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Towards an unbiased estimate of fluctuations in reef abundance and volume during the Phanerozoic

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Abstract

The globally preserved number and volume of ancient biogenic reefs is strongly biased by two factors: geological history and research intensity. These biases are sufficiently strong to cast doubts on the biological meaning of the recorded raw pattern. Without adjustment it is hard or impossible to identify factors potentially controlling the waxing and waning of this important ecosystem through time. Although it is impossible to completely compensate for the biases, I demonstrate herein that spatiotemporal heterogeneities of the biases can largely be evened out by: (1) omitting oceanic reef sites and reef sites only known from subsurface exploration; (2) standardizing for economic factors known to affect research intensity; and (3) adjusting for sedimentary cycling processes. The resulting curves of fossil reef abundance and volume appear quite different from the original ones but neither is the overall volatility reduced, nor are patterns of waxing and waning of the time series significantly altered. Thus, although the differences are sufficiently strong to call for new tests of potential extrinsic controls on Phanerozoic reef proliferation, the raw curves correctly reflect the basic timing of major reef blooms and declines.

1. Introduction

The bias of the fossil record has repeatedly been emphasized in the last few years. Most studies agree that recorded changes of biodiversity are so strongly governed by changes in the quality of the geological record that the biological signal is largely overprinted (Peters and Foote, 2001; Smith, 2001; Crampton et al., 2003). However, little has been done to adjust for this bias in order to receive biologically more meaningful patterns of diversity through geological time. For biodiversity, large-scale heterogeneities of sampling intensity can be balanced by subsampling techniques based on weighted random draws from the available sampling pool (Alroy et al., 2001; Bush et al., 2004). Equivalent adjustments are more difficult when the unit of sampling is a biological community and the pattern of interest is abundance or productivity rather than diversity. These adjustments, however, are an important prerequisite for meaningful analyses at the ecosystem level.

Here I focus on the abundance (N) and volume (V) of tropical reefs through the Phanerozoic. These patterns provide important proxies of the waxing of waning of a well-constrained marine ecosystem. Similar to biodiversity, there is no hope to ever gain a reliable number of the true total that existed at any particular time, but we can standardize the preserved record as much as possible.

The goal of this paper is to remove as much bias as possible from the time series of N and V as recorded in a database on Phanerozoic reefs. The ecosystem dynamics derived from these patterns will allow for a better understanding of potential physico-chemical controls on reef ecosystems through time.

2. Database and methods

The analyses are based on a comprehensive database of Phanerozoic reefs (Kiessling and Flügel, 2002) currently comprising 3340 entries. This database contains information on paleogeographic, paleontological, geometrical, and petrographical attributes on mostly pre-Pleistocene Phanerozoic reef sites, where a site lumps data from reefs of the same age and environment within an area of roughly 350 km^2. Previous analyses have detailed the patterns of reef abundance and calcium carbonate ($CaCO_3$) production through time (Kiessling, 2002; Kiessling et al., 1999, 2000) but potential biases in these patterns were always a matter of concern (Kiessling et al., 1999; Kiessling, 2002, 2005b). The method of calculating the preserved volume of reefs is as in Kiessling et al. (2000), except that I focus on preserved volume (= net accumulation of calcium carbonate) rather than estimates of gross $CaCO_3$ production. This method assumes simple reef geometries and gives very conservative estimates of preserved reef volume. The volume is calculated from just the measured portion of reported reef sites and does not consider reconstructions of reef tracts. Although it is obvious that the calculated volumes are at least one order of magnitude lower than presumed true volumes, there is currently no sound way to extrapolate these measured values using estimates of extensions of reef tracts.

The recorded pattern of the number of reef sites and their cumulative volume through time (Fig. 1) is likely to be a function of true fluctuations and the sum of the distorting factors. The severity of these distortions has recently been quantified (Kiessling, 2005b), focusing on the effects of habitat area, the number of oceanic reefs, reservoir potential, and socioeconomic factors. Socioeconomic factors, most importantly economic productivity per unit area, were identified as introducing the most severe bias in the recorded number and volume of ancient reefs, but the other factors are also likely to distort the biological signal. What was missing in the previous analysis was an approach towards compensation of the variety of biases, so that more realistic time series can be achieved.

Here I present methods and experimental results of adjustment in three logical steps. I first omit all reef sites recorded from geological settings introducing temporal bias. I then adjust for the effects of economic factors and finally I try to compensate for long-term trends of sediment preservation in the geological record. Because temporal resolution does matter, I report raw data and adjustments for two different sample resolutions. The first sample resolution is based on supersequences defined by semi-global unconformities (with an average duration of 17 million years); the second is based on time intervals of roughly ten million years (myr) duration, but adheres to traditional paleontologically defined boundaries (Kiessling, 2005a). Both time series consist of intervals with slightly unequal durations. Therefore all numbers have been normalized to 10 myr intervals following the time scale of Gradstein et al. (2004). Changes in the time series after manipulation are recorded by overall similarity (correlation), changes in standard deviation of the total time series and changes in volatility of the complete time series:

$$\text{Volatility} = std\left(\ln\left(\frac{(N,V)_t}{(N,V)_{t-1}}\right)\right) \tag{1}$$

where (N, V) is the recorded number of reef sites (N) or reef volume (V) in a time interval t and in the previous time interval $t-1$, and std stands for the standard deviation of the log-transformed quotients. Following standard methods used in volatility estimation of financial time series (http://www.riskglossary.com/link/volatility.htm), I apply a log transformed quotient rather the simple first differences as a basis.

