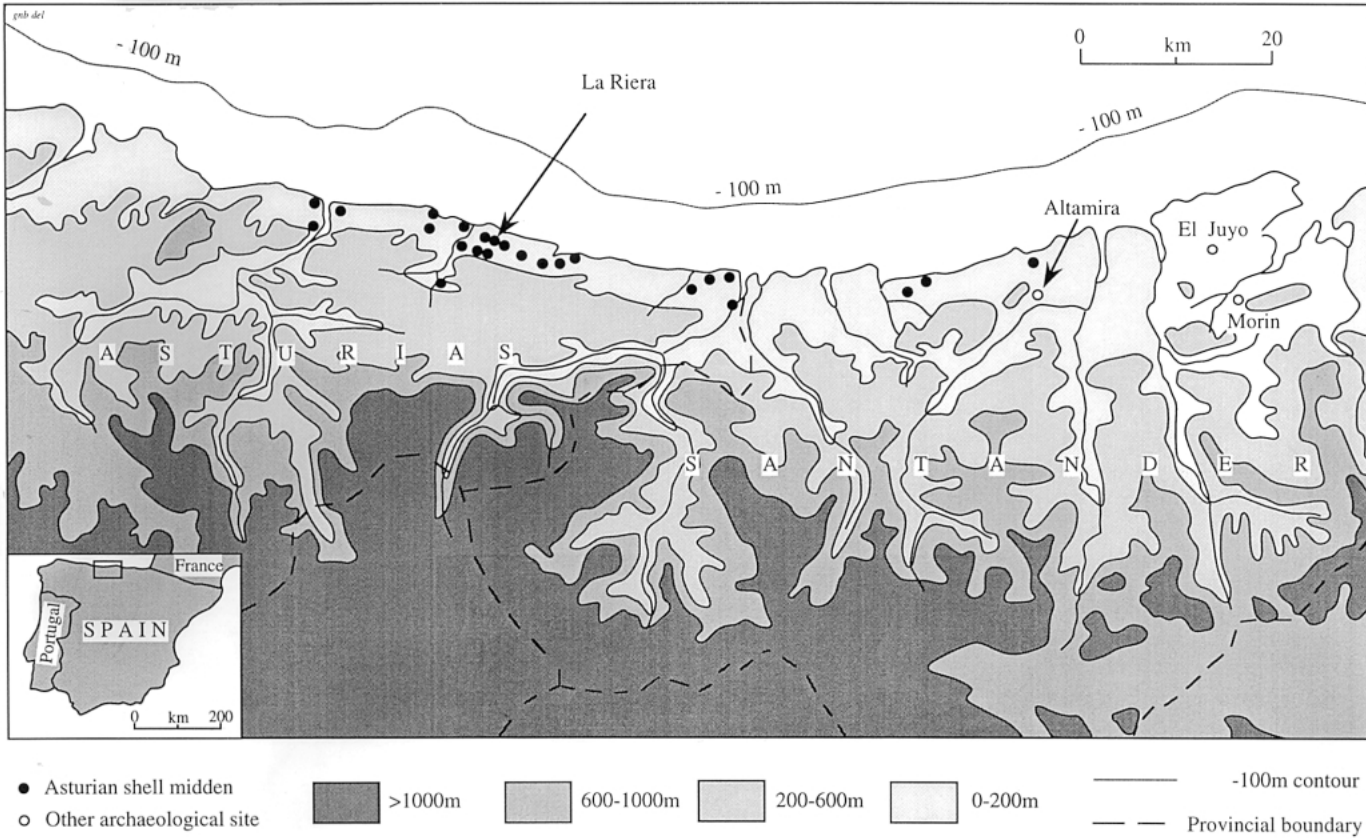


Figure 1. Distribution of Asturian shell middens and other sites in northern Spain. Sources of information: Bailey (1975), Gonzalez Morales (1982), and Straus and Clark (1986).

age structure, palaeotemperature signals, and seasonality evidence in the limpet shells of the La Riera sequence, where a long and well-studied sequence including Asturian and earlier deposits spans the Pleistocene-Holocene boundary. We do not attempt to analyze the full range of palaeoeconomic evidence available and take it as given that the molluscs were only one food resource, albeit an important one, among a broad spectrum of food supplies. Rather our aim is to consider how far the evidence of the molluscs themselves, as one of the most durable and visible indicators of coastal settlement and activity, can be used to test hypotheses of socio-economic and environmental change. First we take a critical look at the evidence for rates of shell accumulation in relation to sea level change.

SHELL QUANTITIES

Mollusc shells have been recorded not only in the Asturian *concheros*, but also in earlier deposits, mostly Upper Palaeolithic in date. The latter are relatively few compared to the number of Asturian sites. Some are stratified beneath Asturian middens in caves and rockshelters, but others are located over a broader territory including the adjacent province of Santander. It is rather difficult to compare shell quantities in a systematic way between sites or between periods, because adequate quantitative data are rarely presented. Many of the Asturian deposits have also been partly removed by erosion, or by excavation earlier in the 20th century.

The largest reported Asturian midden was some 50 m long by 12 m high according to Obermaier (1925:386), which we estimate to represent of the order of one million shells. In contrast, none of the shell deposits reported from earlier contexts, for example from the Magdalenian levels at El Juyo in the neighboring province of Santander (Barandiarán et al., 1985), appears to represent more than a few hundreds or at most thousands of shells. It is difficult to generalize on the basis of such inadequate quantitative records, but our opinion, based on the number and size of deposits that have been recorded, is that the rate of accumulation of mollusc shells in the Asturian middens is orders of magnitude greater than in earlier periods.

For a more detailed study, we rely on the evidence from the cave site of La Riera (Straus and Clark, 1986), which has a cultural sequence extending from the beginning of the Solutrean period at about 20,700 yr B.P. (level 2), and possibly earlier, through to the end of the Asturian period at about 6500 yr B.P. This site offers one of the most comprehensive studies of a long sequence available anywhere in the region and is the only site to have produced a systematic quantification of molluscan remains through a sequence spanning the late Pleistocene and early Holocene. The topmost levels (level 29 and the overlying stalagmitic crust of level 30) represent a classic Asturian shell midden deposit, which originally filled the whole of the cave entrance and extended out in front of it, but only fragments cemented to the cave wall and ceiling still survive.

We use Ortea's figures (1986: Table 15.2), expressed as percentages of shell numbers by stratigraphic level. We also show Straus et al.'s (1986: Table 9.3) weights of shell per cubic meter and combine their data on volumes of excavated deposit

Table I. Representation of mollusc shells by level at La Riera.

Level	Volume (m ³)	Shells (N)	%	Shells (N/m ³)	%	Shell (kg/m ³)	%
1	1.5	34	0.17	22.67	0	0.19	0.07
2	0.128	23	0.12	179.7	0.4	0.66	0.23
3	0.858	99	0.51	115.4	0.3	0.82	0.29
4	0.33	1050	5.36	3182	6.9	27.67	9.68
5	0.385	1380	7.05	3584	7.8	24.1	8.43
6	0.16	127	0.65	793.8	1.7	5.29	1.85
7	0.85	587	3	690.6	1.5	11.85	4.14
8	0.405	589	3.01	1454	3.2	9.63	3.37
9	0.4	117	0.6	292.5	0.6	10.78	3.77
10	0.35	106	0.54	302.9	0.7	2.69	0.94
11	0.165	18	0.09	109.1	0.2	3.48	1.22
12	0.0825	66	0.34	800	1.7	5.01	1.75
13	0.092	209	1.07	2272	5	19.22	6.72
14	0.92	571	2.92	620.7	1.4	11.26	3.94
15	0.32	188	0.96	587.5	1.3	4.9	1.71
16	1.2	147	0.75	122.5	0.3	3.46	1.21
17	0.1875	211	1.08	1125	2.5	12.46	4.36
18	0.56	66	0.34	117.9	0.3	6.56	2.29
19	0.56	56	0.29	100	0.2	3.68	1.29
20	0.4	206	1.05	515	1.1	3.76	1.31
19/20	0.52	208	1.06	400	0.9	3.68	1.29
21/23	2.25	94	0.48	41.78	0.1	0.51	0.18
24	0.6	71	0.36	118.3	0.3	1.97	0.69
25						14.98	5.24
26	0.125	545	2.78	4360	9.5	33.58	11.7
27	2	8383	42.8	4192	9.1	17.15	6
28	0.255	3279	16.8	12,859	28	39.87	13.9
29	0.21	653	3.34	3110	6.8	5.3	1.85
30 ^a	0.13	492	2.51	3785	8.3	1.43	0.5
Totals	15.943	19,575	100	45,852	100	285.9	100

