

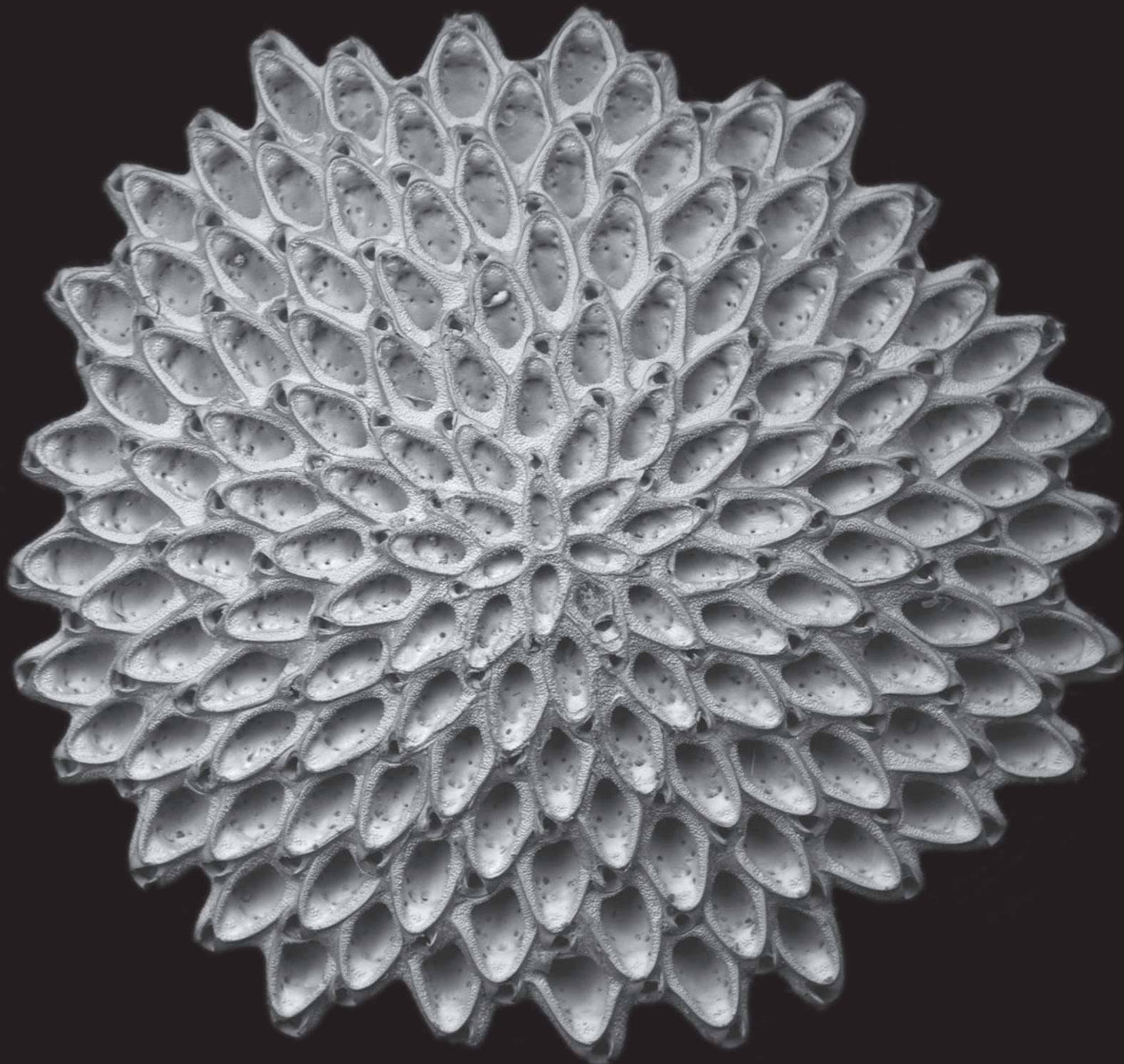
PROCEEDINGS
— OF —
THE ROYAL
SOCIETY **B** **BIOLOGICAL SCIENCES**

ISSN 0962-8452

volume 276

number 1673

pages 3561–3735



Royal Society **Publishing**

*Informing the science
of the future*

22 October 2009

Environmental change drove macroevolution in cupuladriid bryozoans

Aaron O’Dea^{1,2,*} and Jeremy Jackson^{1,3}

¹Center for Tropical Paleocology and Archeology, Smithsonian Tropical Research Institute, Apartado 0843-03092, Panamá, República de Panamá

²Department of Earth and Ocean Sciences, University of British Columbia, Vancouver, British Columbia V6T 1Z4, Canada

³Center for Marine Biodiversity and Conservation, Scripps Institution of Oceanography, University of California, San Diego, La Jolla, CA 92093-0244, USA