2.1. Excluding oceanic reefs

Oceanic atolls are important reef sites today. A survey of Reefbase, a database on modern tropical coral reefs, suggests that 37±2% of all modern tropical coral reefs are situated in oceanic regions (Kiessling, 2005b). Due to plate tectonics, oceanic reef sites have little chance of a lasting geological record. Subduction processes are held responsible for the fact that there is virtually no oceanic crust older than Middle Jurassic. This introduces a severe bias towards higher reef numbers in younger time intervals.

Although it remains to be demonstrated that the proportion of oceanic reefs is similar through time, an adjustment is necessary by either adding a certain proportion of oceanic reefs to each time interval or by just omitting all oceanic reefs. Here I omitted all oceanic reefs to diminish the overrepresentation of oceanic reefs in younger times. This adjustment, while intuitive, implies that the resulting curve is valid only for reefs on continental crust.

2.2. Excluding subsurface data

PaleoReefs contains many reefs known only from subsurface exploration, either from drilling or seismic data (607 out of 3266 non-oceanic reef sites, or 18.6±1.3%). While it is a good thing to have data from the subsurface, where paleontologically relevant information is often scarce, the heterogeneous temporal distribution of the proportion of subsurface reefs suggests a strong bias. The proportion of reefs with hydrocarbon reservoir potential and the proportion of subsurface reefs are significantly cross-correlated (r=0.76, P<0.001 for first differences), which suggests that the recorded number of subsurface reefs is strongly controlled by economic interest. This means that the true number of reefs will be greatly underestimated when reefs have no reservoir potential. Furthermore subsurface reefs tend to be larger in thickness, either due to different methods in estimating reef geometries or due to the fact that only larger reefs are recorded by seismic exploration. This imposes a strong bias on the calculations of preserved reef volume. For these reasons complete removal is the best way to adjust for the bias introduced by subsurface reefs. This adjustment may not be correct for all bias introduced by the economic interest in reefs as hydrocarbon reservoirs. Exposed reefs also tend to be studied more intensely, when they can be used as models for subsurface reservoirs. Although, there is no way to estimate this exploration bias quantitatively, it may not be that strong, because reefs from time intervals without significant hydrocarbon accumulations are also being used as reservoir analogues (e.g. Antonellini and Mollema, 2000).

2.3. Adjustment for variations in gross domestic product

While the number of subsurface reefs is controlled by economic interest, economic wealth in a country may also govern research intensity. I have previously demonstrated that the number of reef sites and their cumulative volume described from each country is strongly dependent on its gross domestic product (GDP), especially when normalized by surface area (Kiessling, 2005b). More reefs are known from countries with a high GDP density (GDP per unit area) than from countries where the GDP density is low. In spite of an increasing mobility of geoscientists in rich countries, this correlation suggests that the number of recorded reefs is strongly controlled by research intensity, which in turn is governed by economic wealth within the countries. The correlation values of Kiessling (2005b) cannot be used directly for this study because he has included oceanic and subsurface reefs. Based on an analysis of the reduced PaleoReefs database (oceanic and subsurface reefs excluded) and economic data from countries with at least 5 reef sites (N=78), the Pearson correlation between log GDP density and log density of reef sites is 0.665 ($P<0.001$). Between log GDP density and log reef volume density, I achieve $R=0.304$, $P=0.007$. The correlation coefficients are somewhat higher for Spearman rank correlations ($R=0.688$ and $R=0.363$, respectively), but since the data are nearly normally distributed on a log scale, the Pearson correlations are used for adjustment. The much stronger correlation of numbers than of volumes is probably due to the overestimation of reef sizes in less developed countries. Nevertheless, a significant bias of GDP is evident both for numbers and volume.

The basic correlation between GDP density and reef density per country is also evident for some individual time intervals, although correlation coefficients are usually smaller. An analysis of the six richest supersequences (S, each with at least 125 reef sites) suggests an increasing dependency through time. Correlations are insignificant in the Ordovician ($S5$) and Silurian ($S7$), significant in the Devonian and Triassic ($S10$: $R=0.50$, $P=0.015$; S18: $R=0.44$, $P=0.012$) and highly significant in the Jurassic and Miocene (S21: $R=0.57$, $P<0.001$; S31: $R=0.48$; $p=0.004$). Although this could mean that the bias of economy is less prevalent in the early Paleozoic (e.g. countries with a low GDP density are better sampled), it could as well be due to random effects of lower sample sizes. The lower correlations are also due to the fact that most of the Paleozoic reefs are recorded from sites which are now situated in large countries with a relatively low GDP density.

It is reasonable to assume that the global number of reefs is overestimated with respect to other time intervals when the majority of reefs from a particular time interval are known from countries with a high GDP density, whereas the number of reefs is underestimated when most of the reefs are known from countries with a low GDP density. With good knowledge of the paleogeology of all time intervals, the adjustment could be made globally. However, due to limitations of this knowledge, I just adjust for those countries where reefs in a particular time interval have actually been recorded. The level of adjustment is to the average log-transformed GDP density of all countries with reefs, which is 5.07, approximately the log GDP density of Romania (as of 2002).