^a Level 30 represents a cemented crust sealing the prehistoric deposits and shell quantities for this and the underlying conchero of level 29 should be treated as minimum estimates.

with Ortea's figures to give numbers of shells per cubic meter (Table I, Figure 2). We believe these figures are a useful proxy measure of differential rates of shell deposition, but with some qualifications. Ortea studied 85–90% of the total shells collected in the 1976–1979 excavations. It is not certain that these are all the shells recovered in excavation (rather than a nonsystematic subsample), although it seems reasonable to assume so in the absence of information to the contrary. In addition, Ortea augmented the figures for the Asturian levels with a 16% sample from a previous excavation. On the other hand, it is likely that both the number and weight of shells in the Asturian level at La Riera may be considerably under-represented because of the fragmented and heavily cemented character of the surviving deposit. Finally, we note that numbers and weights of shell per unit volume

LATE PLEISTOCENE AND HOLOCENE COASTAL PALAEOECONOMIES

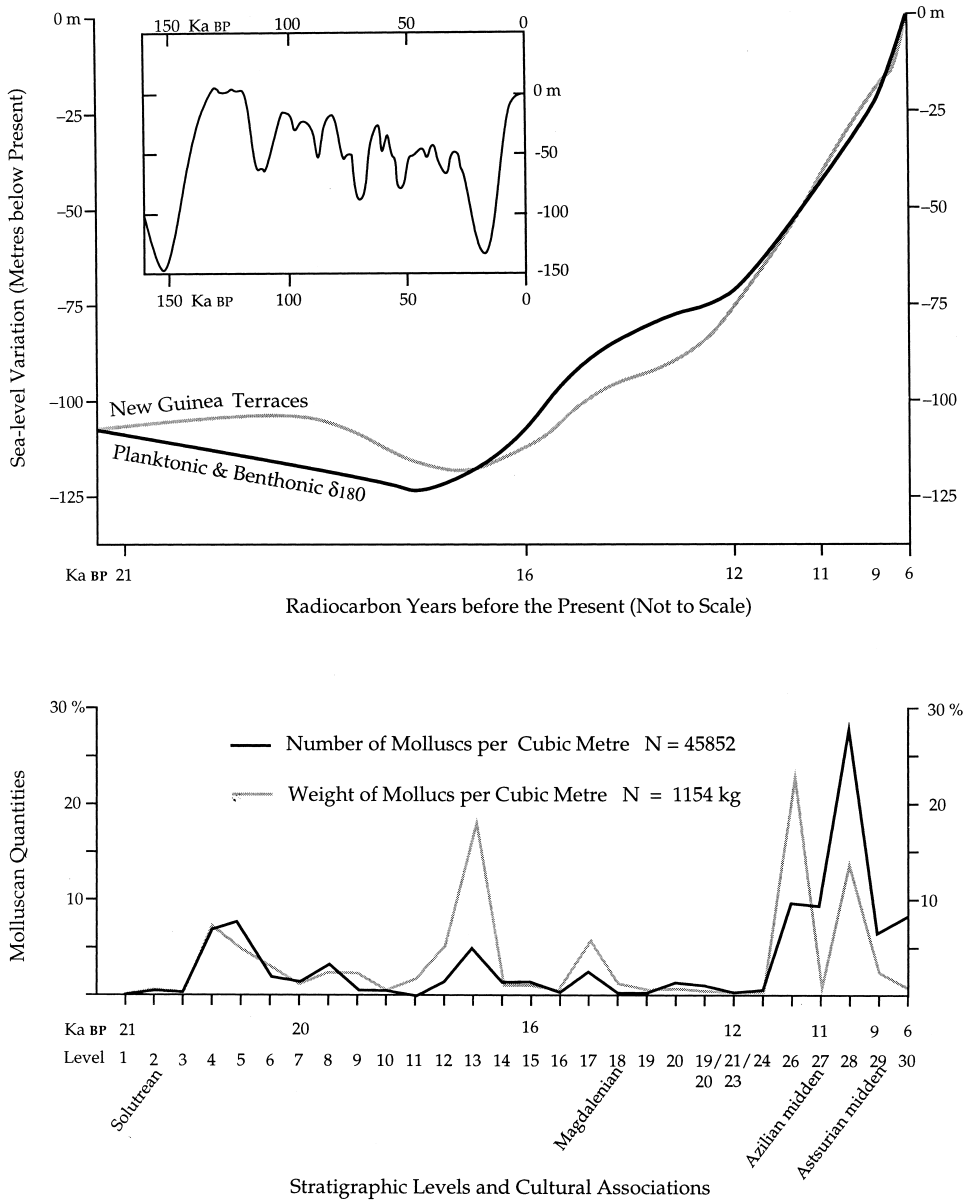


Figure 2. The quantitative representation of marine mollusc shells in the La Riera sequence, plotted alongside sea-level variation. Data from Ortea (1986), Straus et al. (1986), and Chappell and Shackleton (1986). See text for discussion of shell quantities and Table I for raw data.

are a measure of geometric density (cf. Bailey et al., 1983) and do not necessarily accurately reflect rates of accumulation per unit time (or time density)

A sharp and sustained increase in shell deposition is apparent towards the top of the sequence, beginning at the top of the Magdalenian deposits (level 26, dated to about 13,000 yr B.P.) and peaking in the Azilian (level 28) dated to about 10,000 yr B.P. (Straus, 1986: Table 2.2). The drop in the Asturian (levels 29 and 30) is surprising, but we suspect that this may reflect the problems of sampling cemented deposits noted above, and this in any case needs to be seen in the context of the much greater total volume of shell deposit compared with earlier periods. There is another quite sizeable peak of shell deposition in levels 4–5 dated to about 19,000–20,000 yr B.P., and lesser peaks in level 13 (ca. 16,000–17,000 yr B.P.), and perhaps also in level 17 (ca. 16,000 yr B.P.).

Sea Level Change

In order to test the relationship between shell quantities and changing distance to the seashore, we plot the quantitative representation of mollusc shells at La Riera by stratigraphic level alongside Chappell and Shackleton's (1986) data on eustatic sea-level variation (Figure 2). The key point here is that the earlier part of the Riera sequence, between 20,000 and 16,000 yr B.P., coincided with a period when sea level was at its lowest at the Last Glacial Maximum (LGM). From about 15,000 yr B.P. onwards, there was a sustained sea level rise, which slowed somewhat at about 8000 yr B.P. and approximated modern sea level at about 6000 yr B.P. The final sea level rise from about -25 m to the present level coincided with the period of accumulation of the Asturian shell middens.

In plotting the local position of the shoreline, we start with a figure of -125 m for global eustatic lowering of sea level at the LGM, but note that plotting the position of local shorelines is not simply a case of identifying the appropriate bathymetric contour (cf. Van Andel, 1989). Accumulations of sediment on the seabed in subsequent millennia, local hydro-isostatic and glacio-isostatic adjustments of the earth's crust, and other tectonic movements can introduce significant variations. Even allowing for these variables, there are additional inaccuracies and uncertainties in the data available to plot the depth of the seabed. Lambeck (1997) has modeled isostatic effects in NW Europe and shown that the position of the LGM shoreline relative to modern sea level was -70 m on the Atlantic coast of southern France. We suspect that northern Spain was less affected because of its distance from the centers of continental glaciation, its narrow continental shelf, and the presence of a coastal mountain chain that is relatively stable tectonically. Hence we argue that the appropriate bathymetric contour may be closer to the theoretical position of -125 m than elsewhere. But we cannot be sure. We use the -100 m contour as a guide to the LGM shoreline while noting that the correct figure may differ by a margin of up to ± 30 m (Figure 3). We also show bathymetric contours at -50 m and -18 m, approximating sea level positions at about 12,000 yr B.P. and 9000 yr B.P., respectively. Again we note that these are not precise