Most macroevolutionary events are correlated with changes in the environment, but more rigorous evidence of cause and effect has been elusive. We compiled a 10 Myr record of origination and extinction, changes in mode of reproduction, morphologies and abundances of cupuladriid bryozoan species, spanning the time when primary productivity collapsed in the southwestern Caribbean as the Isthmus of Panama closed. The dominant mode of reproduction shifted dramatically from clonal to asexual, due in part to a pulse of origination followed by extinction that was strongly selective in favour of asexual species. Modern-day studies predict reduced clonality in increasingly oligotrophic conditions, thereby providing a mechanistic explanation supporting the hypothesis that the collapse in primary productivity was the cause of turnover. However, whereas originations were synchronous with changing environments, extinctions lagged 1–2 Myr. Extinct species failed to become more robust and reduce their rate of cloning when the new environmental conditions arose, and subsequently saw progressive reductions in abundance towards their delayed demise. Environmental change is therefore established as the root cause of macroevolutionary turnover despite the lag between origination and extinction.

Keywords: faunal turnover; life-history evolution; extinction; Isthmus of Panama

1. INTRODUCTION

A central question in palaeontology concerns the extent to which the major features of evolution are caused by changes in the environment versus intrinsic biological processes or chance (Simpson 1953; Gould 1985; Barnosky 2001; Jackson & Erwin 2006). Much progress has been made in establishing patterns of correlation between rates of environmental and biological change based on stratigraphically well-dated and independent data on fossils and environments (Knoll *et al.* 1996; Wing *et al.* 2005; Grey *et al.* 2008; Smith & Jackson 2009). However, correlations are only suggestive of mechanism and biological responses to environmental change are commonly nonlinear and disguised by time lags (Jablonski 2002; O’Dea *et al.* 2007). Thus, rigorous attribution of cause and effect requires the *a priori* identification of potential causal mechanisms and the formulation of testable hypotheses based on changes in the frequency of morphological, functional or ecological characteristics of fossils in relation to clear and independently measurable changes in the environment (Jackson & Erwin 2006; Jablonski 2008).

To address these issues we evaluated the role of environmental change for rates of speciation and extinction and the evolution of life-history patterns of cupuladriid bryozoans in the southwestern Caribbean

(SWC) over the past 10 Myr. Cupuladriidae are an abundant and diverse family of cheilostome bryozoans in tropical American seas with an exceptional fossil record (Cook & Chimonides 1983; O’Dea *et al.* 2004), and species can be discriminated effectively by morphological methods, as confirmed by molecular sequence data (Dick *et al.* 2003; Herrera-Cubilla *et al.* 2006, 2008). Cupuladriids grow as small, free-living, disc-shaped colonies 2–30 mm in diameter that occur in densities up to several thousand per square metre in continental shelf environments (McKinney & Jackson 1989). Reproduction occurs by asexual (presumably sexual) reproduction of larvae that settle from the plankton to form new colonies, or by clonal fragmentation or fission of previously established colonies (Winston 1988; Hakansson & Thomsen 2001; O’Dea *et al.* 2008).

Colony morphology and level of calcification influence robustness, and thus the likelihood of colony fragmentation, and hence rates of cloning (O’Dea *et al.* 2004; O’Dea *in press*). Some species have also evolved specialized morphologies that appear to be explicitly designed to either induce cloning, such as colony budding (Marcus & Marcus 1962; Hakansson & Thomsen 2001) and auto-fragmentation (O’Dea 2006; O’Dea *et al.* 2008), or to prevent cloning, such as unusually heavily calcified colonies (O’Dea *et al.* 2008). Because reproductive life history is controlled by hard-part morphology, life-history variation is remarkably well preserved in fossil cupuladriids (McKinney & Jackson 1989), something rarely seen in the fossil record. Incidence and rates of clonal reproduction increase with levels of primary productivity in Recent

* Author for correspondence (odeaa@si.edu).

Electronic supplementary material is available at <http://dx.doi.org/10.1098/rspb.2009.0844> or via <http://rspb.royalsocietypublishing.org>.

