Fig. 4 Palaeomagnetic rotation as a function of time for Guam and Saipan islands. Observed rotations (●, ▲) as reported in ref. 11 are also plotted.

Miocene are not expected to show any larger rotation, since the trench is hypothesized to have moved uniformly before the collision with the two aseismic ridges. Because of the excellent agreement between our model and the palaeomagnetic data, the proposed dynamic model for the curvature of the Mariana Trench is believed to be valid. The model is especially attractive because of its ability to explain the differential rotation between Saipan and Guam.

The remaining issue is whether the value of 2.40×10^{-21} chosen for $(1/2\mu)/\mathrm{d}P/\mathrm{d}x)$ is reasonable. To address this question, it is necessary to know the viscosity of the surface layer and the pressure gradient within the overriding plate; neither parameter is very well understood, thus one can only examine the range of possibilities. If the pressure gradient is of the order of a few hundred bars over 1 km, then the viscosity will be about 10^{26}. A pressure difference of a few hundred bars is believed to be reasonable as this is about the strength of surface rocks. Is the required viscosity too low? Although very few studies have been carried out to estimate the viscosity of the surface layer, some laboratory observations have been made in an attempt to provide answers to this question[24]. Based on Ito's experiment on creep deformation of a granite slab over a 10-yr period[24], he found that the deformation of his granite slab can practically be described by a newtonian rheology with a viscosity of $\sim 10^{23}$ Pa s. Thus, our implied value for surface rock rheology is not unreasonable in view of the values derived from Ito's experiments.

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Palaeobiological and sedimentological implications of fossil concentrations

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Concentrations of fossil hardparts are common features of the stratigraphical record and are preferred collecting sites for most palaeontological data. Nonetheless, most investigations into the nature of the fossil record have analysed the biasing effects of selective hardpart transport and destruction[1,2] rather than the consequences of the concentration process itself. Genetic classification is discouraged by the diverse origins of skeletal accumulations, which range from predator gastric residues to shelly shoals and biostratigraphically condensed deposits; concentrations can thus form over time intervals of a few minutes to hundreds of thousands of years. I show here that the close association of shell beds with stratigraphical discontinuities in Miocene shallow marine deposits of Maryland[3,4] provides the basis of a model of skeletal accumulation cast entirely in terms of changes in net sedimentation. This simple sedimentological model is a surprisingly powerful predictor of post-mortem bias and ecological composition of fossil assemblages, suggesting that fossil-rich and fossil-poor strata are qualitatively different, both as repositories of palaeontological information and as settings for biotic interactions. Moreover, the apparent primary importance of rates of sedimentation in skeletal accumulation—despite emphasis usually placed on rates of hardpart input—suggests a new approach to inferring the detailed dynamics of sediment deposition and erosion in the formation of stratigraphical sequences.

Description of the upper and lower contacts of shell (or bone) beds as sharp or gradational has genetic significance because bed contacts not only describe the physical relation of the shell bed to adjacent beds, but also relate the process of hardpart concentration to processes responsible for the accumulation of the surrounding, less fossiliferous sediment. Except for contacts created by bioturbation or diagenesis alone, sharp contacts indicate disjunct shifts in sedimentation and usually record an
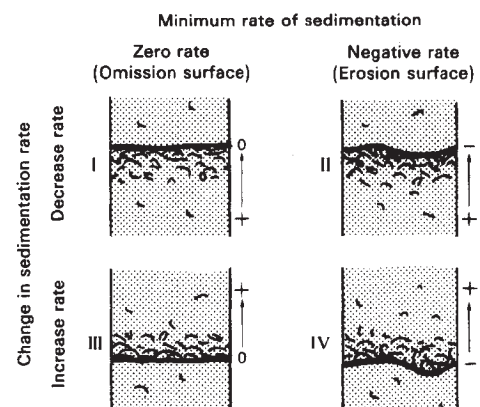

Fig. 1 Field classification of shell beds on the basis of stratigraphical contacts. Type I shell beds grade from less fossiliferous sediment and terminate in a sharp omission surface; type II shell beds also grade upwards with increasing shell-packing density but terminate along an erosion surface; type III shell beds rest on an omission surface and grade upwards into less fossiliferous sediment; and type IV concentrations have erosional basal contacts and grade upwards. Concentrations associated with such surfaces must arise in the context of some change in net sedimentation, since discontinuities indicate conditions of zero (omission) or negative (erosion) net sedimentation, and sediment between discontinuities records positive net sedimentation (deposition).