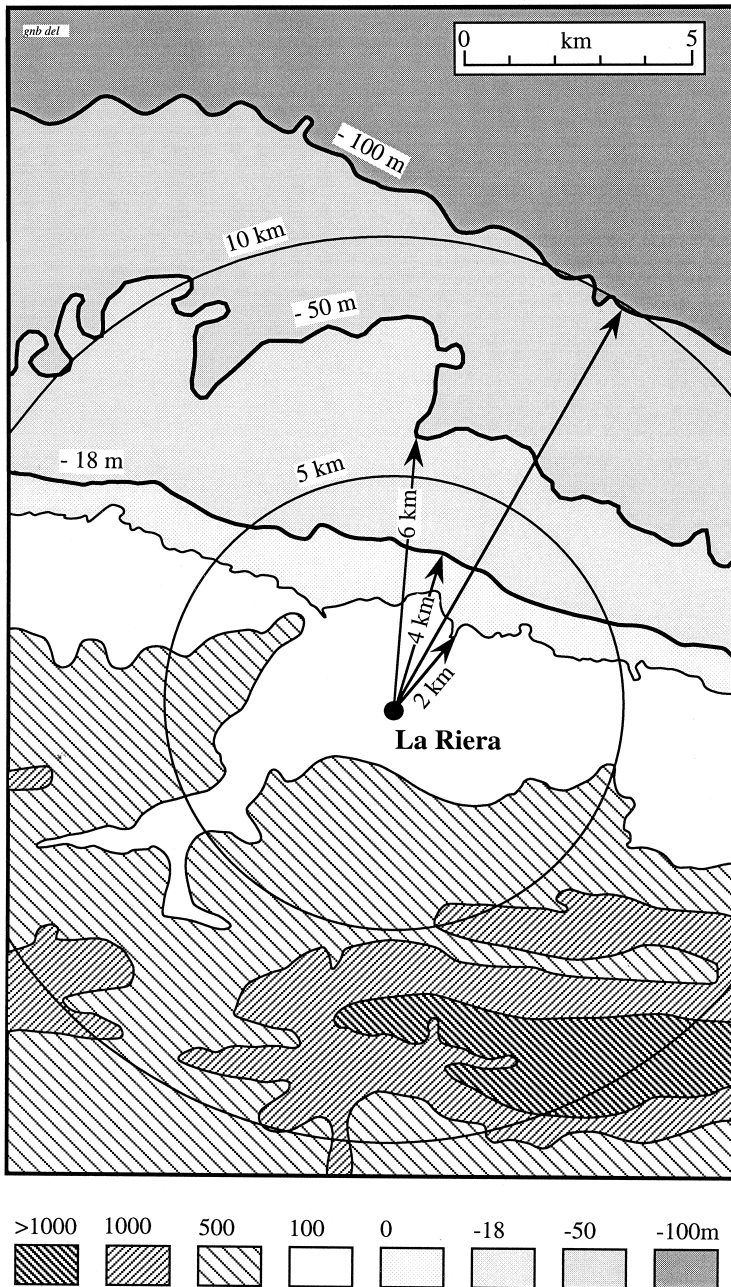


Figure 3. La Riera in its local setting. Sources of information: Bailey (1975) and Straus and Clark (1986).

shoreline positions or dates, but emphasize that the key point is the relative change in distance from seashore to the cave site.

In judging how far people are likely to carry shells for consumption, it is generally assumed that bulk processing takes place as close as possible to the shore because of the high shell to meat-weight ratio of most molluscs and the consequently high transport costs involved. Other factors may override distance constraints and encourage people to carry unshelled molluscs further inland, for example, the longer “shelf-life” of unshelled molluscs, the desire for shelter, availability of freshwater, or patterns of social aggregation (Meehan, 1982). However, the falloff in quantities with increasing distance is likely to be sharp, and 10 km is generally assumed to be a maximum for daily subsistence trips.

The location of known Asturian sites in relation to the modern shoreline provides a useful insight into distance factors. Gonzalez Morales (1982) records 59 rock-shelter sites in eastern Asturias with evidence of Asturian deposits. The shore to site distance for all sites ranges from 0 to 9 km (Figure 4), with the majority (52.5%) falling within 1 km of the modern shoreline, 88% within 3 km, and an overwhelming majority (96.6%) falling within 4 km. Just two sites lie beyond that range, and the fact that both contain typical Asturian shell deposits shows that exceptions to the distance rule do occur, but they are absolutely rare. If we increase these figures by 1 km to allow for the fact that the contemporaneous shoreline during the Asturian period may have been further out than the present one, 4–5 km appears to represent a significant threshold beyond which we should expect very few shells to be carried.

With these factors in mind, it is difficult to resist the conclusion that the increase in shell deposition visible at the top of the Riera sequence is closely correlated with the final stages of sea level rise. The shoreline would have come within the critical 5-km distance from about 12,000 yr B.P. onwards, which is about when the

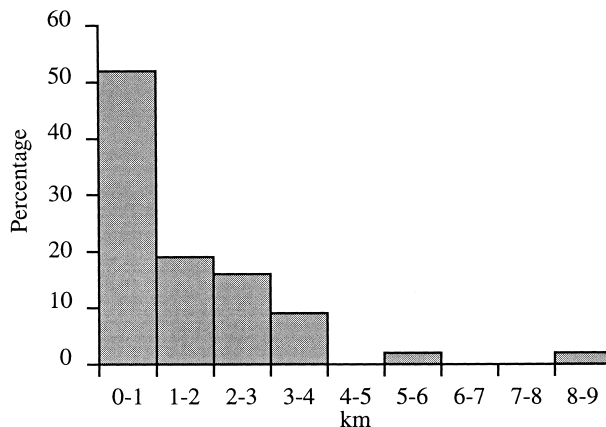


Figure 4. Plot of distances between Asturian sites and the modern shoreline.

sharp increase in shellfood representation becomes apparent (Figure 2). By the beginning of the Asturian period at 9000 yr B.P., sea level would have been close to the -18 m contour, and would have approximated the present position by the end of the Asturian period.

However, this is clearly not the full story, because there is also an earlier peak of shell deposition in levels 4 and 5 at a time when the seashore must have been at its most distant. This accords well with evidence from other Solutrean and Magdalenian sites, notably El Juyo, and suggests that the number of shells, though small relative to the Asturian period, appears significantly greater than in pre-Solutrean periods. If this can be substantiated, it is a point of some interest, because the increased representation of shells occurs at a time when the nearest shorelines would have been as much as 10 km away. Reduction in the distance from seashore to cave site can hardly be invoked to explain the increased representation of limpet shells in Solutrean and Magdalenian levels with respect to earlier periods. We note the presence at La Riera in level 4 of *Patella rustica* and the land snails *Oestophorella bouvinierei* and *Cochlostoma berilloni*, which imply a warmer climate closer to that of the present day than to maximum glacial conditions. But we doubt that this can be equated with an equivalent sea level rise, unless it was so short lived that it is obscured in the deep-sea record of changing ice volumes.

Unfortunately, the La Riera sequence does not extend far enough back in time to the period of higher sea levels at about 28,000 years and earlier (Figure 2). If varying distance to the contemporaneous shoreline were the only factor affecting the numbers of shells deposited at the La Riera location, we should expect to find significantly increased numbers of shells in deposits of these earlier periods. For the moment, we conclude that reduced distance with rising sea level is a major factor in the increased shell deposition apparent in the upper levels at La Riera, but not sufficiently overwhelming to eliminate other possibilities.

SPECIES REPRESENTATION

Four species dominate the La Riera collections (Figure 5): *Patella vulgata* Linnaeus 1758; *Patella intermedia* Murray 1758 (*Patella depressa* Pennant 1777); *Littorina littorea* Linnaeus 1758; and *Monodonta lineata* da Costa 1778. Throughout the greater part of the sequence, *P. vulgata* dominates, with the addition of small percentages of *L. littorea*, but the most striking time trend is the demise of these species in favor of *P. depressa* and *M. lineata* in the late Azilian and Asturian levels (levels 27–30). The replacement of *L. littorea* by *M. lineata* has long been recognized as the result of postglacial climatic warming. *M. lineata* is a southern species with a present-day distribution extending from Southwest Ireland to Morocco and Madeira, whereas *L. littorea* has a more northerly range from the White Sea on the north Russian coast to northern Spain and Portugal (Hayward and Ryland, 1990). Indeed, the complete absence of *L. littorea* in Asturian deposits has been interpreted as evidence of temperatures warmer than the present, since today *L. littorea* is present on the northern Spanish shorelines along with *M. lineata* (Clark, 1971).

