

Demographic history of *Diadema antillarum*, a keystone herbivore on Caribbean reefs

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The sea urchin *Diadema antillarum* was the most important herbivore on Caribbean reefs until 1983, when mass mortality reduced its populations by more than 97%. Knowledge of its past demography is essential to reconstruct reef ecology as it was before human impact, which has been implicated as having caused high pre-mortality *Diadema* abundance. To determine the history of its population size, we sequenced the ATPase 6 and 8 region of mitochondrial DNA from populations in the Caribbean and in the eastern Atlantic (which was not affected by the mass mortality), as well as from the eastern Pacific *D. mexicanum*. The Caribbean population harbours an order of magnitude more molecular diversity than those of the eastern Pacific or the eastern Atlantic and, despite the recent mass mortality, its DNA sequences bear the genetic signature of a previous population expansion. By estimating mutation rates from divergence between *D. antillarum* and *D. mexicanum*, that were separated at a known time by the Isthmus of Panama, and by using estimates of effective population size derived from mismatch distributions and a maximum likelihood coalescence algorithm, we date the expansion as having occurred no more recently than 100 000 years before the present. Thus, *Diadema* was abundant in the Caribbean long before humans could have affected ecological processes; the genetic data contain no evidence of a recent, anthropogenically caused, population increase.

Keywords: mitochondrial DNA; mismatch distribution; coalescence; human impact

1. INTRODUCTION

The long-spined black sea urchin *Diadema antillarum* was, until 1983, the most important herbivore on Caribbean reefs affecting plant (Ogden *et al.* 1973; Carpenter 1981, 1986; Sammarco 1982*a,b*) and coral (Bak & van Eys 1975; Sammarco 1980, 1982*b*) cover, competing with other herbivores (Williams 1980, 1981; Sammarco & Williams 1982; Hay & Taylor 1985), and removing more calcium carbonate from reef framework than any other organism (Ogden 1977; Scoffin *et al.* 1980). In 1983, *D. antillarum* suffered mass mortality due to an unidentified pathogen that reduced its densities throughout the tropical western Atlantic by more than 97%, the most extensive and most severe mass mortality recorded in a marine animal (Lessios *et al.* 1984*a*; Lessios 1988). A decade after the mass mortality, populations had not recovered (Hughes 1994; Lessios 1995*a*). The demise of *D. antillarum* in the Caribbean accelerated the degradation of coral reefs through shifts from coral- to algal-dominated communities (Hughes *et al.* 1987; Lessios 1988; Levitan 1988; Carpenter 1990*a*; Hughes 1994; Ostrander *et al.* 2000). In Jamaica, recent local recovery of *Diadema* was accompanied by reduction of algal cover and increase in coral recruitment (Aronson & Precht 2001; Edmunds & Carpenter 2001). These correlated changes confirmed the importance of the ecological role of this species, and indicated that the magnitude of its previous impact was due to its high abundance.

How long ago *Diadema* reached high population densities is an important question that remains unanswered. Hay (1984), through measurements of the intensity of herbivory in areas of high and low fishing pressure, came to the conclusion that the high abundance of *Diadema* was a recent phenomenon due to the removal of its fish predators and competitors by humans. Post-mortality increases in herbivorous fish abundance in areas of low fishing pressure (Robertson 1991) and extensive overgrowth of corals by algal mats in areas of high fishing pressure (Lessios 1988; Levitan 1988; Hughes 1994) provided support for the hypothesis that *Diadema* competed with fish for plant resources (Carpenter 1990*b*). Levitan (1992) studied the relation between the size of *D. antillarum* jaw apparatus and the diameter of the body in museum specimens collected between 1881 and 1986. He found that in areas of increasing human population density there were signs of increasing *D. antillarum* food limitation, registering as larger relative tooth size (Ebert 1980; Levitan 1991). He reasoned that such food limitation was the result of higher intraspecific competition, and thus that there was a positive correlation between human and *Diadema* population density. However, variation through time was smaller than variation between localities, indicating that human influence played only a small role in regulating the abundance of *Diadema*. Jackson (1997), based on Levitan's conclusion, along with the presence of 125 000 year old diadematoïd skeletal remains in the Falmouth Formation of Jamaica (Donovan & Gordon 1993) and on anecdotal accounts of *Diadema* abundance in the writings of early naturalists going back to 1725, argued that *D. antillarum* was abundant long before humans began to remove fish from the Caribbean. Resolving the question

