Marine mammals through time: when less is more in studying palaeodiversity

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The validity of biological explanations of patterns of palaeodiversity has been called into question owing to an apparent correlation of diversity with the amount of sedimentary rock preserved. However, this claim has largely been based on comprehensive estimates of global marine Phanerozoic diversity, thus raising the question of whether a similar bias applies to the records of smaller, well-defined taxonomic groups. Here, new data on European Caenozoic marine sedimentary rock outcrop area are presented and compared with European occurrences of three groups of marine mammals (cetaceans, pinnipedimorphs and sirenians). Limited evidence was found for a correlation of outcrop area with marine mammal palaeodiversity. In addition, similar patterns were identified in the cetacean and pinnipedimorph diversity data. This may point to the preservation of a genuine biological signal not overwhelmed by geological biases in the marine mammal diversity data, and opens the door to further analyses of both marine mammal evolution and geological bias in other small and well-defined groups of taxa.

Keywords: Cetacea; Pinnipedimorpha; Sirenia; palaeodiversity; rock bias; marine mammal

1. INTRODUCTION

Palaeodiversity, traditionally estimated by counting the number of fossil taxa occurring in a given time interval (e.g. Sepkoski *et al.* 1981; Benton 1995) offers a unique opportunity to study the rise and fall of evolutionary lineages, as well as their biological and environmental drivers. However, a number of studies (Gregory 1955; Raup 1972, 1976; Peters & Foote 2001, 2002; Smith 2001; Smith & McGowan 2007) have cast considerable doubt on whether such estimates truly reflect the variety of taxa that were present in the past. Instead, many of the estimates suggest that palaeodiversity records may be strongly influenced by the amount of available sedimentary rock, the idea being that greater amounts of preserved rock allow larger numbers of fossils, and thus taxa, to be collected per sampled time interval. Several studies on this issue, carried out on both a global (Raup 1972, 1976; Peters & Foote 2002; McGowan & Smith 2008) and a local to regional (Peters & Foote 2001; Smith 2001; Crampton *et al.* 2003; Smith & McGowan 2007) geographical scale, found that the amount of available sedimentary rock correlates with patterns of global Phanerozoic marine palaeodiversity. There is an ongoing discussion on whether this phenomenon is a direct result of preservational bias (bias hypothesis), with the amount of preserved rock directly determining apparent diversity (e.g. Raup 1976; Peters & Foote 2001, 2002; Smith 2001; Smith & McGowan 2007), or whether both sediment abundance and diversity were forced by a third factor, such as global changes in sea level, influencing both the size of sedimentary basins and the amount of habitable area along the continental shelf (common cause hypothesis, Smith 2001; Peters 2005, 2008). Owing to these uncertainties, several researchers have advised great

caution in taking palaeodiversity records at face value, and discouraged any biological interpretation without prior testing for and removal of sampling bias in the data (Raup 1972; Smith 2001; Smith & McGowan 2007).

In contrast to the above findings, Uhen & Pyenson (2007), in their study on factors biasing the past diversity of North American cetaceans (whales, dolphins and porpoises), found that rock outcrop area and generic counts of cetaceans were poorly correlated and concluded that biological factors probably explained most of the observed changes in cetacean diversity. On the basis of their results they suggested that, despite the heavy bias in the Phanerozoic marine fossil record, diversity records of smaller, well-defined groups chosen from comparatively low taxonomic levels may still preserve a large amount of detectable biological information. Here, their idea that changes in the palaeodiversity of comparatively small groups of related taxa can be studied under biological, rather than purely geological assumptions is expanded and tested further by comparing the European diversity records of three groups of marine mammals—Cetacea, Pinnipedimorpha (seals and sea lions) and Sirenia (manatees and dugongs)—to a new database of European Caenozoic marine sediments.

2. MATERIAL AND METHODS

(a) Diversity estimates

Europe was chosen owing to its richness in marine mammal genera, the continent being home to the largest number of extant and extinct cetacean (Uhen & Pyenson 2007) and sirenian genera in the world (the latter together with North America), while second only to North America in terms of pinnipedimorphs. Raw taxon counts for all three groups, sampled at the genus level and recorded at the level of the geological stage, were downloaded from the Palaeobiology Database (Uhen 2008a–c, see the electronic supplementary material).

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(b) Outcrop area estimates

When analysing groups of taxa as small as a mammalian order, the level of lithological resolution of the diversity and outcrop data used may become important, and a facies bias analysis was carried out, following which it was decided to include all types of marine rock in this analysis (see the electronic supplementary material). In order to cover all potential fossil occurrences (Berta 2002; Fordyce 2002; Thewissen & Williams 2002), European outcrop area was estimated at the level of the geological epoch for marine sedimentary rocks ranging in age from the Eocene to the Pleistocene, using a 900 km² equal-grid sampling method applied to the International Geological Map of Europe and the Mediterranean Regions, second/third edition. In order to make fine-scale stage-level comparisons with the diversity estimates possible, outcrop area data for a given epoch were apportioned to geological stages within that epoch (Gradstein *et al.* 2004) according to the number and relative duration of the stages, following a modified version of the approach taken by Crampton *et al.* (2003) (see the electronic supplementary material for detailed methods).