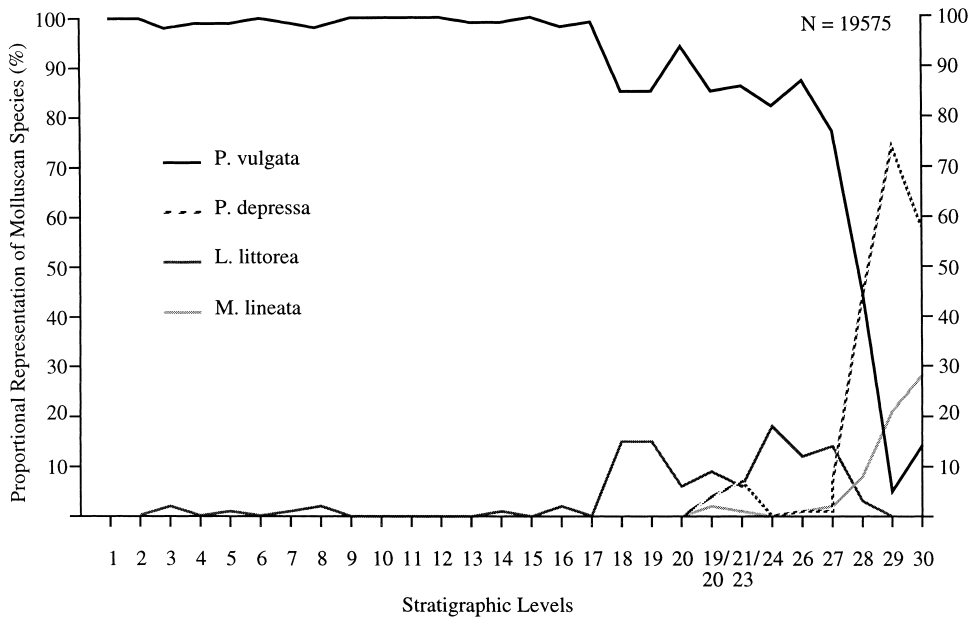


Figure 5. Graphical representation of changes in the proportions of the principal molluscan species in the La Riera sequence, after Ortea (1986).

Patella rustica is also a warm adapted limpet species with a present-day range from Biarritz to the Atlantic coasts of North Africa (Fischer-Piette and Gaillard, 1959; Campbell, 1976) and is present in very small numbers in the La Riera sample. Ortea (1986: Table 15.3) records it in level 4, corresponding to the end of the Laugerie Interstadial. In a reexamination of a sample of 883 limpet shells from levels 5 to 30 sent to Cambridge for oxygen isotope analysis, we have identified *P. rustica* as being certainly present in levels 23/21 and 29. These data confirm a climatic warming trend towards the top of the La Riera sequence.

The rise to dominance of *P. depressa* similarly can be explained in climatic terms. It has a more southerly geographical distribution than *P. vulgata*, ranging from the coast of North Wales to North Africa, whereas *P. vulgata* ranges from northern Norway to Portugal (Hayward and Ryland, 1990). *P. depressa* tolerates more exposed shore conditions than *P. vulgata*, but unlike *P. vulgata* cannot tolerate low salinities or locations high in the intertidal zone (Fischer-Piette, 1948; Fretter and Graham, 1976; Bowman and Lewis, 1977). Accordingly, where the two species are in competition, *P. vulgata* tends to be restricted to estuaries or high shore positions. In Portugal, close to the southern limit of the *P. vulgata* range, *P. depressa* replaces *P. vulgata* as the dominant species on both sheltered and exposed shores (Guerra and Guadencio, 1986). These factors, together with the independent evidence noted above for temperatures warmer than the present, provide a *prima facie* case for attributing the change in limpet species to climatic warming.

Ortea (1986), however, suggests an alternative explanation. *P. depressa* is generally smaller than *P. vulgata* and also prefers more exposed shorelines. In cost-benefit terms it is a less desirable resource for human consumption than *P. vulgata* and may be ignored until rising demand increases human pressure on the food supply. Thus, its appearance in quantity may be due to a widening of the range of shell-gathering activity to include more exposed (and presumably less accessible) stretches of shoreline and smaller limpets. The implication of this argument is that exposed shorelines with abundant populations of *P. depressa* were equally available in earlier periods but neglected by human shell gatherers because of a lack of population pressure or other motivations to exploit less abundant and less accessible resources.

To these climatic and demographic hypotheses can be added a third, and that is that the character of the coastline changed significantly about 9000 years ago to one much more dominated by exposed shores favoring *P. depressa* at the expense of *P. vulgata*. We consider this to be the weakest of the three hypotheses, since the modern coastline is exposed with steep rocky coasts and cliffs but, nevertheless, supports abundant populations of both the principal limpet species. But we concede that this hypothesis is very difficult to test by means of independent evidence and cannot be emphatically excluded.

We also consider the demographic hypothesis to be weak because it seems improbable that a human population under pressure to collect more food would ignore *P. vulgata* shells if they were available, unless we suppose that populations of *P. vulgata* had been virtually wiped out by heavy overexploitation. Nevertheless, the hypothesis of overexploitation is testable, because serious overexploitation should lead to significant reductions in size and modal age of the exploited limpet populations, both of which are measurable. Similarly, additional palaeotemperature evidence can be obtained from the shells themselves to further test the alternative climatic hypothesis.

SIZE CHANGES

By far the most comprehensive series of measurements on limpets has been recorded by Ortea (1986, Table 15.7). As far as we can tell, Ortea measured all of 15,487 identifiable *P. vulgata* shells in his sample, and included not only complete specimens but also estimated the maximum length of broken specimens from the thickness of the apex. We cannot evaluate the reliability of these measurements because Ortea does not give details of the formula for estimating length from apical thickness, or the proportion of specimens measured in this way. We have, therefore, set out to replicate his data by taking independent measurements on a sample of the La Riera material comprising 1610 shells from the original collections stored in the Oviedo Museum plus 518 shells from a sample taken to Cambridge for isotope analysis (Craighead, 1995). Only complete shells were measured, and all measurements were taken with vernier calipers to the nearest 0.5 mm. The results are set out in Table II alongside Ortea's original data, and in Figure 6. Comparison of the

Table II. Metrical data for *Patella vulgata* samples from the La Riera sequence.^a

Level	Mean Length		Mean Length			Mean Width			Mean Height			Low Shore		Sheltered Shore	
	mm	<i>n</i>	mm	s.e.	<i>n</i>	mm	s.e.	<i>n</i>	mm	s.e.	<i>n</i>	%	<i>n</i>	%	<i>n</i>
	(Ortea)		(Craighead)												
30.1	31.0	68	35.8	1.67	15	33.1	0.87	7	12.9	0.66	14	79	15	100	6
29	26.8	34	42.4	3.32	5	36.7	3.77	3	16.6	1.65	5	100	5	100	3
28	28.1	1466	31.8	0.46	107	25.7	0.43	107	11.4	0.24	107	63	107	46	107
27	35.2	3154	37.7	0.38	183	31.4	0.37	179	14.2	0.46	183	76	183	91	176
27 Upper	24.8	502	—	—	—	—	—	—	—	—	—	—	—	—	—
27 Lower	27.9	3630	—	—	—	—	—	—	—	—	—	—	—	—	—
26	34.2	474	33.2	0.50	126	26.8	0.44	122	12.4	0.23	126	60	126	50	122
25	—	—	33.6	0.96	27	27.7	0.84	24	12.9	0.43	27	46	27	54	23
24	33.8	58	31.4	0.71	49	25.8	0.88	26	11.8	0.38	49	68	49	46	24
21/3	43.0	81	39.3	1.24	45	33.3	1.31	42	13.5	0.63	44	82	45	79	39
20	42.5	194	43.4	0.78	43	38.2	0.80	43	15.9	0.39	37	95	43	100	36
19/20	44.5	176	42.7	0.66	64	37.0	0.73	62	15.8	0.37	56	91	64	100	60
19	45.0	47	41.8	0.79	92	37.3	0.69	80	14.8	0.41	64	89	92	93	75
18	45.0	56	43.7	0.50	114	38.7	0.57	107	16.6	0.24	72	87	114	98	105
17	46.2	210	44.7	0.40	119	39.2	0.42	118	16.3	0.33	97	97	119	100	115
16	41.3	144	41.5	0.35	142	36.1	0.37	135	16.1	0.26	74	91	142	99	134
15	38.6	188	38.7	0.84	43	33.1	0.89	42	15.1	0.58	28	67	43	95	42
14	40.1	567	42.0	0.69	112	36.5	0.69	110	16.4	0.39	61	87	112	87	109
13	44.5	208	47.8	1.38	15	42.5	1.45	15	18.3	0.66	3	100	15	100	15
12	45.4	66	44.7	1.76	10	38.5	1.86	10	—	—	—	100	10	100	10
11	40.8	18	47.0	1.91	10	40.9	2.10	10	—	—	—	100	10	100	10
10	35.0	106	38.5	1.55	22	33.0	1.55	22	15.8	0.72	5	68	22	100	22
9	40.3	117	44.6	0.61	76	38.9	0.62	73	16.7	0.44	31	92	76	92	73
8	38.4	576	43.6	0.62	78	37.8	0.63	77	17.6	0.76	27	87	78	93	75
7	44.3	582	43.2	0.52	167	37.3	0.55	157	17.3	0.32	108	80	167	95	152
6	44.4	127	44.0	1.73	16	38.2	2.21	15	20.1	2.14	4	88	16	93	15
5	42.4	1370	43.6	0.60	135	38.2	0.60	129	17.2	0.83	32	91	135	94	126
4	46.1	1045	43.4	0.41	247	37.4	0.41	246	17.8	0.28	109	85	247	84	246
3	42.8	97	35.4	1.04	61	29.4	1.00	61	10.4	0.91	15	79	61	61	61
2	42.3	23	—	—	—	—	—	—	—	—	—	—	—	—	—
1	41.5	34	35.2	1.08	5	27.8	0.87	5	—	—	—	100	5	60	5
Totals		11,286			2128										

^a Data from Craighead (1995) and Ortea (1986).