Table 1 Taphonomic and palaeobiological predictions for four simple patterns of fossil accumulation as modelled in Fig. 1

Shell bed type	Modelled change in sediment-ation	Hardpart residence time on seafloor	Hardpart abundance on seafloor	Severity of post-mortem bias					Community composition			Species morphology		
				Physical abrasion & fragmentation	Bio-erosion	Dissolu-tion	Transport addition or removal	Time-averaging	Deep or mobile infauna	Encrusting & boring taxa	Shell gravel taxa	Shell gravel morphs	Variance owing to: Time-averaging	Selective destruc-tion
I	Decrease from + to 0	Increase	Increase	Increase	Increase	Increase	+/− Increase	Increase	Decrease	Increase	Increase	Increase	Increase	+/− Decrease
II	Decrease from + to −	Increase	Increase	Strong increase	Increase	Increase	Increase	Strong increase	Decrease	Increase	Increase	Increase	Strong increase	Decrease
III	Increase from 0 to +	Decrease	Decrease	Decrease	Decrease	Decrease	+/− Decrease	Decrease	Increase	Decrease	Decrease	Decrease	Decrease	+/− Increase
IV	Increase from − to +	Decrease	Decrease	Strong decrease	Decrease	Decrease	Decrease	Strong decrease	Increase	Decrease	Decrease	Decrease	Strong decrease	Increase

Hardpart abundance and hardpart residence time at or near the sea floor are treated as simple functions of rate of sedimentation (hardpart input is assumed to be constant); fossil assemblages sampled from different horizons within any particular shell bed will be characterized by different degrees of post-mortem bias and patterns of biotic response.

episode of erosion or omission (non-deposition)[5-7]. Hardpart concentrations associated with sharp discontinuities thus must have formed in the context of some change in net sedimentation. These concentrations can be divided into four basic types (Fig. 1), depending on whether hardparts lie on top of or directly underneath the discontinuity surface (as in the "Sohlbanke" and "Dachbanke" of Brinkmann[8]), and whether the surface exhibits scour and truncation features of erosion (negative sedimentation rate) or merely omission (zero net sedimentation rate). As an initial simplifying assumption, hardpart input is assumed to be constant throughout the accumulation period; the model is later shown to hold even after relaxation of this unrealistic assumption.

Type I and type II shell beds (Fig. 1) indicate hardpart accumulation during a slowing down in net sedimentation from high initial rates which exceed hardpart input. Hardpart packing density increases upwards as sedimentation approaches a zero or negative net rate. Type III and type IV beds record an acceleration in sediment accumulation from initially very low rates that foster the concentration of hardparts towards higher positive rates which exceed the background rate of hardpart input. These dynamics of sedimentation have immediate implications for assemblages collected from both fossil-rich and fossil-poor strata.

As rates of sedimentation decrease during the formation of types I and II shell beds, individual hardparts are exposed at the depositional interface for increasingly long periods of time. Assemblages collected from successively higher horizons within the shell bed should thus exhibit a higher frequency and severity of shell damage by abrasion, fragmentation and bio-erosion (Table 1). This trend would be reversed in types III and IV beds. In addition to suffering more pronounced bias owing to selective destruction of hardparts, assemblages that accumulate during the phase of lowest net sedimentation are also more likely to be time-averaged, that is, composite records of a series of populations that occupied the site at different points in time. Time-averaging should be more severe in types II and IV beds than in types I and III beds because of vertical mixing of faunas during erosional reworking. Types II and IV beds are also most likely to be biased by the addition and removal of hardparts through selective transport.