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of when population abundance of *Diadema* attained its pre-1983 levels is important, not just for a successful reconstruction of the ecology of Caribbean palaeo-reefs, but also for deciding the issue, important for modern reef management, of whether such high abundances were 'natural'.

Because the ossicles of *Diadema* fall apart soon after death (Greenstein 1989), there are no known *Diadema* fossils in the Caribbean other than the microscopic fragments found in Jamaica (Lessios 1998). Another means of reconstructing historical demographic fluctuations is the study of DNA sequence variation in contemporary populations. This approach has been extensively applied to populations of humans (Rogers & Harpending 1992; Harpending 1994; Sherry *et al.* 1994; Rogers 1995; Takahata 1995; Harding *et al.* 1997; Jorde *et al.* 1997; Di Rienzo *et al.* 1998; Harpending *et al.* 1998; Kimmel *et al.* 1998; Polanski *et al.* 1998; Reich & Goldstein 1998; Wilson & Balding 1998; Zietkiewicz *et al.* 1998; Pritchard *et al.* 1999; Schneider & Excoffier 1999; Zhao *et al.* 2000; Alonso & Armour 2001) and of other species (Lavery *et al.* 1996; Petit *et al.* 1999), sometimes with conflicting results (Fullerton *et al.* 1994; Marjoram & Donnelly 1994; Bertorelle & Slatkin 1995; Harris & Hey 1999; Hey & Harris 1999; Gonser *et al.* 2000; Hawks *et al.* 2000; Wall & Przeworski 2000; Rogers 2001). Here, we present data from mitochondrial DNA (mtDNA) sequences from 110 individuals of Caribbean *D. antillarum*, analysed with two conceptually different models. Both analyses indicate that major population expansion of this sea urchin in the Caribbean occurred earlier than 100 000 years before present (yr BP).

2. METHODS

We sequenced a stretch of 642 base pairs of the ATPase region of mtDNA from 110 *D. antillarum* individuals collected in eight localities in the Caribbean between 1987 and 1999. Collections were made at Belize ($n=10$) in September 1997; Cayman Brac ($n=10$) in May 1997; Cayos Cochinos, Honduras ($n=10$) in May 1995; Isla Margarita, Panama ($n=35$) in June 1994 and in May 1998; San Blas Islands, Panama ($n=30$) in April 1999; Puerto Rico ($n=10$) in June 1987; San Andrés ($n=2$) in November 1996; St John, US Virgin Islands ($n=3$) in July 1997. Analysis of molecular variance (Excoffier *et al.* 1992), with time of collection nested within localities, using the program ARLEQUIN v. 2.0 (Schneider *et al.* 2000) with the distance of Tamura and Nei (1993) and a gamma distribution with $\alpha=0.164$, showed a great deal of genetic homogeneity in time and space. The value of F_{ST} between collections within localities was 0.03; the value of F_{ST} between localities was 0.04. We therefore treated all sequences as coming from a single sample.

Because the samples were gathered after the mass mortality, it was necessary to consider the possibility that the 1983 population bottleneck might have erased the genetic signature of earlier population expansions. To answer this question, and to obtain a reliable estimate of the rate with which mutations accumulate in *Diadema*, we also sampled 44 *D. mexicanum* in the eastern Pacific and 126 *D. antillarum* in the eastern Atlantic. It is known that *Diadema* in both the eastern Atlantic (Lessios 1988; Casañas *et al.* 1998) and the eastern Pacific (Lessios *et al.* 1984b; Lessios 1988) were not affected by the 1983 pandemic and can thus serve as controls for the effects of recent population