LATE PLEISTOCENE AND HOLOCENE COASTAL PALAEOECONOMIES

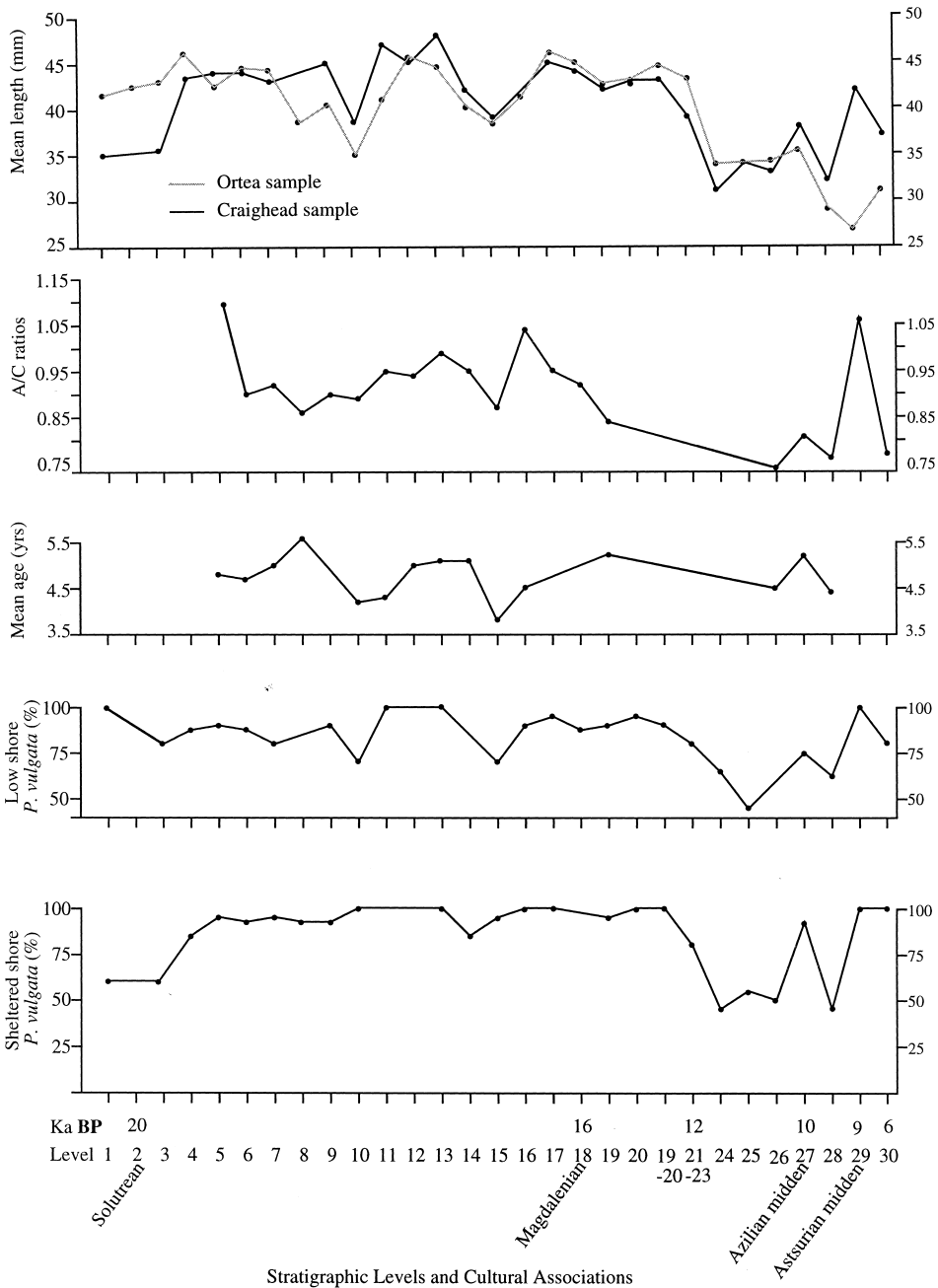


Figure 6. Data on *P. vulgata* from the La Riera sequence: mean length, A/C ratio, low shore and sheltered shore specimens, and mean age. See Tables II and III for raw data.

means of both samples shows no significant difference (Student's $t = 0.85$, less than the significant value of $t = 2.056$ using a 2-tailed test at the 0.05 significance level with 26 degrees of freedom). In broad terms, both sets of data show a general tendency for shells to be smaller in the Azilian and Asturian levels, although both data sets, interestingly, show that the trend to small shell size begins somewhat earlier, in level 24. There are, however, some notable differences for individual levels, the most glaring being level 29, where Ortea's data give a mean of 26.8 mm and Craighead's data a mean of 42.4 mm. It is regrettable that only 5 complete specimens of *P. vulgata* were available for measurement from this level (Ortea records measurements from 34 shells in his sample), especially since it is a level so critical to the interpretation of the sequence. Further evaluation of this difference for level 29 is seriously compromised by the small sample sizes.

Interpreting size changes in samples of limpet shells from archaeological sequences is a complex issue because a reduction in the mean maximum dimension (length) may be the result of any one of at least four independent variables: climate change resulting in a reduction in mean annual sea surface temperatures; increased exposure, involving collection of shells from more exposed shores; a change of zonation, that is collection of shells from higher in the intertidal zone; or a shift to a predominance of younger age classes because of increased predation pressure, whether human or otherwise. The impact of these variables on limpet size is well established, the reduction in growth rates of limpets on exposed shores and high in the intertidal zone being due to the reduced time available for feeding (Ebling et al., 1962; Lewis and Bowman, 1975; Fretter and Graham, 1976; Jones, 1984). Increased predation pressure, by removing the older and larger animals, can also result in size reduction, although animals of a given age class may actually be larger than their counterparts in a less heavily exploited population because of higher growth rates (Swadling, 1976; Luff and Bailey, 2000). The impact of nonhuman predators such as starfish or aquatic birds should not be underestimated, since they can remove huge quantities of molluscs, with a corresponding impact on abundance, growth rates, and demographic structure. But we have no way of distinguishing human and nonhuman predation impacts. Additional habitat variables such as salinity variations in estuaries or variations in food supply may have additional effects. To these should be added uncertainties of measurement because of sample bias and measurement inaccuracies. We comment further on size variation after consideration of other lines of evidence.

Palaeotemperature Variation

The best known technique for identifying palaeotemperature variation is the use of oxygen isotope ratios. However, as Deith and Shackleton (1986) have shown, the technique produces erratic and unreliable results when applied to *P. vulgata* shells from the La Riera deposits because of irregular growth patterns and shell recrystallization and post-depositional diagenesis. Cohen and Branch (1992) have established an alternative method on the South African limpet, *Patella granularis*.

They have shown that the interior surface of the limpet shell is composed of separate, sometimes overlapping, bands of calcite and aragonite. These bands are defined with respect to the m band, the myostracum or muscle attachment scar. The two inner bands ($m - 1$ and $m - 2$) are composed of aragonite and calcite respectively, while the first outer band ($m + 1$) is composed of aragonite, and the second and third outer bands ($m + 2$ and $m + 3$) are composed of calcite. They have demonstrated that the overall percentages of aragonite and calcite in the shell structure as measured by X-ray diffractometry are directly proportional to variations in sea-surface temperature, and that there is also a strong correlation ($r = 0.91$) between sea-surface temperature and the width of the $m + 1$ aragonite band relative to the $m + 2$ and $m + 3$ calcitic bands.