Once apportioned to geological stages, the outcrop data of this study were tested by comparing them with previous outcrop area estimates from Western Europe (Smith & McGowan 2007) and the USA (Peters 2006, 2008, personal communication 2008) as well as global sea-level change (Miller *et al.* 2005) as a potential driving factor of sedimentation rates. Because neither the Western European nor the North American estimates completely record their data at the stage level, the data of this study were reassigned to fit the time scales of the two studies according to the apportioning procedure described above. Also, to facilitate a fair comparison, the Western European part of the data of this study was compared with Smith & McGowan's (2007) estimate separately.

(c) Data manipulation

Because autocorrelation of individual time series can give rise to spurious correlations, all data were detrended for all analyses by calculating their first differences. The outcrop area estimate of this study was then compared with the Western European and North American estimates, as well as global sea-level change using Pearson's product moment correlation. All three diversity datasets were first compared with each other using Pearson's product moment correlation, following which they were compared with the outcrop data, apportioned according to the Gradstein *et al.* (2004) time scale, using cross-correlation, and incorporating three lags of time either side of zero. Both the diversity and the rock data were square-root transformed prior to detrending for the latter two analyses in order to achieve normality. Because the cetacean data were still slightly non-normal following this procedure (Jarque-Bera p (normal)=0.048), the Pearson correlations were cross-checked using the non-parametric Spearman's rank test. In order to counteract the inflation of type I error rates (alpha inflation) caused by multiple comparisons, individual significance levels within families of comparisons were adjusted using the false discovery rate (FDR) procedure (Benjamini *et al.* 2001). Definitions of the different families were based on the hypothesis being tested, and application of this procedure is indicated in figure captions. All tests were performed in PAST (Hammer *et al.* 2001) and MINITAB (v. 14), and alpha was set to be 0.05.

Figure 1. Comparison of the data of this study with previous rock estimates for (a) Western Europe (black curve) (grey curve, Smith & McGowan 2007) and (b) the USA (grey curve), excluding the Pleistocene (Peters 2006, 2008, personal communication 2008). Only the Western European part of the data of this study is shown in (a).

3. RESULTS

Visual comparison of the 900 km² grid square data of this study with the Western European (Smith & McGowan 2007) and North American (Peters 2006, 2008, personal communication 2008) rock volume estimates revealed similar, though somewhat time-shifted, patterns with the data of this study lagging behind those of Smith & McGowan (2007) (figure 1a). Surprisingly, the Western European data failed to correlate with the Western European part of the data of this study ($r=0.14$, $p=0.698$) despite the apparent similarities; however, when the data of this study were moved one stage backward in time, as suggested by visual inspection of the data, the correlation greatly improved and became significant ($r=0.72$, $p=0.027$). A similar, though weaker correlation ($r=0.69$, $p=0.042$) was also found when the whole dataset of the present study was shifted backwards and compared with Smith & McGowan's (2007) estimate. Unlike the Western European estimate, the North American data showed a direct positive correlation with the data of this study ($r=0.70$, $p=0.037$). The greatest mismatch of the latter two sets of data appeared to rest mainly on the diverging Pleistocene records of the two continents, and removal of the Pleistocene from the analysis greatly improved the correlation ($r=0.83$, $p=0.011$; figure 1b). The European data of this study failed to show a significant correlation ($r=0.41$, $p=0.132$) with global sea-level change (Miller *et al.* 2005).

Plots of marine mammal palaeodiversities revealed a general similarity in the diversity curves of cetaceans (figure 2b) and pinnipedimorphs (figure 2c), with a diversity peak during the Late Miocene followed by an apparent crash during the Messinian. This apparent similarity was supported by a significant positive correlation (Pearson:

Figure 2. Plots of raw European marine sediment outcrop area data, attributed to geological stages according to their relative durations and numbers, shown in plot (a). Below there are plots of (b) cetacean, (c) pinnipedimorph and (d) sirenian taxon counts.

Figure 3. Cross-correlation charts of European outcrop area versus (a) cetacean, (b) pinnipedimorph and (c) sirenian palaeodiversity. The length of the bars indicates the strength of the correlation at various lags of time. All correlations pertaining to the same taxon were treated as a family of comparisons in the FDR procedure (Benjamini *et al.* 2001), which rendered all previously significant correlations (p -values referring to the bars below them) non-significant.