There are basically two ways to adjust for the GDP density effect on reef distribution. I have used the most conservative method (that is, the one providing the lowest correction coefficient) for N and V. To correct for N in each country where reefs are preserved, I have first extracted the equation of the regression analysis:

$$\ln\left(\frac{N}{\text{area}}\right) = 1.69 + 0.46 \ln\left(\frac{\text{GDP}}{\text{area}}\right) \tag{2}$$

where N is the number of reef sites, area is the land area in million square kilometers and GDP is the gross domestic product in billion dollars. From this I have calculated the expected number of reef sites (N_{exd}) by

$$N_{exd} = \text{area} \cdot e^{1.69+0.46 \cdot \ln(\text{GDP\_area})} \tag{3}$$

To reduce noise, the residuals (res) of the regression were accounted for by

$$N_{exd} = \text{area} \cdot e^{1.69+0.46 \cdot \ln(\text{GDP\_area})+\text{res}} \tag{4}$$

The quotient of N_{exd} and the recorded total number of reef sites in a country was then used to derive a factor for adjustment of N for each country (Nfact). The expected number of reefs in a country at a particular time is then the observed value (N_{obs}) multiplied by Nfact. The sum of all N_{exd} then gives the expected total of reefs when GDP density would be uniform.

For volumes, the most conservative estimate (due to the low correlation coefficient) is to use the difference between the log-transformed GDP density and the adjusted GDP density. The GDP-adjusted volume per country is then calculated by

$$V_{exd} = V_O \cdot e^{R(\Delta(\ln(\text{GDP\_area})))} \tag{5}$$

where V_{exd} is the GDP-adjusted reef volume in a country, V_O is the original reef volume, R is the correlation coefficient derived from all reefs and countries and Δ (ln(GDP_area)) is the difference of the level of adjustment to the log-transformed GDP density of the country in question. The term $\exp(R \times (\Delta(\ln(\text{GDP\_area}))))$ is used as the factor for adjustment of V for each country (Vfact).

N_{obs} and V_{obs} were tabulated for each country and time interval, the corrected values were calculated for each country, and then summed up to derive N_{exd} and V_{exd} for the GDP-adjusted level.

2.4. Compensation of sediment cycling

The amount of preserved sediment is well known to fit an exponential decay curve (Gregor, 1985; Wilkinson and Walker, 1989; Wold and Hay, 1990, 1993). Although the fit to actual data is quite poor for sedimentary carbonates in general (Morse and Mackenzie, 1990; Mackenzie and Morse, 1992) and in reefs in particular (Kiessling, 2002), there is no reason to assume that the basic principles of sediment decay through time do not apply for $CaCO_3$. An exponential decay can thus be assumed as a first approximation.

$$(N,V)_O = (N,V)_P \cdot e^{kt} \tag{6}$$

where $(N,V)_0$=reconstructed number of reef sites or reef volume; $(N,V)_p$=preserved amount of reef sites or reef volume; k=decay constant; t=midpoint of time interval in myr.

The experimentally derived decay constants for the raw data are suspiciously low for reef numbers and even negative for all GDP-adjusted data (Table 1). This is a common observation when looking at carbonate preservation through the Phanerozoic. The Phanerozoic shift of $CaCO_3$ production to the open ocean (Wilkinson and Walker, 1989) and the drift of shelf areas to latitudes unsuitable for prolific carbonate sedimentation has resulted in the paradox of negative decay constants for shallow water carbonates (Walker et al., 2002). Just as systematic long-term shifts in the carbonate reservoir size obscure the reliable identification of decay constants for sedimentary carbonates in general, true fluctuations in reef proliferation hinder the experimental determination of a decay constant for the erosional destruction of reefs. The only benefit from the experimental determination of decay constants in reefs is to show that these are comparable for numbers and volumes (Table 1). It may thus be permitted to apply a single decay constant for both measures, which however has to be derived from an independent data source.

I derived a decay constant from the known mass/age distribution of all Phanerozoic sediments. Hay and Wold (1990) have compiled information of earlier work (Ronov et al., 1980; Budyko et al., 1987) and normalized the data to 10 myr intervals. I have extracted their data for the mass/age distribution of sediments on the continents and passive continental margins, modeled the data into the time scale used in this study and fitted an exponential decay curve. The resulting decay constant of 0.0014 is used as a first approximation of reef survival rates (both for V and N) through the sedimentary record.

Apart from true fluctuations in reef proliferation, the imperfect fit of decay curves can also be explained by cyclic changes in weathering intensity due to large-scale sea-level fluctuations, which in turn are controlled by plate tectonic processes (Mackenzie and Morse, 1992). Global phases of plate assembly and disassembly are known to alter sedimentation and erosion regimes at global scales (Ronov, 1994). A potential proxy tracing these changes is the percentage of continental area covered by seawater, which is a function of eustatic sea-level and hypsometry. Empirical evidence confirms that changes in continental flooding are indeed significantly cross-correlated with changes in preserved reef abundance (Kiessling, 2002). I have previously suggested introducing an additional factor to adjust for the effect of continental flooding (Kiessling, 2002).