Craighead (1995, 1999) has tested this relationship on 224 modern *P. vulgata* shells collected from 8 locations around European coastlines with local data on mean annual sea surface temperatures. Shells were cleaned and a stripe of reagent solution, prepared in accordance with Feigle and Anger (1972:542–543), applied with a watercolor brush to the interior of each shell. This solution is absorbed more rapidly by the aragonite portions of the shell, which show up as a dark silver color. The widths of the bands were then measured to the nearest 0.01 mm using a dendrochronology increment measurer incorporating a 10× microscope and designed by V.R. Switsur for counting and measuring tree rings. Because of difficulties in identifying the muscle attachment scar, a modified formula has been used to measure the aragonite/calcite (A/C) ratio, namely, the ratio of the width of the aragonite layers (m and $m + 1$) to the width of the calcite layers ($m + 2$ and $m + 3$). Because of a slight fuzziness in the boundary between bands, and variation in measurements taken to the outer edge of the shell because of indentations in the shell edge, the A/C ratio for each shell is based on the mean of 4 sets of measurements. The results produce a very strong correlation between the A/C ratio and mean annual sea surface temperatures ($r = 0.96$), and the relationship between the two is expressed by the following formula:

$$\text{SST } ^\circ\text{C} = \text{Exponent} [1.83 (\text{Ln A/C ratio}) + 2.65] \quad (1)$$

This technique was applied to 393 shells from the La Riera sequence, drawn from the Cambridge sample. The average A/C ratio was calculated from up to 4 measurements on each shell and the mean determined for each of 21 stratigraphic levels (Table III). As a further check on the method, 19 specimens from 5 levels (levels 14–17 and level 18) were selected for oxygen isotope analysis. Recrystallized calcitic shell and aragonite material were ground away from the edges and surfaces of each specimen and up to 8 samples were taken along the axis of growth at about 2.0 mm intervals to cover at least one year's growth. The mean $\delta^{18}\text{O}$ values were compared with the A/C ratios from the corresponding levels and show a moderately strong correlation ($r = -0.84$). We conclude that A/C ratios provide a reliable guide to palaeotemperature variation, but we caution against placing too much reliance on the absolute values of the estimated sea-surface temperatures. Many of the

Table III. Aragonite/calcite ratios, estimated sea surface temperatures, and mean limpet ages in selected levels of the La Riera sequence.^a

Level	A/C Ratio	N	SST (°C)	<i>Patella vulgata</i>		<i>Patella depressa</i>		
				Mean Age		Mean Age		Mean Length
				Years	N	Years	N	mm
30	0.77	8	8.8	—	—	—	—	—
29	1.06	12	15.8	—	—	4.0	34	25.1
28	0.76	30	8.6	4.4	36	4.4	5	28.2
27	0.81	36	9.6	5.2	40	4.6	23	30.9
26	0.74	14	8.2	4.5	29	—	—	—
21/23	0.79	10	9.2	—	—	—	—	—
19	0.84	32	10.3	5.2	32	—	—	—
18	0.92	18	12.2	—	—	—	—	—
17	0.95	10	12.9	—	—	—	—	—
16	1.04	36	15.2	4.5	34	—	—	—
15	0.87	16	11.0	3.8	15	—	—	—
14	0.95	16	12.9	5.0	10	—	—	—
13	0.99	17	13.9	5.1	14	—	—	—
12	0.94	11	12.6	5.0	10	—	—	—
11	0.95	13	12.9	4.3	11	—	—	—
10	0.89	9	11.4	4.2	9	—	—	—
9	0.90	33	11.7	4.9	42	—	—	—
8	0.86	20	10.7	5.6	30	—	—	—
7	0.93	33	12.4	5.0	51	—	—	—
6	0.90	10	11.7	4.7	11	—	—	—
5	1.25	9	21.3	4.8	12	—	—	—

^a Data from Craighead (1995).

archaeological specimens have slightly abraded edges, and removal of a few mm of edge material may result in overestimates of temperature by as much as 1–2°C. Cohen and Branch (1992) also draw attention to other minor measurement errors. They also note that the formation of calcite and aragonite crystals may be affected by other factors such as variable microhabitat conditions (resulting in interindividual variation of A/C ratios by as much as 0.18), differential solubility of aragonite and calcite at different temperatures, and different phylogenetic histories. For all these reasons, quite large margins of error should be attached to the temperature estimates, of the order of ±1–2°C. Some of the absolute values in Table II are questionable, notably the result from level 5, which produces an anomalously high value well outside the range of any other climatic indicators for this period. The value for level 16 is also strikingly high. This level is associated with the middle of the Lascaux Interstadial, so that a relatively high value is not unreasonable, especially given the presence of the warmth-loving snail *Oestophorella bouvinieri*. However, these figures seem too high in relation to level 29, since other evidence from level 29, noted above, suggests temperatures warmer than the present day. We conclude that the A/C ratios provide a useful guide to palaeotemperature variation but that the absolute values should be treated with caution.

Figure 6 compares the A/C ratios with the mean maximum size of *P. vulgata* from the Craighead sample, and shows that the two variables track each other very closely, the direction of change being the same for all levels except levels 7 and 17. If the level 5 outlier is excluded, the two variables are quite strongly correlated ($r = 0.76$), from which we conclude that the mean size of *P. vulgata* was quite strongly dependent on sea surface temperatures. However, these results do not exclude the influence of other factors, especially if Ortea's figure for the mean size of *P. vulgata* shells in level 29 is preferred.

Exposure and Zonation

We can use our metrical data to test Ortea's hypothesis in another way by looking at variations in the proportion of limpets that grow in low-shore positions or on sheltered shores. In cost-benefit terms, we would expect low-shore limpets on sheltered shores to be the preferred target of shell gathering because this is where the larger limpets tend to grow. Increased proportions of high shore limpets might indicate greater pressure on food resources. It is well known that shells of *P. vulgata* on exposed shores or in high-shore positions, in addition to being smaller than those in sheltered or low-shore positions, tend also to have a more conical shape (Orton, 1928a, 1928b; Fretter and Graham, 1976; Jones, 1984).

Measurements of length/height and length/width ratios of modern limpet shells demonstrate that low-shore shells tend to be longer, flatter and wider than high-shore animals. Discriminant analysis gives an unstandardized discriminant function, which assigns shells to high shore and low shore positions with a success rate of 86%, using the following formula:

$$\text{Zone} = \text{Length} (-0.123) + \text{Height} (0.52) + \text{Width} (0.191) + 2.289 \quad (2)$$

Values more positive than -0.25 are assigned to high-shore locations, while more negative values are assigned to low-shore locations.

Similarly, exposed-shore limpets tend to be slightly narrower and flatter than those from sheltered shores, and discriminant analysis produces an unstandardized discriminant function as follows:

$$\text{Exposure} = \text{Length} (0.142) - \text{Height} (0.06) + \text{Width} (0.0489) - 5.328 \quad (3)$$

Values more positive than -0.15 are associated with sheltered shores and values more negative with exposed shores. Use of these values resulted in shells being assigned to their correct position with a 68% success rate.

Length/width and length/height ratios also vary with latitude and climate, but the nature of the variation is similar to that caused by variations in exposure. Thus, it is possible to discriminate between high-shore, low-shore, exposed-shore, and sheltered-shore limpets in a given sample, provided that climate is constant. If we

assume that climate remained constant within each stratigraphic level of the La Riera sequence, then the discriminant functions can be applied to the raw data from La Riera to produce reasonably reliable measures of the source of origin of the *P. vulgata* shells (Table II, Figure 6).

Proportions of low shore and sheltered shore specimens track each other quite closely, and both types of limpets are more common in the earlier levels, with more dramatic fluctuations towards the end of the sequence. If the reduction in these specimens is evidence of increased pressure on food, then the period of greatest stress appears to have been in levels 24–26, coinciding with the sharp increase in shell quantities towards the end of the sequence (Figure 2). However, there is another factor to consider.

Figure 6 plots the variation in percentage of low shore and sheltered shore specimens against variations in the A/C ratio. It is apparent that these variables track each other quite closely. Regression analysis gives moderately strong coefficients of correlation: for the relationship between the A/C ratio and low shore specimens $r = 0.76$, and for the relationship between the A/C ratio and sheltered shore specimens $r = 0.79$ (excluding in both comparisons the anomalous A/C value for level 5). The implication of these results is that during colder periods limpet gathering tended to focus more on high-shore locations and exposed shores.