reduction. *D. mexicanum* has been separated from *D. antillarum* by the Isthmus of Panama for a minimum of two million years (Myr). Eastern Atlantic *Diadema*, although given the same specific name, contains a distinct phylogenetic lineage of mtDNA, diverged from that in Caribbean *D. antillarum* for at least 1 Myr, with no evidence of gene flow between the two sides of the Atlantic since that date (Lessios *et al.* 2001). Collections of *D. mexicanum* were made at Clipperton Atoll ($n=11$) in April 1994; Isla del Coco ($n=12$) in December 1987; Galápagos Islands ($n=4$) in April 1990; Sea of Cortez ($n=9$) in February 1987; Bay of Panama ($n=5$) in April 1987, September 1992 and December 1995; Gulf of Chiriqui, Panama ($n=3$) in December 1995. Collections of the eastern Atlantic *D. antillarum* were made at São Tomé, Gulf of Guinea ($n=10$) in December 1997; Gran Canaria, Canary Islands ($n=51$) in December 1995, April 1996 and November 1998; La Palma, Canary Islands ($n=4$) in January 1998; Boa Vista, Cape Verde ($n=29$) in September 1996 and August 1998; Desertas Island, Madeira ($n=32$) in May 1996 and October 1998.

All sequencing was done in both directions. For details of the methods see Lessios *et al.* (2001). Sequences have been deposited in GenBank under accession numbers AF366077–AF366222, AY12836–12876, AY12908–12951 and AY12766–AY12815.

3. RESULTS AND DISCUSSION

Diadema from the Caribbean, with 43 unique haplotypes in a sample of 110 individuals, harboured significantly higher levels of variation than did populations from either the eastern Atlantic (eight unique haplotypes in a sample of 126) or from the eastern Pacific (four unique haplotypes in a sample of 44), the opposite of what would be expected if the Caribbean pandemic had acted as a genetic bottleneck (figure 1a). The higher apparent diversity of the Caribbean populations was not the result of pooling individuals from genetically different localities, because the diversity excess remained when populations from each locality were analysed separately (figure 1b). These results from mtDNA sequencing agree with previous conclusions drawn from comparisons of isozymes in Caribbean *D. antillarum* collected before and after the mass mortality. The isozyme results had indicated that there was no loss of genetic variability in nine polymorphic loci sampled every year for 10 years following the mass mortality (Lessios 1985, 1995b).

Two statistics used to determine from DNA sequences whether populations have been expanding, remaining constant, or contracting are Tajima's (1989) D and Fu's (1997) F_s . In all three *Diadema* populations, including the one from the Caribbean, both D and F_s have values significantly smaller than zero (table 1), indicating an excess of 'new' mutations relative to the equilibrium expectation based on the number of segregating sites (the Tajima test), or on the number of observed alleles (the Fu test). Such negative values could be the result of either a recent expansion in effective population size, or of selective sweeps. Selective sweeps that occurred after the lineages became separated would be expected to manifest themselves in higher ratios of amino acid replacement to silent substitutions between lineages relative to within lineages (McDonald & Kreitman 1991). This, however, is not the case in any of the pairwise comparisons between the three mitochondrial lineages of *Diadema* (Fisher's