$r=0.69$, $p=0.013$; Spearman: $r_s=0.68$, $p=0.015$) of these two curves. The cetacean/pinnipedimorph pattern contrasted with a sirenian (figure 2d) diversity peak during the Early Miocene, followed by a rapid decline and continuous low levels of diversity, including intermittent absence from Europe, from Mid-Miocene times onwards. Sirenian palaeodiversity correlated with neither that of cetaceans (Pearson: $r=0.52$, $p=0.057$; Spearman: $r_s=0.44$, $p=0.119$) nor that of pinnipedimorphs (Pearson: $r=0.21$, $p=0.522$; Spearman: $r_s=0.16$, $p=0.616$).

The results of the cross-correlation of the rock outcrop data (figure 2a) with the diversity curves (figure 2b–d) showed correlations of varying strength at a number of lags for all three groups of marine mammals (figure 3a–c). However, all of these results were rendered non-significant following application of the FDR procedure.

4. DISCUSSION

In trying to answer the question to what extent palaeodiversity has been biased by the amount of preserved rock, obtaining detailed and accurate databases of outcrop area is a crucial first step, often made difficult and time-consuming by the comparatively crude temporal level at which geological maps typically present information. This often makes it necessary to restrict detailed studies to comparatively small areas (e.g. Smith 2001; Smith & McGowan 2007) or infer, rather than observe, the amount of rock preserved at a finer time scale than the geological epoch (Crampton *et al.* 2003).

(a) The European marine sedimentary record

The data of this study showed a strong positive correlation with previous rock estimates from both Western Europe

(Smith & McGowan 2007) and North America (Peters 2006, 2008, personal communication 2008), indicating that relative duration of geological stages might be considered a suitable way of constructing fine-scale outcrop databases at a reasonable expense of time. The discrepancies between the Western European record of Smith & McGowan (2007) and the data of this study, as well as the stronger correlation of the latter with the North American data, was unexpected, but might simply be a result of the combined error introduced by their incomplete coverage of Western Europe (ranging from 17 to 80%, McGowan & Smith 2008) necessitated by their method of high-quality data collection, local distortion of the record caused by Pleistocene glaciation (McGowan & Smith 2008), which may also have been responsible for the improvement of fit with the North American data following the exclusion of the Pleistocene, and the unavoidably imperfect estimate of the present study. In addition, the strong correlation of the data of this study with the North American estimate supports the findings of McGowan & Smith (2008) who, despite not finding any evidence for a correlation during the entire Phanerozoic, reported a better fit of the European and North American records from the Cretaceous onwards. Assuming that this suggests similar Caenozoic sedimentary histories of these two continents caused by their geographical proximity and similar climates, it is likely that the worsening fit of the European and North American curves towards the present time, as observed in this study, reflects the increasing separation of these two landmasses by the Atlantic. The lack of correlation of the European data with global sea-level change also corroborates the results of McGowan & Smith (2008) who cast doubt on the existence of a uniform global sedimentary record simply driven by eustatic sea-level fluctuations, and mirrors a similar lack of association in the Caenozoic of New Zealand, where any correlation between sea-level changes and outcrop area may have been obscured by tectonic activity (Crampton *et al.* 2003, 2006). It is possible that events related to the Alpine orogeny, the closing of Tethys and the drying up of Paratethys and some of its remnant basins had a similar effect in Europe.

(b) *Outcrop areal diversity associations*

Several workers have made a strong case that changes in outcrop preservation and availability exert a substantial bias on coincident changes in Phanerozoic biodiversity (e.g. Raup 1972; Peters & Foote 2001, 2002; Smith 2001; Smith & McGowan 2007). However, most of the studies corroborating the prevalence of such a bias have focused on global marine diversity (Peters & Foote 2001, 2002; Smith 2001; Smith & McGowan 2007) or large faunal groups at high taxonomic levels, such as Mollusca (Crampton *et al.* 2003). The results of the present study stand in contrast to both their main conclusions and the comprehensiveness of the faunal groups investigated. None of the three groups of marine mammals examined here exceeds the level of a mammalian order. More importantly, the results of this study provide only limited evidence for a strong influence of the amount of available rock on marine mammal palaeodiversity, since all of the correlations of marine mammal diversity with outcrop area observed here are weak enough to be rendered non-significant by an adjustment of the data for alpha inflation.

However, it would be both unrealistic and unwise to assume that the diversity records of any group of taxa, however small or well defined, will be completely unaffected by geological biases, and thus the fact that these correlations were strong enough to be detected at all should suggest caution in any further analysis of cetacean palaeodiversity. Overall, however, the results of this study seem to corroborate those of Uhen & Pyenson (2007) who failed to find a strong association between outcrop area and cetacean palaeodiversity in North America.