The increase in high-shore limpets in cold weather might be due to more restricted access to the low shore because of cold temperatures and bad weather, or to food stress caused by a drop in other food supplies, rather than to increased population pressure per se.

The reasons for the increase in exposed shore specimens are less certain. As is clearly shown in Figure 6, the preference for sheltered shore specimens is very strongly marked throughout the La Riera sequence, with sharp reductions being apparent only towards the end of the sequence, notably in levels 26 and 28. It is possible that we are seeing here the additional effect of a widening of shell-gathering activity to include less favorable stretches of shoreline. However, there are two other possibilities. The first is that changes in the morphology of the shore profile increased the exposure of the shoreline as a whole. A second possibility is that the figures are an artifact of the measuring technique. As noted above, the discriminant function for distinguishing exposed shore and sheltered shore limpets is very similar to that which discriminates between shells growing in cold climates from those growing in warmer climates. It is not possible to disentangle the two effects unless one is known to be constant. The interpretation of the La Riera data is based on the assumption that climate remained constant within each stratigraphic level. However, we know that climate underwent rapid fluctuations between climatic extremes over as little as a few decades towards the end of the Last Glacial (Johnsen et al., 1992; Taylor et al., 1993). If climate were changing within a stratigraphic level, it is possible that the effects of climatic change and differential exposure would be confounded in our data.

We conclude that changes in the proportions of sheltered shore limpets are primarily the result of climatic changes, either acting directly on the L/W and L/H

ratios, or indirectly on the availability or accessibility of sheltered shore locations. Changes in proportions of exposed shore limpets are more ambiguous. We cannot fully rule out the hypothesis that shell gathering intensified towards the end of the La Riera sequence. But if these changes were taking place, their effect on the metrical characteristics of the limpet shells is too weak to be detected with confidence in our data.

Age Data

Incremental growth structures in *P. vulgata* show a similar pattern to other molluscan species. Microscopic banding is related to periodic tidal immersion, and macroscopic bands visible on the shell surface represent a break in normal growth due to cold sea-surface temperatures in winter (Ekaratne and Crisp, 1982, 1984). The winter growth check may show up as a dark ring and provides a basis for estimating the age at death of individual specimens. Rings representing minor growth checks may also occur as a result of spawning, or as a result of high summer temperatures near the southern limits of the geographical range, but these checks are usually less pronounced and more irregularly spaced and can be distinguished from the winter growth checks. The winter growth checks form a regularly spaced series, the interval between rings showing a slight but successive decrease as the growth rate of the individual slows down with increasing age.

A total of 448 limpets from 17 La Riera levels was available for study. Visible winter growth checks were counted on each shell, and the average minimum age for each level established (Table III, Figure 6). In 60 cases, the apices of the shell were missing, and the ages of these shells were estimated using a formula to derive the missing growth increments from the ratio of growth increments between the final three years' of growth, or the final two years' growth in the case of younger shells (Hamai, 1937; Monks and Johnston, 1993). This formula was applied to *P. vulgata* specimens of known age and growth characteristics from a variety of habitats (Craighead, 1995) and gives a close correlation between observed and estimated age ($r = 0.93$ where the estimated age was based on the final 3 years of growth and $r = 0.77$ where based on the final 2 years of growth).

P. vulgata is a protandrous hermaphrodite (Fretter and Graham, 1976). The animal becomes a mature male at an average age of nine months with a shell length of 10–15 mm. Sex change to female generally occurs during the second and third years. Thus the vast majority of older individuals are female with size ranges for 2-year-olds and 3-year olds respectively of 11–25 mm and 13–38 mm. If human gatherers removed large quantities of the bigger 2- and 3-year-old females, the remaining population would be predominantly male and recruitment drastically reduced.

The La Riera data show that mean age in the levels studied never falls below 4 years and therefore that limpet populations during these periods were not subjected to dangerously high levels of predation. Nor is there any significant correlation between shell ages and mean lengths in the sequence as a whole (Figure 6),

as would be expected if reduction in length were solely a function of reduction in the mean age of the collected shells. On the other hand, it is worth noting that the dip in mean age in levels 15, 26, and 28 is correlated with a dip in mean length, suggesting, at least for these levels, the possibility of a link between the two variables. But the age reduction is quite slight in all three cases and certainly not sufficient to endanger the recruitment of subsequent generations of limpets. In any case, since the drop in mean age also correlates with a drop in estimated sea surface temperatures, we consider climatic change to be the more likely cause of the size changes. We should also emphasize the regrettable lack of ageable *P. vulgata* specimens in the samples available from levels 29 and 30. In the absence of age data, we have to fall back on indirect inferences from the length data. In this regard, it is worth noting that one of the smallest mean lengths in the whole sequence in both Ortea's and Craighead's samples is in level 28 (28.1mm and 31.8 mm respectively, Table II). Yet the mean age of shells in this level is 4.4 years (compared with a mean age from the whole sequence of 4.7 years). Clearly the reduction in mean length in this level is not primarily related to increased predation pressure. This is also the level in which the proportion of *P. depressa* shells draws nearly level with the proportion of *P. vulgata* shells (Figure 5), and when we might therefore expect the effects of overexploitation on *P. vulgata* populations to become apparent, if that were the reason for the increase in *P. depressa* populations. As for levels 29 and 30, although we have no age data for *P. vulgata*, the mean length of *P. vulgata* is actually higher in level 29 than in level 28 in both Ortea's and Craighead's samples (Table II). It seems most unlikely that limpet populations that had been subjected to greatly intensified levels of predation with respect to those in level 28 would show an *increase* in mean length; the expected trend under heavy predation pressure would be a decrease. We conclude that there is no evidence to support the hypothesis that the greatly reduced proportions of *P. vulgata* in the uppermost levels of the La Riera sequence are due to overexploitation by human shell gatherers.

Equally we should observe that, although both the mean length and age of *P. vulgata* are highly variable through time, there is a slight decrease in mean size and mean age in the upper levels. This may be plausibly interpreted as the consequence of a slight but progressive increase in exploitation pressure.

Finally, we present age and length data for samples of *P. depressa* from levels 28–30 (Table III). In this species, the sexes remain separate throughout life and both sexes mature in their second year (Orton and Southward, 1961; Guerra and Guadencio, 1986). Individuals of both sexes are found in all size ranges with the bulk of the breeding population in the 24–30 mm length range. Because the sexes remain separate and the smaller limpets can reproduce, it is likely that recovery would be rapid even after the removal of large numbers of the breeding population. As it is, our data on both age and mean length suggest that the level of human predation fell far short of endangering recruitment in any of the levels for which we have measurements.

SEASONALITY

Deith and Shackleton (1986) have provided a comprehensive review of seasonality issues at La Riera, based on the application of the oxygen isotope technique to shells of *M. lineata* from the upper levels. Their results, however, are limited by their inability to obtain reliable measurements from *Patella* shells because of slow and erratic growth patterns, recrystallisation of shell carbonate, and irregularities in the growing edge. In a more recent study, Craighead (1995) has estimated seasonality by measuring the amount of growth relative to the last winter growth check on a sample of 413 limpet shells from 17 La Riera levels (Table IV). Several difficulties should be recognized with this technique. Very small variations in measurement can substantially alter the estimate of season, particularly in limpets, where the shell edge is sometimes deeply serrated and measurement from the last winter growth line to the shell edge can vary considerably depending on the point from which the measurement is taken. In this study, a conscious effort was made to use the midpoint of an indentation on the shell edge. Another potential source of error is the loss of material from the shell edge by abrasion. Accordingly, the seasonality estimates should be treated with some caution, although they appear to provide consistent general trends, even allowing for these measurement errors.

The results in Table IV show that *P. vulgata* shells were collected throughout the year but with the majority falling in the summer and autumn periods, whereas the majority of the *P. depressa* shells were collected in autumn and winter. If these figures are adjusted to allow for a loss of up to 0.5 mm of material from the shell edge, this advances the estimates by as much as a season. For the most part, winter and spring estimates remain low for *P. vulgata*, while the percentage of winter estimates for *P. depressa* increases. Even a loss of 1.0 mm of edge material does not substantially alter the general shape of the seasonality distributions for the two species.