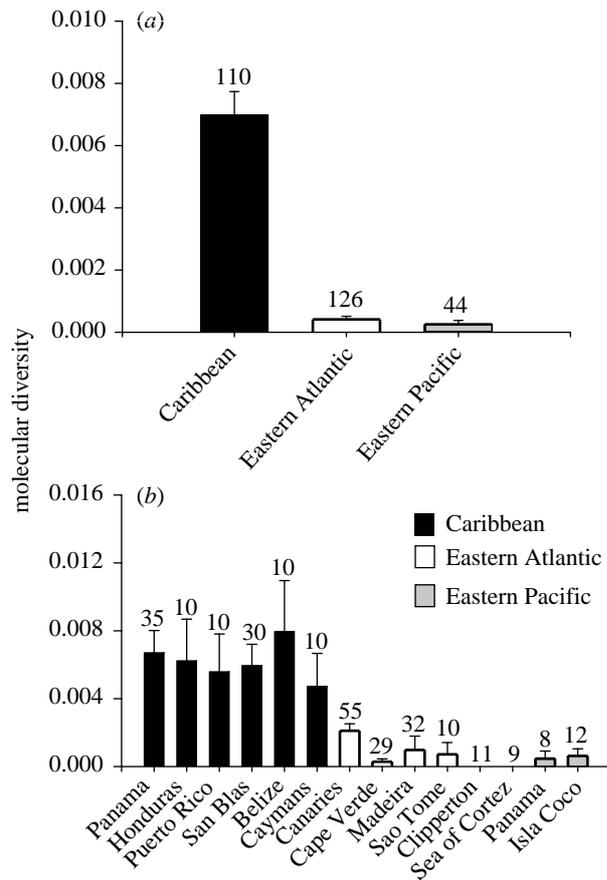


Figure 1. Molecular diversity (π) + 95% confidence intervals in populations of *Diadema* in the Caribbean, the eastern Atlantic, and the eastern Pacific: (a) samples from each region pooled; (b) individual localities in which $N > 7$. Molecular diversity incorporates the correction of Tamura and Nei (1993), based on a gamma distribution of substitutions, with $\alpha = 0.164$. Sample size for each population is indicated above the bars.

Table 1. Values of D (Tajima 1989) and F_s (Fu 1997) for three mitochondrial DNA lineages of *Diadema*.

(Significance is based on 10 000 random samples generated under the assumption of selective neutrality and population equilibrium, using coalescent simulations as implemented in ARLEQUIN 2.0 (Schneider *et al.* 2000).)

	D	F_s
Caribbean	-2.12 ^b	-26.46 ^c
eastern Atlantic	-2.29 ^c	-10.24 ^c
eastern Pacific	-1.70 ^a	-4.06 ^c

^a $0.005 < p < 0.01$.

^b $0.001 < p < 0.005$.

^c $p < 0.001$.

exact test, $p > 0.15$ in all comparisons). A more likely explanation for the negative values of D and F_s is that they are the result of population expansion. Thus, both a comparison of molecular diversity in Caribbean *Diadema* to that in other populations that did not suffer recent mass mortality and an analysis of the inherent pattern of variation of its own mtDNA indicate that the 1983 mass

