

Predicting climate change effects on marine biodiversity: comparison of recent and fossil molluscan death assemblages

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The death assemblage of molluscs (gastropods and bivalves) from the sandy beach at Harlyn Bay, north Cornwall is shown to be fully representative of the biodiversity of the regional species pool from all habitat types. The biodiversity measures used are average taxonomic distinctness (Δ^+ , the average degree to which species in an assemblage are related to each other) and variation in taxonomic distinctness (Λ^+ , the evenness of the spread of taxa across the taxonomic spectrum). A late Pliocene fossil assemblage of molluscs from St Erth Pits, north Cornwall, UK, is also not significantly different in biodiversity, in these terms, from the present-day regional species pool. The climate in the late Pliocene was similar to the present-day Mediterranean, suggesting that predicted changes in climate, by the end of this century, will not affect molluscan biodiversity, although the species composition will undoubtedly change.

INTRODUCTION

There is increasing concern about the effects of global warming on biological diversity (Peters & Lovejoy, 1992). In coastal marine ecosystems, widespread extinctions seem unlikely, but changes in community distributions and compositions will inevitably occur. These will track the timing of global warming quite closely because of the high fecundity and dispersal capabilities of most marine organisms (Ray et al., 1992). Community level changes on decadal timescales cannot be predicted from short term experiments, and currently there is little predictive ability regarding the effects of global climate change on the marine biota (Fields et al., 1993). A useful approach to predicting the effects of future climatic conditions on marine biodiversity is by an analysis of biodiversity patterns where such conditions currently pertain. However, this may be rather too simplistic. For example, we would not expect coastal biodiversity in Britain to become equivalent to that of the Mediterranean if temperature rose to a comparable level, because other environmental factors (tidal regime, range of habitats etc.) differ considerably between the two. Another possibility, for taxa with a good fossil record, is to compare current patterns of biodiversity with fossil death assemblages in the same region laid down under different climatic conditions to the present. This will of course depend on whether the death assemblages are fully representative of the biodiversity of the regional living species pool.

Kidwell (2001) compared the living and dead species composition of shell-bearing molluscs (gastropods and bivalves) in 85 studies of marine sedimentary habitats. She found that these 'time averaged' death assemblages retain a strong signal of the rank order of relative species abundances in the original living source community. Nevertheless, the rank order of abundances of dead species

may be opposite, random or consistent with the live species in individual studies. However, these are within-habitat comparisons, and the question to be addressed in the context of regional biodiversity is whether death assemblages are spatially averaged as well as time averaged, i.e. is their composition representative of the regional living species pool from all habitats within the region, not just the habitat in which they were found?

The choice of an appropriate biodiversity metric for making such comparisons also requires consideration. We could not expect the relative abundances of species in death assemblages to be representative of the living fauna from both near and distant habitats (and in any case, these abundances would be almost impossible to determine on a regional scale). Also, because of the sampling effort dependence of species richness measures (Warwick & Clarke, 2001), we would not expect the number of species found in the death assemblage to reflect the living fauna.

In this paper, using appropriate measures of biodiversity, we first test whether a molluscan death assemblage from a single sandy beach on the north Cornish coast is representative of the biodiversity of the regional species pool. We then compare the biodiversity of a fossil death assemblage from the same coast, laid down when the climate was similar to that of the present Mediterranean, to assess possible climate change effects.

MATERIALS AND METHODS

Sources of data

The region under consideration is Sea Area 20, as defined by Seaward (1982), north Cornwall, UK (Figure 1). Records of shell-bearing molluscs from this area date back to the 19th century (Tregelles, 1885; Clark, 1906). A list of all



Figure 1. Map showing the extent of Sea Area 20 off the north coast of Cornwall, UK, and the locations of the Harlyn Bay and St Erth Pits sites.