By controlling rates of hardpart burial, net sedimentation also determines the abundance of hardparts in the substratum and thereby influences the physical characteristics of benthic habitats. Ecologically, type I shell beds record the transformation of an initial soft-bottom habitat into an increasingly shelly and thus coarser-textured, firmer and topographically more complex substratum. This change in the physical environment facilitates colonization by borers and encrusters of dead hardparts and by free-living and attached epifauna which prefer or require stable substrata[9]. At the same time, the in situ development of a shell gravel inhibits mobile and sedentary burrowers which occupied the original soft sediment habitat[9]. Types I and II beds should thus exhibit an upward increase in the abundance and diversity of epifaunal species and a concomitant decrease in the numbers of mobile and of especially large or deep-burrowing infauna (Table 1). Assemblages from the most densely fossiliferous parts of the beds will be characterized by ecologically mixed assemblages produced by later shell-gravel taxa occupying the same volume of sediment as earlier soft-bottom taxa; types III and IV beds should exhibit the opposite trend. These shifts in faunal composition should arise regardless of whether the dead hardparts that bring about the change in benthic habitat were produced in situ or delivered from allochthonous sources[9,10].

Another expected biotic response to variation in shell-packing density is a shift in average shell shape of morphologically plastic taxa—most notably epifauna—which can occupy both soft and shelly bottoms[10]. Shell gravel morphs should occur most frequently in assemblages from the most densely packed part of a shell bed (Table 1). Apparent morphometric variance within sampled fossil populations of species should also be greatest there, owing to the time-averaging of the directional shift from soft-bottom and shell gravel morphs and of random non-directional fluctuations in morphology. In types III and IV shell beds, the expected burst of variation followed by a gradual dwindling of variance mimics patterns predicted by some theories of speciation[11,12].

The robustness of the sedimentological model is evaluated by relaxing the assumptions, using a series of hypothetical histories of sedimentation and hardpart input (Fig. 2). When hardpart input is allowed to vary (Fig. 2b-e), classification and interpretation of shell beds using the bed contact criterion yields a correct interpretation of sedimentary dynamics in all but one situation: when peaks in hardpart input coincide precisely with maxima in sedimentation (Fig. 2d). This relationship is biologically improbable, because most shelly benthos avoid colonizing settings with high rates of sedimentation. Coincident maxima can occur when hardparts are hydraulically equivalent to enclosing sediments, such as macroinvertebrate shell debris in turbidity current or other high-energy conditions, and microfossil tests in deep-sea environments. These pitfalls can be diagnosed in the field by visual comparison of the hardpart and sediment grain sizes. Figure 2e,f illustrates the results of more complicated patterns of change in sedimentation and hardpart input and more closely mimics real fossiliferous sequences. The robustness of the model for these, as well as for endmember conditions, suggests that the model can be applied successfully to the spectrum of possible combinations of rate changes.

Changes in net sedimentation inferred from bed contacts provide working hypotheses that can be tested by their palaeontological predictions (Table 1) as well as by independent evidence for reduced net sedimentation within the shell bed (glauconite concentration, winnowed sedimentary matrix, physically amalgamated beds). In the Maryland Miocene sequence,
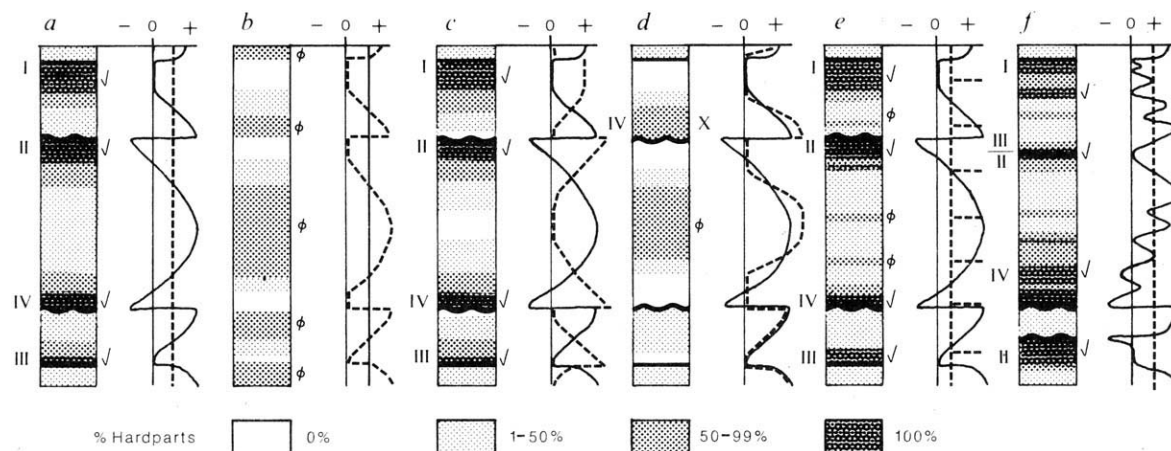
% Hardparts ☐ 0% ▒ 1–50% ▓ 50–99% ■ 100%