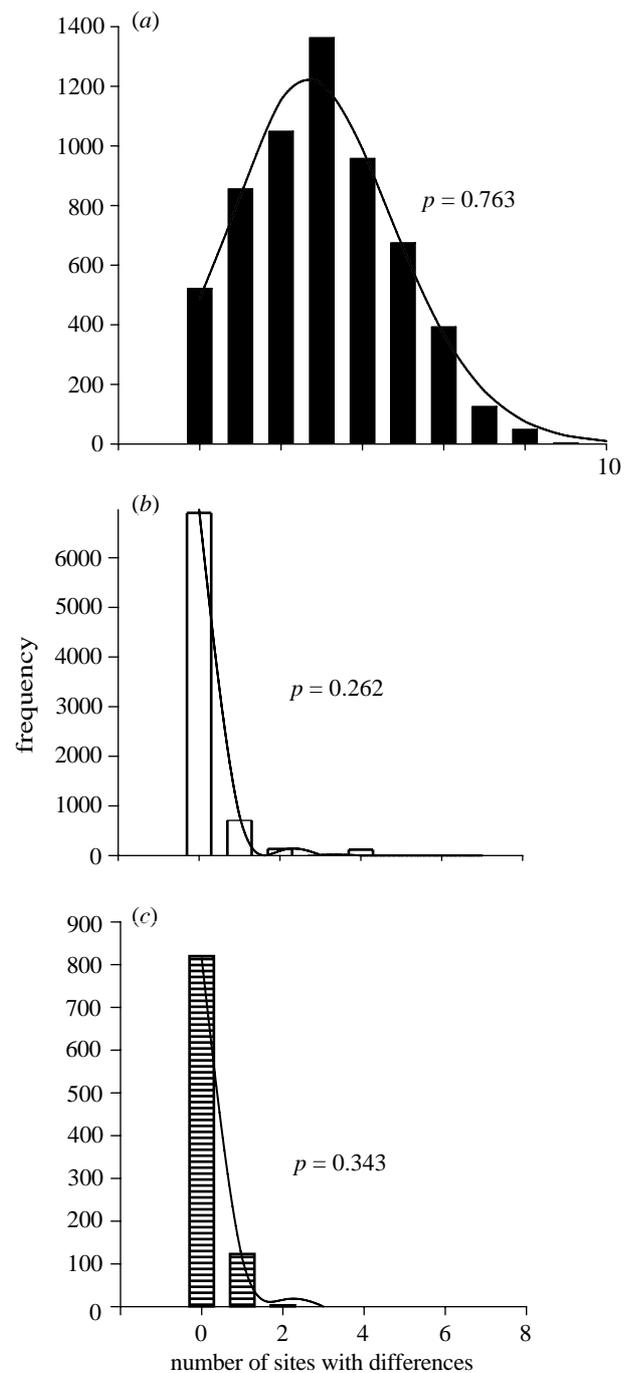


Figure 2. Mismatch distributions (Rogers & Harpending 1992; Harpending 1994; Rogers 1995) of haplotypes of *Diadema* in (a) the Caribbean, (b) the eastern Atlantic, and (c) the eastern Pacific. The continuous line represents the mismatch distribution expected from sudden expansion. Probability values (p) for rejection of the sudden expansion model are based on a comparison of the sums of squares of expected and observed mismatch distributions, using parametric bootstrap with 10 000 iterations (Schneider & Excoffier 1999).

mortality in the western Atlantic did not erase the genetic signature of past population history. It may have removed 97% of individuals in the Caribbean but, as might be expected, in the 4–16 generations (*D. antillarum* reaches sexual maturity in one year (Carpenter 1997)) that elapsed between the mass mortality event and the time of

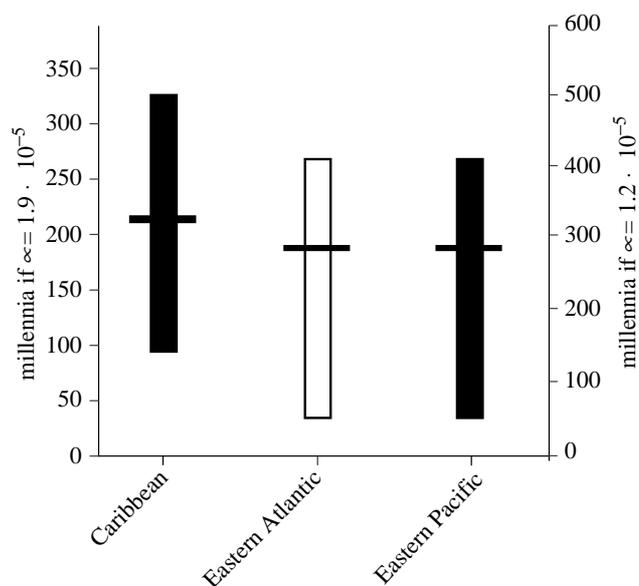


Figure 3. Time since the beginning of the expansion of modern day populations, as estimated from the observed distribution of haplotype differences (Rogers & Harpending 1992; Harpending 1994; Rogers 1995). Parameters were estimated from the mismatch distribution by generalized nonlinear least squares, allowing for variable mutation rates and multiple hits per site; 95% confidence intervals were estimated from parametric bootstrap (Schneider & Excoffier 1999) with 10 000 iterations. Mutation rates μ are expressed as substitutions per site per millennium.

sampling for this study, there were no obvious bottleneck effects on its genetic variability.