However, continental flooding or its inverse, continental freeboard, acts in two ways on reefs. The first is the biological control of flooding on habitat area. As tropical reefs have a strong preference for shallow water habitats, the reduction of shelf area by relative sea-level fall may considerably lower the available habitat area and thereby global reef carbonate production (Kleypas, 1997). The second is the effect of continental flooding on the volume of preserved sediment. Increases in continental freeboard are associated with erosion of older sediments. While at relatively fine temporal scales (stage level and finer) the biasing effect of low sea level is suspected to occur at a temporal lag (the backward and forward smearing effects; Foote, 2001) it is reasonable to assume that over longer time intervals, the erosion effect will be strongest within a time interval. Mackenzie and Morse (1992) have previously noted a good match between declining rates of carbonate preservation and orogenic cycles, with survival rates declining when approaching the Slossian (Sloss, 1963, 1976) megasequence boundaries.

At this point it is hard to decide which of the two effects will stronger influence the preserved number and volume of reefs. In any case, a simple adjustment for continental flooding will always result in a mixed signal. Therefore, proxies of actual weathering rates are required. It is reasonable to assume that the bias on preserved reef carbonate production is proportional to the deviation from mean weathering rates. Unusually low rates will result in a positive departure from the exponential decay curve. Higher than normal weathering rates will result in a negative departure and an elevated decay constant. I used the chemical weathering rates derived by Berner and Kothavala (2001) from volumes of terrigenous rocks (Ronov, 1993). These values for siliciclastic rocks, are conservative estimates of carbonate weathering, which are usually much more prone to chemical weathering (Blum et al., 1998). The epic level chemical weathering rates ($f_R(t)$) were interpolated and adjusted to the stratigraphic bins used herein. As the $f_R(t)$ values of Berner and Kothavala (2001) are already standardized to the Miocene level of chemical weathering, they can be directly applied to adjust the decay constants and achieve a corrected curve of reef volumes by:

$$(N,V)_0 = (N,V)_P \cdot e^{ktf_R(t)} \quad (7)$$

The effect of $f_R(t)$ is such that the decay constant at time t is lowered when the intensity of chemical weathering is less strong than in the Miocene. Thereby the corrected values of N and V are lowered with respect to the simple correction for sedimentary decay.

3. Results

The various levels of adjustment had a quite different impact on the observed curves on N and V. The effect of removing oceanic reefs results in a moderate modification of the original pattern. Noticeable changes are limited to the Cretaceous and Cenozoic. A significant decline is observable in the Neogene, when 11±3% of known reefs are from oceanic areas. The additional exclusion of subsurface reefs results in a visibly modified pattern of temporal reef distribution (Figs. 2a and 2b). Major peaks are reduced, whereas the depressions in the raw data a little affected by the exclusion of subsurface reefs. However, the overall volatility is not strongly reduced (Table 2). The major time intervals of reef growth are basically the same as in the raw data, but the ranking has changed. In the raw data, the Neogene represents by far the most prominent peak in terms of reef numbers and also shows the major peak in preserved reef volume. The reduced dataset has the major peak of reef numbers in the Silurian followed by the Neogene and Jurassic. Preserved volumes peak in the Silurian and Devonian, which have approximately equal values, whereas in the raw data, the Devonian peak is by far the most pronounced in the Paleozoic. Significant changes are also evident in the late Paleozoic and early Mesozoic.

The correction for GDP density has substantial effects, especially in the early Paleozoic. The strong concentration of reefs in countries with a fairly low GDP density (such as Russia, central Asian states and Mongolia) at this time, suggests that there are many undetected reefs in these countries. The adjustments often result in substantial additions to the previous datasets. Due to the higher dependency of reef density than volume density from GDP density, the GDP-adjusted curves of N (Figs. 3a and 3b) differ most strongly from the previous curves. The original values are more than doubled in several intervals and usually raised by around 50% in the Paleozoic. Reductions of the raw values are common in the Mesozoic and Cenozoic. The strongest reductions are evident in the Middle Triassic, at around 230 million years before present (Ma), Early Cretaceous and Late Miocene/Pliocene. The apparent rapid recovery of reefs after the Permian/Triassic extinction thus has to be revised, as it is likely to be an artifact of several reefs observed in countries with a higher than average GDP density such as Austria and Italy. The adjustment for GDP density makes the Middle Miocene reef bloom more pronounced because the Late Miocene/Pliocene (last point in time series) turns out to be inflated in the raw data, due to the strong concentration of reefs in Italy and Spain. For volumes, the GDP density effect is much less pronounced (Figs. 4a and 4b), with a maximum of +80−90% in the Emsian-Eifelian time interval, when many reefs are recorded from Mongolia, the country with the lowest GDP density in the analysis. The direction of changes is usually the same as for numbers. One notable exception is the Late Jurassic reef bloom (at around 155 Ma), which is interpreted to be overestimated by the analysis based on numbers, whereas in the volume analyses the original values are raised. This is due to the concentration of recorded reef sites in countries with a high GDP density (France, Germany, Slovenia) and the few reefs with large estimated volume in countries with a low GDP density (Russia and Uzbekistan). At the supersequence level, the most prominent, peak in reef proliferation is now seen in the Wenlock-Ludlovian time interval (at 425 Ma), whereas the 10 myr interval adjustments suggest a peak in the Emsian-Eifelian interval (at 398 Ma). The overall volatility in the time series is raised with respect to the previous adjustment level and is close to the volatility in the raw data (Table 2).