These differences between the two species can be explained by reference to seasonal variations in meat weight, which are closely related to the timing of spawning. *P. vulgata* meat weight values are lowest in winter, building up to a maximum just before the spawning period in autumn (Jones, 1984). Conversely *P. depressa* spawns in winter/spring and again in summer/autumn (Bowman and Lewis, 1986), so that optimum meat values would occur in winter and again in autumn. If human shell gatherers were optimizing their subsistence activities in cost-benefit terms, we would expect them to concentrate their collection of *P. vulgata* in the summer and early autumn and of *P. depressa* in the winter and autumn. On the whole, this is what the archaeological results show, although *P. depressa* seems to have been ignored during the potentially favorable autumn period. These results provide an interesting comparison with *M. lineata*, which, according to Deith and Shackleton's (1986) isotope analyses, were collected mainly in winter. *M. lineata* spawns in spring (Fretter and Graham, 1976), so that winter would be predicted as the optimum season of collection.

Table IV. Seasonality estimates of limpet shells from La Riera.^a

Level	Unadjusted				Adjusted for 0.5 mm Edge Loss				Adjusted for 1.0 mm Edge Loss				Total N
	W (%)	Sp (%)	Su (%)	Au (%)	W (%)	Sp (%)	Su (%)	Au (%)	W (%)	Sp (%)	Su (%)	Au (%)	
29 ^a	5.9	8.8	35.3	50.0	41.8	—	14.7	44.1	41.2	—	8.8	50.0	34
28 ^a	20.0	20.0	20.0	40.0	60.0	—	20.0	20.0	60.0	—	20.0	20.0	5
28	2.8	25.0	38.9	33.3	22.2	—	33.3	44.4	25.0	—	27.8	47.2	36
27	12.5	7.5	55.0	25.0	25.0	—	20.0	55.0	37.5	2.5	17.5	42.5	40
26 ^a	35.7	14.2	21.4	28.6	64.3	7.1	21.4	7.1	63.4	7.1	24.1	7.1	14
26	—	26.3	47.4	26.3	36.3	5.3	42.1	26.3	37.6	5.3	37.6	37.6	19
19	13.3	20.0	50.0	16.7	26.7	10.0	26.7	36.6	26.7	—	26.7	46.6	30
16	9.5	11.9	61.9	23.8	23.8	2.4	35.7	38.1	33.3	2.4	26.2	38.1	42
15	—	24.3	54.5	18.2	—	9.1	36.4	54.5	18.2	9.0	36.4	36.4	11
14	6.7	13.3	33.3	46.7	26.7	—	30.0	53.3	46.7	—	13.3	40.0	15
13	6.2	12.5	25.0	58.3	25.0	6.2	31.2	37.5	37.4	—	31.3	31.3	16
12	11.1	22.2	22.2	44.4	44.4	—	44.4	11.1	33.3	11.1	33.3	22.2	9
11	—	30.0	60.0	10.0	—	—	60.0	40.0	10.0	—	40.0	50.0	10
10	9.1	36.4	54.5	—	9.1	—	63.6	27.3	18.2	—	35.4	45.4	11
9	29.3	7.3	56.1	7.3	34.1	4.9	24.4	36.6	39.0	2.4	17.1	41.5	41
8	19.2	15.4	19.2	46.2	53.2	—	19.2	26.9	57.7	—	15.4	26.9	26
7	17.6	14.7	52.9	14.7	29.4	—	35.3	35.3	35.3	—	29.4	35.3	34
6	—	11.1	55.6	33.3	11.1	—	44.4	44.4	22.2	—	33.3	44.4	9
5	9.1	18.2	45.3	27.3	27.2	—	36.4	36.4	36.4	—	45.4	18.2	11

^a Results for *Patella depressa*; all other figures are for *Patella vulgata*. Figures in bold highlight the seasons with the highest percentages. W = Winter = January, February, and March. Sp = Spring = April, May, and June. S = Summer = July, August, and September. Au = Autumn = October, November, and December.

Notwithstanding the uncertainties of the method, it produces consistent results within quite wide margins of error, from which three general conclusions can be drawn. First, it is clear that La Riera was visited at all periods of the year, not confined to a narrow season of use or a narrowly specialist function. This does not, of course, exclude the use of sites and resources in the hinterland, but it does strengthen the case for associating sites such as La Riera with residential bases. Second, the seasonality data suggest that the exploitation of different molluscan species was scheduled so as to concentrate their collection in those seasons that would have generated the optimum return of food. Third, the pattern of seasonal use of the molluscs appears to have remained quite stable throughout the sequence. These results do not provide unequivocal evidence to argue either for or against the hypothesis of intensification, but they do show that, in terms of site function and seasonal scheduling of mollusc collection, the Asturian period maintained a very similar pattern to that established in preceding millennia.

CONCLUSIONS

The main outcome of the above analyses is to show that the changes in molluscan representation and metrical characteristics observable in the La Riera sequence are most likely the result of climatic and habitat changes, rather than the result of increased pressure of human populations on the food supply. There are hints of slight changes that might be attributable to human predation pressure, but these are weak and insufficient to account for the major changes observed throughout the sequence. The results also demonstrate that analysis and interpretation of long-term shell-gathering trends associated with a period of changing and in all likelihood quite rapidly oscillating climate is a complex procedure involving consideration of a number of variables. Nevertheless, we have shown that analytical techniques based on the metrical, chemical, and physical characteristics of the exploited mollusc shells, backed up by studies of modern control populations, can be devised to disentangle the relative influence of palaeoclimatic, palaeoecological, and palaeoeconomic factors.

To the extent that there are remaining ambiguities in the Spanish data, this is as much due to the inadequacy of some of the samples available for study as to the inadequacy of the analytical techniques. For example, it would certainly be desirable to examine larger samples of *P. vulgata* shells from the deposits of the Asturian period. Nevertheless, we do not rule out the possibility that human populations were increasing in the late Pleistocene–early Holocene period. There is, of course, a range of other food resources and palaeoeconomic and palaeoclimatic indicators represented at La Riera and discussed by Clark and Straus (1986), which we have not attempted to incorporate into this discussion. What our results indicate is that any such population increase, if it did occur, failed to have a measurable or unequivocal impact on the growth characteristics and availability of the principal edible molluscan species. The corollary of this is that the evidence for changes in molluscan species and reduction in shell size cannot be used as a strong argument for increased population pressure.

There are two remaining sources of uncertainty that are worth a final comment. The first is the quantitative representation of mollusc shells in the Asturian deposits. There is little doubt in our opinion that the quantity of shells and the rate of shell deposition represented by the known deposits in this period are substantially greater than in the known deposits from earlier periods. Our preferred interpretation is that just as many limpet shells were being collected during the Upper Palaeolithic period as during the Mesolithic period, but that the majority were discarded in now-submerged locations closer to the contemporaneous shoreline. On this interpretation, the increased quantities visible from Azilian times onwards are primarily the result of sea-level rise and increased proximity of the shoreline to the existing cave sites, rather than to increased rates of shell gathering. Whether this is correct is another matter. What we can say with some confidence is that if there was a genuine time trend towards increased rates of shellfood consumption during Azilian and Asturian times, this appears to have had little discernible impact on the size, growth rates, or age structure of the exploited limpet populations. What we lack in the northern Spanish case, as on most other coastlines, is adequately excavated and quantified control data from earlier deposits associated with comparable periods of high sea level. Indeed, here as in most areas of the world, we would have to go back to about 125,000 years ago to find an equivalent configuration of palaeogeographical and climatic circumstances (Figure 2).

The second uncertainty is over possible changes in the ecological character of the shoreline at different sea-level stands during the late Pleistocene with respect to such variables as the width and substrate of the intertidal zone, the degree of exposure, and the presence of embayments and river estuaries. We have tended to discount this variable on the grounds that rocky shorelines with a relatively steep off-shore gradient are less liable to major changes of this sort with changing sea level than shallower coastlines. However, this is probably an oversimplification.

What both these uncertainties highlight is our ignorance about the character, and indeed the precise position, of the coastline during the periods of lower sea level that prevailed throughout most of the late Pleistocene period, the marine resources available on these now submerged coastlines, and the human exploitation of those resources. We know that archaeological sites can, under favorable circumstances, be preserved underwater, and that a variety of remote sensing techniques are available to aid in reconstructing now submerged coastal landscapes and coastlines (Masters and Flemming, 1983; Shackleton and Van Andel, 1986; Fischer, 1995). The development and application of techniques of underwater exploration is a costly enterprise and the chances of success uncertain, but our understanding of the archaeological issues associated with periods of lowered sea level is now sufficiently developed to suggest that such an investment would be worthwhile. It is time that a sustained attack was mounted on this last frontier of archaeological discovery.

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