Fig. 2 Synthetic fossiliferous sequences generated from hypothetical patterns of change in sedimentation (solid curve) and hardpart input (dashed curve) provide a test of the robustness of the simple sedimentation model of fossil concentration (Fig. 1). *a*, Condition of constant hardpart input (original model conditions). The sedimentation model correctly interprets the mode of formation of all hardpart concentrations that can be classified as type I, II, III or IV (indicated by √). *b*, Constant sedimentation, only hardpart input varies. Concentrations form when hardpart input is relatively high, but none is associated with sharp discontinuity surfaces that permit classification by the model; the model does not lead to erroneous interpretations of the mode of formation (indicated by ϕ). *c*, Hardpart input varies inversely with sedimentation. Variation in hardpart input simply accentuates concentrations produced by excursions in sedimentation, and thus the model correctly interprets shell beds. *d*, Hardpart input varies directly with sedimentation. When the two rates are identical, fossil abundance does not vary stratigraphically (lower part of synthetic section), but relative concentrations do arise when hardpart input is allowed to exceed sedimentation. The model yields incorrect interpretations (indicated by X) of only those shell beds actually assocociated with discontinuities. This requires a very particular pattern of sedimentation plus perfect hydraulic equivalence of hardparts with sediment or preferential colonization by macrobenthos during the episode of maximum sedimentation. *e*, Variable net sedimentation, constant background rate of hardpart input with brief positive excursions (for example, mass mortality, allochthonous input). Synthetic pattern of fossil abundance closely mimics real stratigraphical sequences wherein some concentrations are associated with stratigraphical discontinuities, concentrations that can be classified by bed contacts are correctly interpreted by the simple sedimentation model despite random variation in hardpart input. *f*, Complex changes in sedimentation plotted against constant hardpart input. Short-term fluctuations during overall decrease or increase in net sedimentation produce internally complex fossil concentrations; back-to-back monotonic changes produce composite types I–III and II–IV deposits which share an internal discontinuity surface, and composite type III–I and IV–II beds in which both upper and lower contacts are sharp; the model is robust to any pattern of change in sedimentation.

all four large-scale shell beds (Beds 10, 14, 17 and 19 (ref. 13) in Fig. 3*a*) and most smaller-scale shell concentrations can be classified on the basis of bed contacts as type I, II, III or IV. These exhibit physical evidence of accumulation during intervals of reduced net sedimentation (letter-coded in Fig. 3). Expected palaeontological trends are best developed in the large-scale accumulations, which record skeletal accumulation over prolonged periods of time (estimated at 10^{-3}–10^{-4} yr each[3]). As evident in the expanded columnar sections of beds 10 and 17 (Fig. 3*b*, *c*), these shell beds exhibit similar vertical sequences: a basal shell hash of largely fragmental infaunal and unbroken epifaunal hardparts; this grades into the main body of the shell bed which contains ecologically mixed and highly amalgamated assemblages of both whole and broken closely packed shells; and an upper interval of closely spaced but discrete shell horizons by which the shell bed grades into less fossiliferous overlying strata. The small-scale types I and IV shell beds which characterize the upper transitional part of these thick, complex type IV shell beds are lags of reworked hardparts from soft-bottom communities, and in some instances have been colonized by epifauna[9]. Directional shifts in bivalve morphology documented within each of the major Miocene shell beds have been interpreted as microevolutionary in origin[14], but might also represent the predicted ecological response to changing substratum characteristics or to concomitant increases in water depth deepening during transgression, or the expected effects of time-averaging. Expected palaeontological trends are thus borne out on several hierarchical scales of skeletal accumulation in this particular setting[4].