gastropod and bivalve species recorded from the area has been compiled from Seaward (1982, 1990, 1993), which for this area was based on the field record sheets of the second author (S.M.T.), and on subsequent unpublished data again collated by S.M.T. All records are contained in the ERICA database which is now under the aegis of the Environmental Centre for Cornwall and the Isles of Scilly housed by the Cornwall Wildlife Trust. The recent death assemblage studied is from Harlyn Bay on the north Cornish coast (Figure 1), a 'sand catchment' beach fully exposed to the open sea. The list of dead shells from this beach has been compiled from the unpublished records of various members of the Conchological Society of Great Britain and Ireland, notably Enid Harvey, Jean and Gill Charlsh and J.E. Phorson: all records are on the ERICA database. The fossil assemblage was from the long abandoned sand and clay pits at St Erth, Cornwall, laid down some 2 my ago in the late Pliocene when the waters were as warm as the Mediterranean is today and reached a depth of up to 10 m. The fossiliferous blue clays were laid down in a shallow arm of the sea that separated West Penwith from the rest of Cornwall, the sea level at that time being some 45 m higher than it is today, so that St Erth Pits are now some kilometres inland. Records of molluscs from this site have been compiled by N.F. McMillan (in Mitchell et al., 1973).

Biodiversity measures

Biodiversity measures of the taxonomic spread of species, rather than the numbers of species, are appropriate for the comparisons involved here. They are independent of sample size and sampling effort, they can be used with simple non-quantitative species lists, and there are possibilities of testing for representativeness using permutation tests (review by Warwick & Clarke, 2001).

Average taxonomic distinctness (AvTD, denoted by Δ^+) is a measure of the average degree to which species in an assemblage are related to each other, and is defined as:

$$\Delta^+ = [\sum \sum_{i < j} \omega_{ij}] / [s(s-1)/2] \quad (1)$$

where s is the number of species present, the double summation is over the set $\{i = 1, \dots, s; j = 1, \dots, s, \text{ such that } i < j\}$, and ω_{ij} is the 'distinctness weight' between species i and j traced through a hierarchical taxonomic tree. The degree to which certain taxa are over- or under-represented in samples is another biodiversity attribute of ecological relevance and is reflected in *variability* of the full set of pairwise distinctness weights making up the average. Variation in taxonomic distinctness (VarTD, denoted by Λ^+) is defined mathematically as:

$$\Lambda^+ = [\sum \sum_{i \neq j} (\omega_{ij} - \bar{\omega})^2] / [s(s-1)] \quad (2)$$

For Δ^+ and Λ^+ , a simple permutation test of the hypothesis that the death assemblage has a taxonomic structure that is representative of the full biodiversity can be constructed. Say the death assemblage comprises m species, then the measured values of Δ^+ and Λ^+ can be compared with the range of values from, perhaps, 1000 random selections of m species from the full regional species list. If the measured value falls outside the 95% probability limits of this null distribution, then statistically it cannot be considered representative of the full list. If the values fall within these limits then the assemblage is not significantly different in taxonomic structure from the full list, at least in terms of these summary criteria. Results of this type are visualized here as a bivariate plot of Δ^+ and Λ^+ in which the 95% probability limits become ellipses of increasing size for decreasing numbers of species. All analyses were implemented using PRIMER version 5.

RESULTS

Altogether a total of 252 species of gastropods and bivalves has been recorded from Sea Area 20. A rather astonishing total of 175 species has been found as dead shells from the sands at Harlyn Bay, and 53 species of fossil Mollusca from St Erth Pits. Values of Δ^+ and Λ^+ are plotted in Figure 2, and are based on equal step lengths between six taxonomic levels (species, genus, family, superfamily, order, class) together totalling 100. Values for both Δ^+ and Λ^+ , and for both Harlyn Bay and St Erth Pits, fall within the 95% limits of the probability ellipses for the appropriate numbers of species randomly drawn from the regional species pool (each based on 1000 random selections). The recent death assemblage at Harlyn Bay is not significantly different in taxonomic structure from the regional species pool, and is thus fully representative of its biodiversity in terms of both average taxonomic distinctness and variation in taxonomic distinctness. The biodiversity of the fossil assemblage at St Erth is also not significantly different, in these terms, from the present day regional species pool, although of course the number of species found there is much lower.