The final steps in adjustments (sediment cycling) consistently intensify the early Paleozoic reef bloom. For supersequences, the Silurian peak now becomes extremely pronounced (Figs. 5a and 6a). At the finer stratigraphic resolution (Figs. 5b and 6b) the (middle and late) Silurian is also identified as the major time of Phanerozoic reef expansion, but this peak is not much greater than the latest Ordovician and Devonian spikes. Except for volumes at the 10 myr sample resolution, this step of adjustment results in further increases of volatility (Table 2).

The overall similarity of the curves is greater than discernible at first glance (Fig. 7). The correlation between two subsequent levels of adjustment varies between 0.47 and 0.95 with generally higher similarities between time series of N than between time series of V. There even is a surprisingly great similarity between the raw data and the final step of adjustment. It is only for reef volumes at the supersequence level where this similarity in not significant (R=0.28, P=0.12). The pattern of changes in both N and V are even less affected by the adjustments. Although the magnitude of changes between adjacent time intervals varies considerably, the direction of change is hardly affected. Detrended time series (first differences) have a highly significant cross-correlation for all time series and between all levels of adjustments (Table 3). The basic pattern of waxing and waning in the reef ecosystem seen in the raw data is thus confirmed by the corrected curves.

4. Discussion and conclusions

The adjustments to the original time series of Phanerozoic reef abundance and volume are just first steps towards unbiased curves. In spite of the conservative approach, the adjustment for GDP density is perhaps exaggerated, because it assumes the same correlation between GDP density and reef/volume density over all time intervals, irrespective of regional variations in geological characteristics. Due to low sample sizes, especially in some of the 10 myr intervals, the effect of the adjustment is probably too strong. One detailed survey in a country with a low GDP density (perhaps by scientists from another country) can substantially inflate the adjusted values. Problems are also involved in the effects of sedimentary cycling processes. I have applied the same decay constant for reef numbers and reef volumes, although the decay constant derived from the mass-age distribution of all sedimentary rocks strictly can only be applied to volumes in a straightforward fashion. Additionally, I have applied variations in chemical weathering intensity of siliciclastic rocks to modify the exponential decay function, although carbonates somewhat different in their weathering behavior (Bluth and Kump, 1994).

In any case, I am confident that the methods presented here show the correct basic steps towards "unbiasing" the fossil record. A further refinement of (1) the actual

GDP-density effect, (2) the decay constant for both reef numbers and volumes, (3) and changes in carbonate weathering intensity will then permit the reconstruction of an unbiased time series of Phanerozoic reef $CaCO_3$ production. These refinements, however, are unlikely to modify the conclusions that can be drawn from the current results:

(1) Fluctuations in Phanerozoic reef proliferation were indeed profound. All adjustments failed to substantially reduce volatility in the dataset suggesting that the great fluctuations already seen in the raw data are real and of biological significance. Time series of reef volumes show greater volatility than time series of reef numbers (Table 2) suggesting that smaller reefs may behave differently from larger reefs.

(2) The most prolific reef growth of the Phanerozoic was in the early Paleozoic and probably in the Silurian period. The result of an unparalleled reef bloom in the early Paleozoic is surprising and counter-intuitive given the common perception of the Cenozoic or even Neogene as the age of modern-type tropical coral reefs (Veron, 1995; Perrin, 2002). However, there are previous qualitative statements of a maximum reef expansion in the Silurian and Devonian periods with reef areas up to 10 times the ones in the modern ocean (Copper, 1994).

At the current level of reliability, it is perhaps premature to repeat the whole suite of tests for cross-correlations between time series of reef proliferation and earth system parameters such as climate, ocean chemistry and sea-level (Kiessling, 2002). However, that there was almost no significant cross-correlation of detrended values in the analysis of Kiessling (2002) is most likely due to the biased original curve, rather than simply due to prevailing biological controls.

My results have more general implications, because they are principally also applicable to other ecosystems, sedimentary units and estimates of biomass. To mention just a few examples, one could think of rainforests, radiolarites or the biomass of shelly invertebrates as future applications of the methods presented here.

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BGD
2, 1487–1514, 2005

Table 1. Empirical decay constants (k, in myr^{-1}) for Phanerozoic reefs.

	Supersequences		10 myr intervals	
	N	V	N	V
Raw data	0.0012	0.0016	0.0013	0.002
Oceanic and subsurface reef excluded	0.0006	−0.0014	0.0008	0.0007
GDP-adjusted data	−0.0005	−0.0019	−0.0004	−0.0002

Table 2. Standard deviations (std) and volatility (volat) of time series (volatility calculated according to Eq. 1).

		Supersequences		10 myr intervals	
		N	V	N	V
Raw data	std	50.0	123.1	45.9	112.2
	volat	0.67	0.94	0.81	2.16
Oceanic and subsurface reef excluded	std	32.3	37.9	33.1	47.2
	volat	0.62	0.93	0.77	1.91
GDP-adjusted data	std	65.3	45.57	45.4	51.1
	volat	0.67	1.02	0.79	1.99
Adjusted for sedimentary cycling	std	75.9	76.8	75.0	55.1
	volat	0.69	1.04	0.80	1.69

Table 3. Cross-correlations between detrended time series of raw data and detrended time series after final level of adjustment.