These results with both synthetic and real stratigraphical sections suggest that the model has more than heuristic value. The model should promote palaeobiological comparison of fossil assemblages because it can be used as a testable hypothesis to address a wide variety of skeletal concentrations. Hardpart accumulations can be evaluated regardless of their timescale of
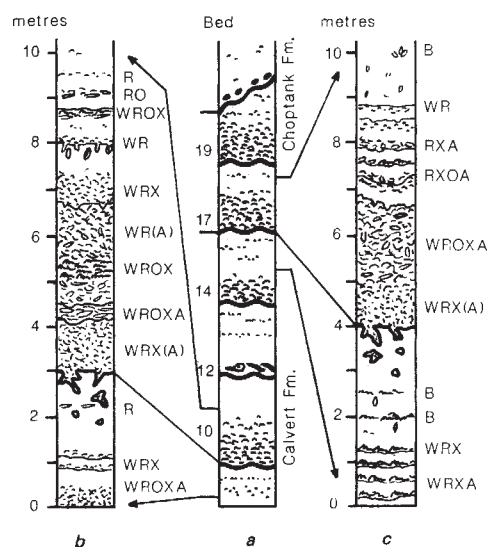

Fig. 3 The Middle Miocene Calvert and Choptank formations (composite section, middle column *a*) include four thick (1–10 m) and laterally extensive (2,500–7,000 km²) shell beds (numbered 10, 14, 17 and 19 in column *a*) and many small-scale concentrations. Most of these are associated with stratigraphical discontinuities—disconformities in the case of the four major shell beds, and scoured or winnowed bedding planes in the case of the minor accumulations (see schematic columns *b* and *c* for expanded scales)—and exhibit independent evidence of concentration during low net rates of sedimentation[15]. W, Winnowed matrix; R, hydraulically reoriented specimens; O, overpacked infauna; A, physically amalgamated beds; X, exhumed specimens; B, concentrations of biogenic origin, for example, clumps of shells recording concentration through biological processes, such as gregarious behaviour of the skeletized fauna or reworking by other organisms.

accumulation (for example, both rapidly formed storm beds and slowly accumulated basal lags on unconformities have type IV structures), physical dimensions, taxonomic composition, proportion of allochthonous hardparts, depositional environment and geological age. Detailed palaeoecological and evolutionary comparisons across environmental gradients or through geological time thus become feasible if a single type of shell bed is sampled throughout. For example, a transect based on erosive washover deposits, swash zone shell laminae, lags produced by channel and shoal migration, inner shelf storm concentrations and shelly proximal turbidites—which are all short-term type IV deposits—should yield assemblages that are ecologically and taphonomically more comparable with one another than to assemblages from short-term types I, II or III deposits. In addition, the absence (or otherwise divergence) of taphonomic trends from those predicted by the model permit the detection of more complex histories and conditions of fossil concentration. Successive horizons within a shell bed might be palaeontologically identical because of: very rapid concentration and burial which sequesters hardparts from destructive processes at the sea floor so that trends never develop; accumulation in environmental conditions (for example anoxia) which exclude potential colonists of dead hardparts; and homogenization by bioturbation. Very rapid formation and burial relative to rates of hardpart destruction and benthic colonization probably explain the less consistent development of expected trends within the small-scale shell beds of the Maryland Miocene, and bioturbation of shell bed contacts may well obscure the sedimentological origin of many others. The complex internal stratigraphies of the major shell beds, on the other hand, record the physical amalgamation of many small-scale concentrations into a single fossil deposit by the superposition of short-term fluctuations on a longer, overall trend in sedimentation rate, such as examined synthetically in Fig. 2f.