How recently did the expansion of effective population size occur in the Caribbean? If the mutation rate μ is known, changes in effective population size N_e can be calculated from estimates of θ , where $\theta = 2N_e\mu$. One means of estimating the trajectory of θ through time is the 'mismatch distribution', i.e. the distribution of pairwise differences between haplotypes in a sample (Rogers & Harpending 1992; Harpending 1994; Rogers 1995). For populations that have undergone a sudden expansion (and thus display a unimodal distribution of haplotype differences), the mismatch distribution permits the calculation of initial and final values of θ , and also of τ , the product of 2μ multiplied by the time since expansion started. All three populations of *Diadema* fit the sudden expansion model (figure 2). However, the mean number of sites with nucleotide differences between haplotypes in the Caribbean is 2.99, whereas the mean number in the eastern Atlantic is 0.19 and in the eastern Pacific 0.14, indicating an earlier expansion and/or a larger N_e in the Caribbean.

To date the initiation of each expansion, it is necessary to estimate the rates at which mutations accumulate in *Diadema*. Such an estimate can be obtained by comparing sequences of Atlantic and eastern Pacific populations. The two oceans were separated by the emergence of the Isthmus of Panama. The Central American landbridge was completed 3.1 Myr BP (Coates & Obando 1996), but there is a possibility that it was breached by sea intrusions as recently as 2.0 Myr BP (Cronin & Dowsett 1996). Because *Diadema* shows less transisthmian divergence

than six other genera of sea urchins in both mitochondrial and nuclear markers, the possibility exists that its populations on the two coasts of Central America may have re-established genetic contact during the breach (Lessios *et al.* 2001). The rate of mutation for the sequenced segment can, therefore, be either 1.2×10^{-5} substitutions per site per millennium (if separation between *D. antillarum* and *D. mexicanum* is assumed to have lasted 3.1 Myr) or 1.9×10^{-5} substitutions per site per millennium (if separation lasted 2 Myr). The slower rate of substitution dates the beginning of *Diadema* population expansion in the Caribbean at 330 000 yr BP, with a lower 95% confidence limit at 146 000 yr BP (figure 3). The faster rate produces an estimate of 213 000 yr BP with a lower 95% confidence limit of 94 000 yr BP. Thus even the 95% confidence limit of the most recent estimate of the initiation of population expansion pre-dates by far the onset of any possible fishing pressure in the Caribbean.

The mismatch approach has been criticized for not incorporating the genealogical information inherent in DNA sequences (Felsenstein 1992). An approach that takes this information into account is based on the distribution of the estimates of common ancestors between sequences. This distribution depends on mutation rate and effective population size. We used the procedure of Kuhner *et al.* (1998) to obtain maximum likelihood estimates of population growth rate r and of θ . This algorithm uses initial values of θ and r , and samples possible genealogies based on their posterior probability given the data; the sampled genealogies are then used to evaluate the likelihood of other values of θ and r . Using the program FLUCTUATE of Kuhner *et al.* (1998), we obtained the maximum likelihood estimates of the two parameters and then calculated effective population size through time, based on our estimates of mutation rates of *Diadema*. Based on these estimates, N_e of Caribbean *Diadema* becomes zero 940 000 yr BP by the fast mutation rate and 1.52 Myr BP by the slow mutation rate. An effective population size of 1 million females is reached at 180 000 yr BP and 320 000 yr BP, respectively (figure 4). Thus, the results from the maximum likelihood analysis of coalescence agree rather well with those obtained from mismatch distributions in dating the initiation of the population expansion of *Diadema* populations in the Caribbean at about 200 000 yr BP, a time which strongly suggests that there were large populations of *D. antillarum* on Caribbean reefs long before humans could remove their predators and competitors.