	Supersequences		10 myr intervals	
	N	V	N	V
R	0.82	0.56	0.70	0.69
N	31	31	52	52
P	<0.001	<0.001	<0.001	<0.001

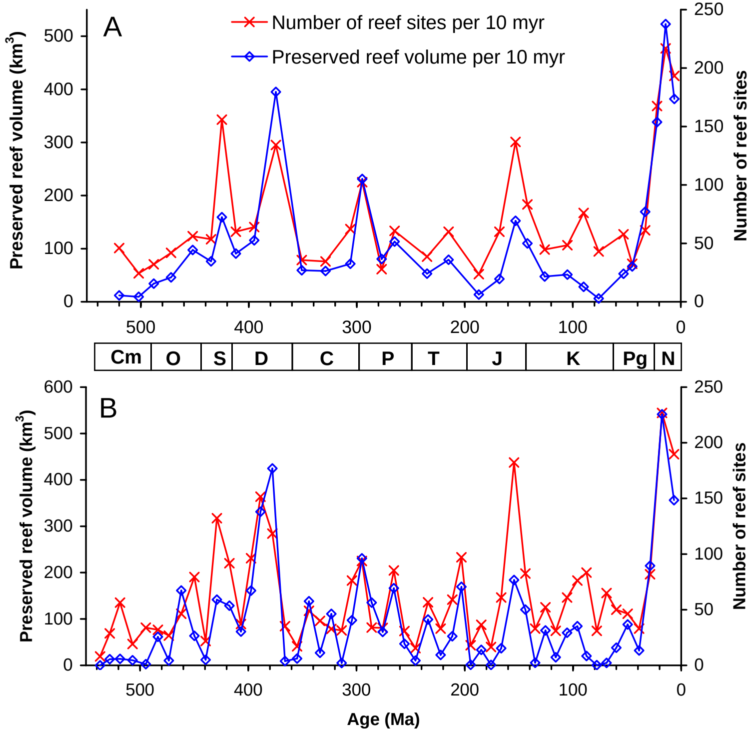

Fig. 1. Time series of the recorded number of reef sites and calculated total reef volume through the Phanerozoic. Raw values, normalized to 10 myr intervals. Bold letter codes indicate geological periods: Cm, Cambrian; O, Ordovician; S, Silurian; D, Devonian; C, Carboniferous; P, Permian; T, Triassic; J, Jurassic; K, Cretaceous, Pg, Paleogene; N, Neogene. **(a)** Data resolved to supersequences. **(b)** Data resolved to 10 myr intervals.

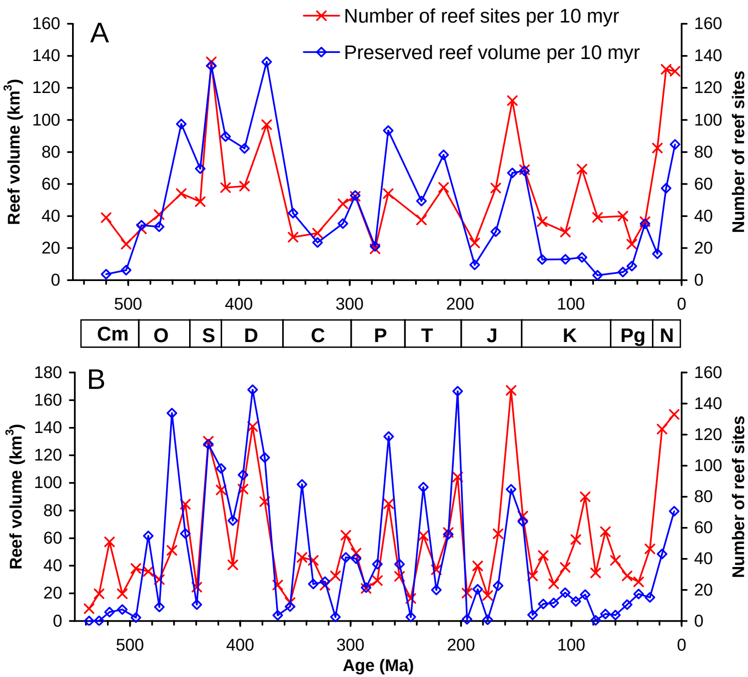

Fig. 2. Time series of the recorded number of reef sites and total reef volume after removal of oceanic and subsurface reef sites. **(a)** Data resolved to supersequences. **(b)** Data resolved to 10 myr intervals.