If sedimentation is the primary control on skeletal acccumulation as indicated by the initial tests reported here, fossil concentrations can yield insights into the basic dynamics (timing and magnitude) of stratigraphical accumulation. The relative frequency of type I, II, III and IV beds should vary among depositional environments owing to differences in sediment supply and hydrodynamics, and suggests a new approach to the mapping and interpretation of sedimentary facies. Qualitatively different patterns of fossil accumulation can also be expected between transgressive and regressive phases of marine deposition, and among basins of different tectonic and latitudinal settings. By referring to fundamental rates and patterns of hardput input and sedimentation, this approach to modelling has the potential to generate testable hypotheses for a systematic exploration of the nature of the fossil record on several scales.

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Sex ratios of an aphid subject to local mate competition with variable maternal condition

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Fisher[1] was the first to argue that natural selection would adjust the sex ratio so as to equalize parental investment (PI) in the two sexes, where mating is at random. Hamilton[2] then showed that female-biased sex ratios would be favoured where male siblings compete for matings, a situation referred to as 'local mate competition' (LMC). In Hamilton's original model and in most subsequent LMC models, the females founding a local breeding population have equal amounts of PI to be allocated between sons and daughters. But in nature, females may differ in total PI and, as a consequence, in fecundity. Here I describe a model for the sex ratios of n co-foundresses, all of which differ in total PI. The model shows that each female with more than a specified minimum amount of PI is selected to make the same absolute investment in sons. All previously published cases of dramatic sex-ratio control occur in haplodiploid species. Here I test my theoretical model against sex-ratio data for an aphid, Prociphilus oriens, which has a normal diploid genetic system.

Several theorists have considered the sex-ratio strategies of two co-foundresses with different clutch sizes, and they have found that the more fecund female should always produce the more female-biased ratio of investment[3,4]. 'Double parasitism' of hosts often occurs in natural populations of parasitoid wasps, leading to local competition for mates among the offspring of two females. But in aphids, such LMC often occurs among the offspring of more than two females. Thus for aphids, a more general LMC model is needed.

The model described here embodies the following assumptions. Each local breeding population ('patch') is founded by n inseminated females selected at random from the total population at large. These females differ in their total PI: $P_1 < P_2 < \cdots < P_n$, where P_i is the total PI of the ith female. Each female can control her offspring sex ratio, S_i, which is the proportion of P_i invested in sons. Mating occurs at random among the offspring born in the same patch, and all of the female offspring are successfully inseminated. Then the mated female offspring disperse, becoming thoroughly mixed with the rest of the population at large before the next generation's patches are established by taking samples of n females.

Natural selection will favour offspring sex ratios that maximize each mother's inclusive fitness. With a diploid genetic system and autosomal control of the sex ratio, mothers are related equally to their sons and daughters. At the end of the period of parental investment, the expected reproductive success of female offspring (R_f) can be taken to be a constant, equal for all daughters of all mothers. But the reproductive success of a son (R_m) depends directly and immediately on the sex ratios of the mothers in the patch. Thus the inclusive fitness of each mother is a function of her own sex ratio and of the sex ratios of the other mothers, and sex-ratio evolution takes the form of a game in which the best move for each individual depends on what all the others are doing[5]. Below, I derive the optimal sex ratios as the Nash solution or non-cooperative equilibrium of an n-person game, which in this context is the same as an evolutionarily stable strategy[6].

The inclusive fitness of the ith mother (F_i) in a patch founded by n mothers can be written as[7]

$$F_i = r_d \frac{P_i(1-S_i)}{w_d} R_f + r_s \frac{\dot{P}_i S_i}{w_s} R_m \quad (i = 1, 2, \ldots, n) \quad (1)$$

where S_i = sex ratio of the ith mother; P_i = total PI of the ith mother ($P_1 < P_2 < \cdots < P_n$); r_d, r_s = relatedness of a mother to