How accurate are these estimates of time since the expansion of *Diadema* population size? Many assumptions of this analysis can induce errors, but almost all such possible errors would cause underestimation, rather than overestimation, of the age of the Caribbean populations. Obviously, the actual number of individuals in the population at any given time would be at least double the effective number of females, estimated by mtDNA. Both of the genetic models assume that growth of the populations has been monotonic, whereas it is more likely to have been fluctuating. The model of Kuhner *et al.* (1998) also assumes exponential population growth, which *Diadema* is not likely to have attained for long periods of time. If selective sweeps, undetected by the McDonald-Kreitman (1991) test, have occurred, their

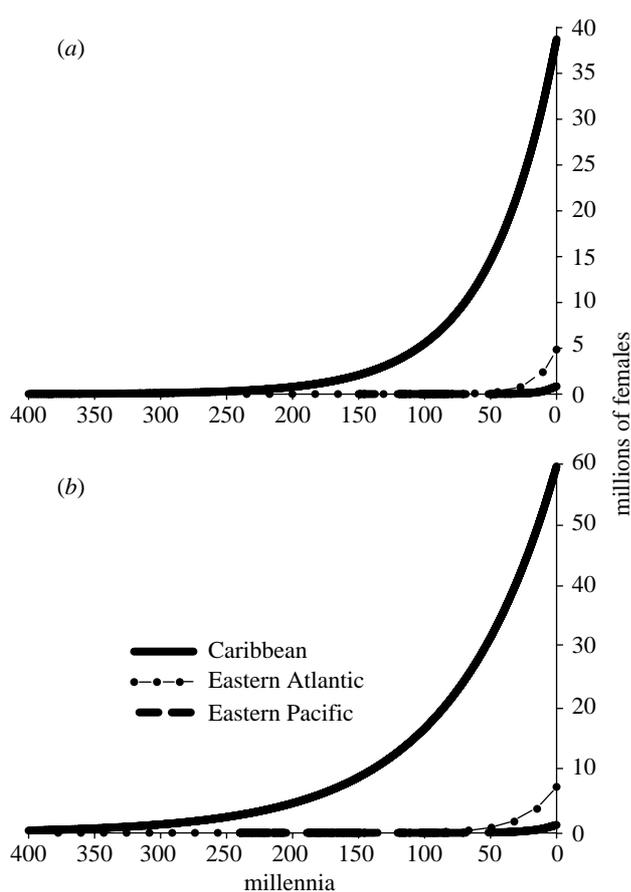


Figure 4. Estimates of effective population size N_e through time in three clades of *Diadema*, based on two possible mutation rates μ and maximum likelihood estimates of growth rate and of $\theta = 2\mu N_e$ (Kuhner *et al.* 1998): (a) $\mu = 1.9 \times 10^{-5}$ substitutions per site per millennium; (b) $\mu = 1.2 \times 10^{-5}$ substitutions per site per millennium.

effect on the present population genetic structure would be to mimic recent restrictions of effective population size. If the 1983 mass mortality has decreased pre-existing mtDNA variability, its effect on the estimates of time to coalescence would be to cause them to appear shorter. Indeed, the only two violations of assumptions that could produce an overestimate of the time since Caribbean *Diadema* expanded its populations are diversifying selection and population subdivision. Within-clade diversifying selection would have registered as a higher proportion of replacement versus silent substitutions within the Caribbean relative to the differences between the Caribbean, on the one hand, and the eastern Pacific or eastern Atlantic on the other. Population subdivision within the Caribbean is absent today. Historical subdivision with subsequent mixing could have increased molecular diversity, but it would have also caused a multimodal mismatch distribution (Marjoram & Donnelly 1994); this is clearly not the case (figure 2). Given the relative magnitudes of molecular diversity, both of these processes would have had to take place in the Caribbean, but not in the eastern Pacific or the eastern Atlantic. Thus, the real time at which *Diadema* became abundant in the Caribbean could well have been earlier than the minimum of 100 000 yr BP we have calculated from its mtDNA variability, but it is very

unlikely to have been more recent. The major expansion documented by the genetic data could not have been caused by reduction of competitors and predators due to human fishing pressure. Though fish reductions may have affected *Diadema* population density, they must have done so to a minor degree, relative to the expansion that has occurred over evolutionary time. When we think of pristine Caribbean reefs before the arrival of humans, we should consider *Diadema* as having been present in high abundance.

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As this paper exceeds the maximum length normally permitted, the authors have agreed to contribute to production costs.