Accepting, with some reservations, the absence of an overwhelming geological bias in the marine mammal data, the question arises of why the level of bias in these groups should be lower than in the total Phanerozoic marine dataset. One explanation may lie in the nature of the animals studied, with aspects of their biology such as size or preferred habitat setting them apart from many other marine taxa, for example by raising their preservation potential to such a degree that fluctuations in the amount of preserved rock fail to affect overall preserved diversity. In order to test this, all European marine mammal occurrences scored at least at the level of the geological epoch were downloaded from the Palaeobiology Database (Uhen 2008a–c). Of the 129 cetacean genera downloaded, 73.6 per cent were known from fewer than five occurrences, with 40.3 per cent being known from just a single occurrence. The figures were similar for pinnipedimorphs (62.1% fewer than five occurrences, 31.0% single occurrences) and sirenians (80.0% fewer than five occurrences, 33.3% single occurrences). Given these relatively low abundances, high preservation potential becomes unlikely.

An alternative explanation for the apparent weakness of the geological bias in the marine mammal data may be the nature of diversity itself. Diversity is linked to evolution, and hence different taxa may react differently to changes in the environment, such as temperature fluctuations, changes in nutrient availability or biotic interactions. Thus, while some may diversify in response to a warming event, others may decline at the same time. It is reasonable to assume that closely related taxa with a similar biology, such as cetaceans or pinnipedimorphs, will react in a broadly similar way to a given environmental change, resulting in a net change in the diversity of the whole group, which may be strong enough to be detectable in a palaeodiversity study. By contrast, taxa with widely differing biological attributes are more likely to show different or even opposite reactions to a given change. It follows that groups comprising a variety of biologically very different taxa, such as those included in the global marine palaeodiversity record, will probably lack any coherent response to environmental change with the multitude of diversification events and declines in diversity effectively cancelling each other out. While this effect may be unlikely to result in a flat diversity curve over time, it may still severely dampen any genuine biological signal, thus raising the relative importance of geological factors in determining the shape of the curve and making the search for a genuine biological signal in the diversity of large groups of taxa rather difficult. It should be said that this line of reasoning only applies to diversity, not measures of origination or extinction. Nonetheless, if true, this problem of biological signal dampening may add merit to the study of smaller, taxonomically defined groups.

(c) Biology: the major cause behind marine mammal palaeodiversity?

Given the apparent absence of a strong outcrop area bias, could the marine mammal diversity data analysed here contain a strong and valid biological signal? Various other biasing factors, such as the 'pull of the recent' (Cutbill & Funnell 1967; Raup 1972) or varying research effort (Raup 1972; Tarver *et al.* 2007; Uhen & Pyenson 2007), have been proposed, and it is difficult to determine whether and to what degree these might bias marine mammal palaeodiversity records. Comparisons of the palaeodiversity records of the three groups do, however, provide some grounds for assuming the presence of a genuine and detectable biological signal in the data. While the similar shapes of the cetacean and pinnipedimorph diversity curves indicate a similar response of both groups to external influences, sirenian palaeodiversity looks unlike either of the others. This difference is also reflected in ecology and habitat: while cetaceans and pinnipedimorphs are carnivorous, sirenians are almost exclusively herbivorous (Berta *et al.* 2006). In addition, while cetaceans and pinnipedimorphs inhabit both coastal and open waters (Balance 2002; Bowen 2002) and include migratory species (Stern 2002), sirenians are mainly restricted to shallow areas within the photic zone, often located within the tropics (Domning 2002). Given the comparatively low taxonomic level of the groups in question, such a difference in lifestyle could conceivably produce a signal such as that in the palaeodiversity records, thus again supporting the hypothesis that smaller, well-defined groups at lower taxonomic levels can preserve a genuine biological signal not obscured by sampling biases. More work is needed on other taxonomic groups to determine the general validity of such a statement.

It should be said that the line of reasoning developed here relies on the assumption that there is such a thing as a valid biological signal in any kind of taxonomically, rather than ecologically defined group. It has been argued that diversity patterns are meaningless when measured above the level of the local community (e.g. Vermeij & Leighton 2003) due to the absence of biologically meaningful interactions. This statement needs to be tested for marine mammals, and an investigation into environmental and biological factors, such as sea-level change, temperature or upwelling (Fordyce 1977, 1980; Berger 2007) potentially affecting marine mammal palaeodiversity on a global level are currently underway. Apart from providing valuable insights into marine mammal evolution, the results of such a study may help to answer the question whether there can be meaningful patterns in a global, taxonomically defined dataset, and whether there is common factor responsible for changes in both palaeodiversity and rock abundance, as proposed by the common cause hypothesis (Peters 2005, 2008).

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