BGD

2, 1487–1514, 2005

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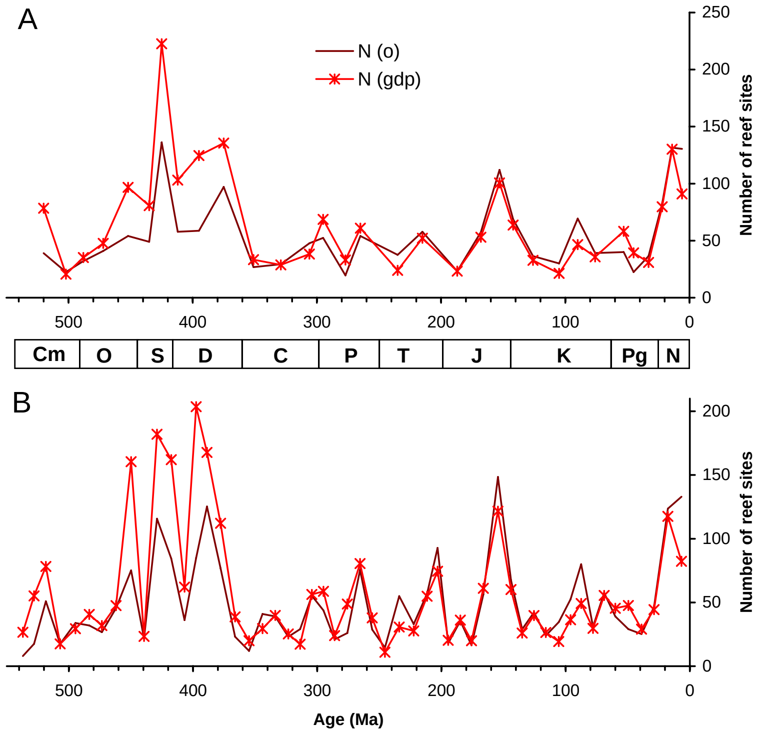

Fig. 3. Time series of the recorded number of non-oceanic, exposed reef sites without (lines) and with (lines with markers) adjustment for the GDP effect with Eq. (4). **(a)** Data resolved to supersequences. **(b)** Data resolved to 10 myr intervals.

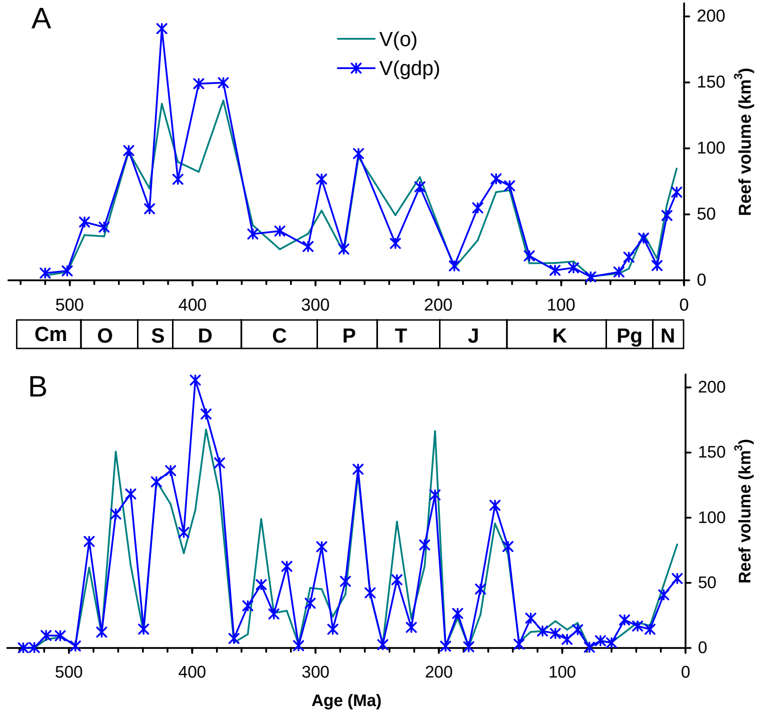

Fig. 4. Time series of the calculated non-oceanic, exposed reef volume without (lines) and with (lines with markers) adjustment for the GDP effect with Eq. (5). **(a)** Data resolved to supersequences. **(b)** Data resolved to 10 myr intervals.

BGD

2, 1487–1514, 2005

Title Page
Abstract
Introduction
Conclusions
References
Tables
Figures
◀
▶
Back
Close
Full Screen / Esc
Print Version
Interactive Discussion

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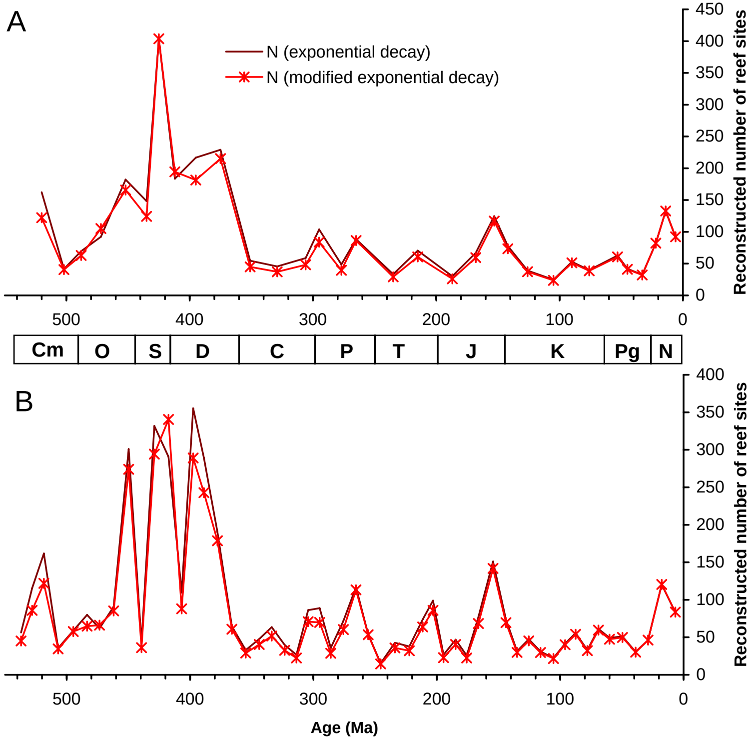