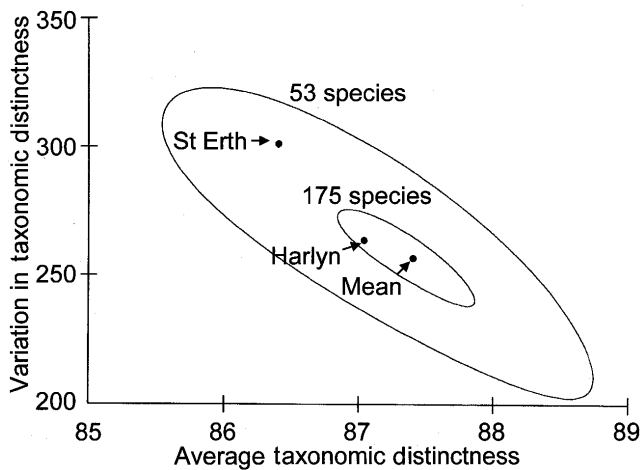


Figure 2. Average taxonomic distinctness (Δ^+), variation in taxonomic distinctness (Λ^+) plots for the regional species pool in Sea Area 20 (mean) and the death assemblages at Harlyn Bay and St Erth Pits (indicated by dots). Modelled 95% probability contours using an algorithm for back-transformed, bivariate normal ellipses are shown for sublists from the regional species pool of size 53 (equivalent to the species number at St Erth) and 175 (Harlyn Bay), based on 1000 simulations for each.

DISCUSSION

Warwick & Light (2002) made a similar comparison of death assemblages on St Martin's Flats, Isles of Scilly with the regional species pool for Sea Area 19 (Isles of Scilly). They found that Δ^+ for the gastropods was fully representative of the regional living fauna, but for bivalves it was significantly lower. This is because most of the bivalves were characteristic of the sandflat habitat, which introduced a bias, whereas post-mortem transport of gastropods, characterizing exotic habitats, is more random. For both gastropods and bivalves, Λ^+ was significantly higher than expected from a random sample of the regional species pool, suggesting the over-representation of some taxa and the under-representation of others. For the total shelled molluscan fauna (gastropods + bivalves) all Δ^+ values were below, and all Λ^+ values above, expectation. St Martin's Flats, unlike Harlyn Bay, are very enclosed and sheltered and this situation is likely to impede transport of species from certain habitats to the site, particularly for example bivalves such as *Nucula* spp. and *Abra* spp. that are characteristic of fine offshore sediments. Harlyn Bay is fully exposed to the open sea with no such transport barriers. The geological evidence for the presence of coastal sand-dunes suggests that the coastline at St Erth in the late Pliocene was similar to that of the present day nearest coast at Hayle Towans, which is similar in situation and exposure to Harlyn Bay. The fossil death assemblage is therefore likely to be representative of the biodiversity of the regional species pool at that time.

Many of the fossil molluscan species found at St Erth are not found in the region at the present day. Ten of the 34 gastropod species found at St Erth still exist in the region, and 14 of the 19 bivalve species. Several of the St Erth species now extinct in the region are currently present in the Mediterranean. The fact that the St Erth species are not a proper subset of the species in the regional species pool

to which it is compared is of course unimportant, since it is the taxonomic structure that is being compared and not the actual species involved.

This study suggests that death assemblages of molluscs from exposed sandy beaches may prove to be good surrogates for the biodiversity of the regional species pool, and thus a good means of rapid biodiversity assessment in less well studied areas. For example, in a 15-min walk along the beach at Sopot, North Poland, the first author collected shells of all five mollusc species known to occur in the region of the Baltic Sea. Generally, of course, the species found on beaches will only be a small subset of the regional species pool, but assessment of biodiversity is possible using indices like Δ^+ and Λ^+ , provided that the species in the death assemblages can be regarded as a random selection from the regional pool.

From climate models that indicate rises of mean temperature of 2°C in the next 50 years, and from the observed changes, we can expect future latitudinal shifts in the marine biota of 300–600 km (Southward et al., 1995). This means that the climate in north Cornwall may be equivalent to that of the Mediterranean by the end of this century. On the basis of this study, there is no evidence that this will significantly affect the biodiversity of the molluscan fauna, although the species composition will undoubtedly change.

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