Fig. 5. Time series of the number of GDP-adjusted, non-oceanic, exposed reef sites adjusted for sedimentary decay. Simple lines refer to a simple decay function as in Eq. (6), whereas lines with marker refer to a variable decay as in Eq. (7). **(a)** Data resolved to supersequences. **(b)** Data resolved to 10 myr intervals.

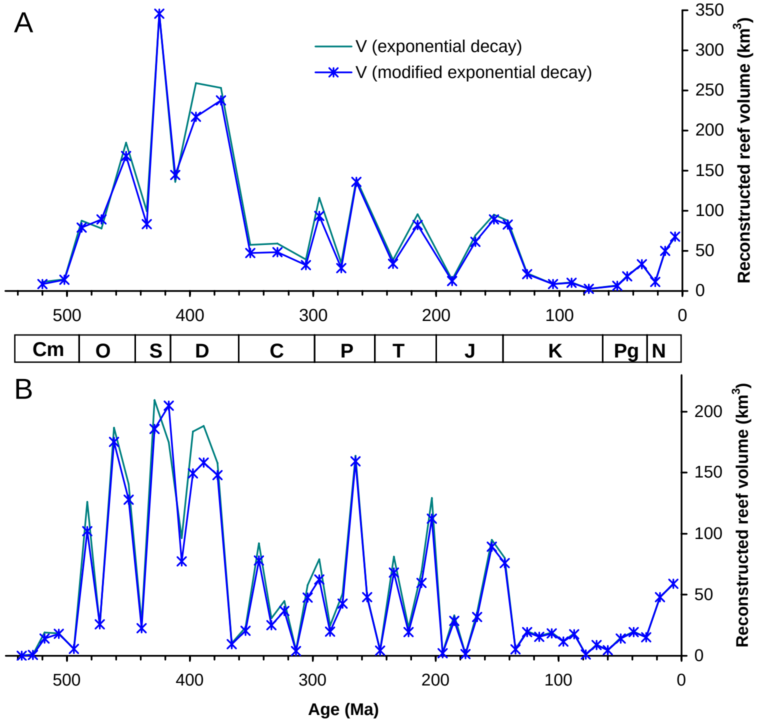

Fig. 6. Time series of GDP-adjusted, non-oceanic, exposed reef volumes adjusted for sedimentary decay. Simple lines refer to a simple decay function as in Eq. (6), whereas lines with marker refer to a variable decay as in Eq. (7). **(a)** Data resolved to supersequences. **(b)** Data resolved to 10 myr intervals.

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2, 1487–1514, 2005

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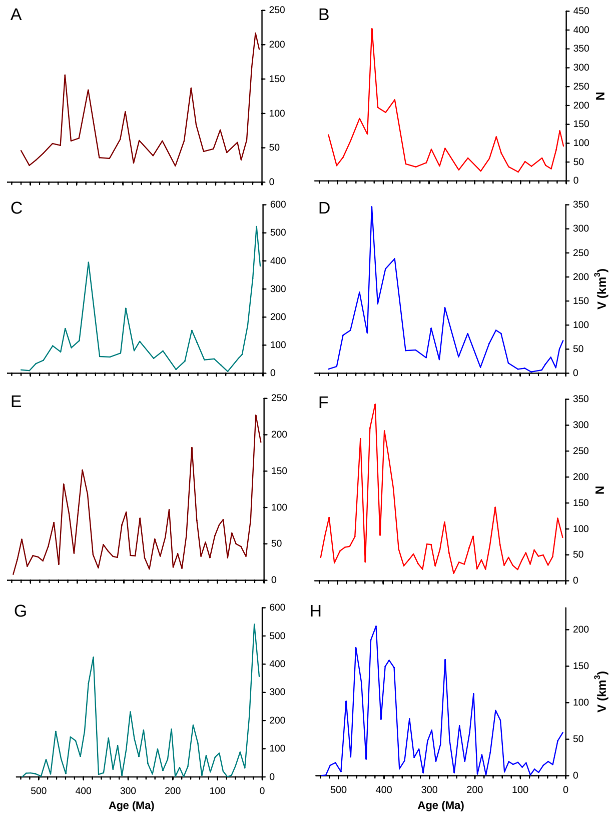

Fig. 7. Comparison of original time series (compare Fig. 1) and time series after all adjustments (compare Figs. 5 and 6). **(a)**–**(d)** Data resolved to supersequences; (a) original time series of reef abundance; (b) time series of reef abundance after adjustments; (c) original time series of reef volumes; (d) time series of reef volumes after adjustments. **(e)**–**(h)** Data resolved to 10 myr intervals; (e) original time series of reef abundance; (f) time series of reef abundance after adjustments; (g) original time series of reef volumes; (h) time series of reef volumes after adjustments.