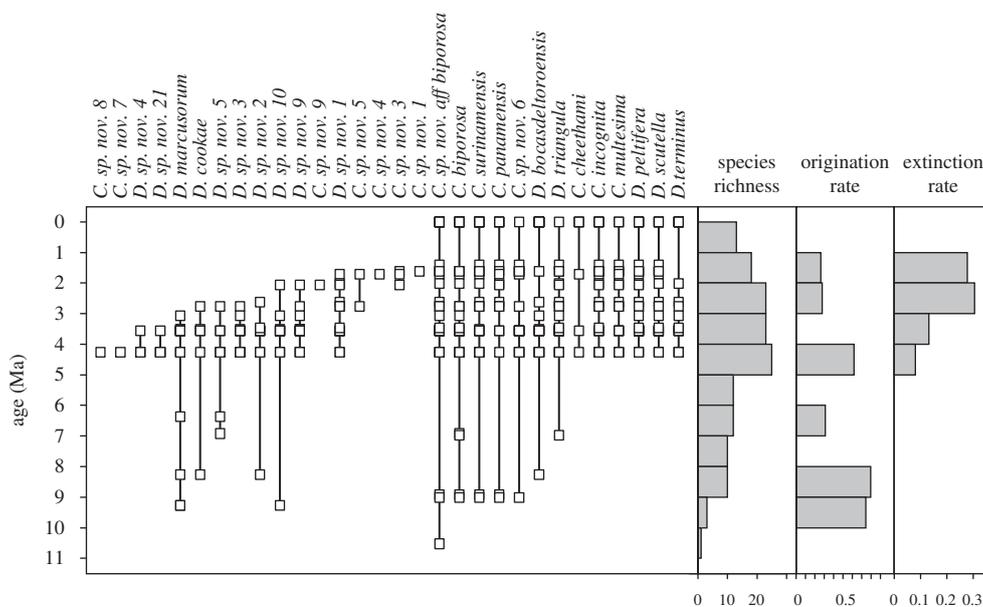


Figure 1. Stratigraphic ranges of cupuladriid species in the southwestern Caribbean ordered by their last then first occurrences with species richness, origination and extinction rates per million years. Open squares indicate actual occurrences in different faunules.

seas (O'Dea *et al.* 2004) because cloning requires rapid colony growth (O'Dea 2006) and abundant food (Winston 1977; Hakansson & Thomsen 2001). Moreover, species with specialized modes of cloning only occur in very productive regions (O'Dea *et al.* 2008) and cloning coincides with peaks in planktonic productivity in seasonal upwelling regimes (O'Dea 2006).

Thus, cupuladriids offer an exceptional window into macroevolutionary patterns of life-history evolution in response to long-term changes in primary productivity. We predict that the reduction in primary productivity in the SWC as the Caribbean became isolated from the tropical eastern Pacific by the emerging Isthmus of Panama (Coates *et al.* 1992; Haug & Tiedemann 1998; O'Dea *et al.* 2004; D'Croz & O'Dea 2007; O'Dea *et al.* 2008) coincided with major shifts in the reproductive life histories of cupuladriids, including reduced clonality, extinctions of specialized modes of cloning and the proliferation of aclonality.

2. MATERIAL AND METHODS

We compiled the occurrences, relative abundances and the proportion of clonal versus aclonal colonies of 30 species of cupuladriid bryozoans in the SWC over the past 10 Myr. Data were derived from more than 148 000 fossil and Recent cupuladriid colonies (see electronic supplementary material).

Recent collections were made with 171 dredge samples at shelf depths along the Caribbean coast of Central America from 1995 to 2006. Samples were washed on deck with a 2 mm mesh and dried for sorting and picking of all cupuladriid colonies in the laboratory. Fossil collections were made with 1317 bulk samples (each approx. 10 kg) from fossiliferous Neogene shelf and shallow slope sediments on the Caribbean slopes of Panama and Costa Rica. Both Recent and fossil samples were grouped in 40 faunules best described as ecological units in time and space that share sedimentary and environmental conditions (Jackson *et al.*

1999; O'Dea *et al.* 2007). Ages of fossil samples are median values of minimum and maximum ages based on microfossils from the sample or interpolated from ages of samples stratigraphically above and below (see electronic supplementary material). Fossiliferous bulk samples were disaggregated by soaking, sieved with a 2 mm mesh, dried, sorted and picked for cupuladriid colonies using the same methods as for the Recent samples.

All well-preserved colonies were classified using skeletal morphological features according to the methods described in Herrera-Cubilla *et al.* (2006, 2008), which are confirmed by molecular sequence data (Dick *et al.* 2003). In total, 148 648 colonies were identifiable to species. Several thousand more colonies were unidentifiable to the level of species due to dissolution, abrasion or their small size. The proportion of unidentifiable colonies tended to increase with increasing age. Of those identifiable, 76 894 colonies could be classified as either clonal or aclonal. Those that preserved an ancestrula derived from a sexually produced larva were classed as aclonal. Colonies that showed any sign of regeneration from a previous fragment (no matter how small), colonial budding or autofragmentation were classed as clonal (O'Dea 2006; O'Dea *et al.* 2008). A small number of colonies had both an ancestrula and evidence of fragmentation and regeneration, and were classed as aclonal. The remaining 71 754 identifiable colonies preserved no evidence of their mode of propagation and were classed as fragments. Identifiable fragments were used to construct age ranges of species, species richness and origination and extinction rates but were not used to address patterns of life history or relative abundance.

Numbers of identifiable clonal and aclonal colonies were used to calculate percentage clonality and percentage relative abundances for each species per faunule. Only species that occurred in two or more faunules were used and only faunules with at least five colonies were used. However, two species (*Discoporella* sp. nov. 9 and *D. sp. nov.* 10) were represented by fewer than five colonies in a faunule for which its

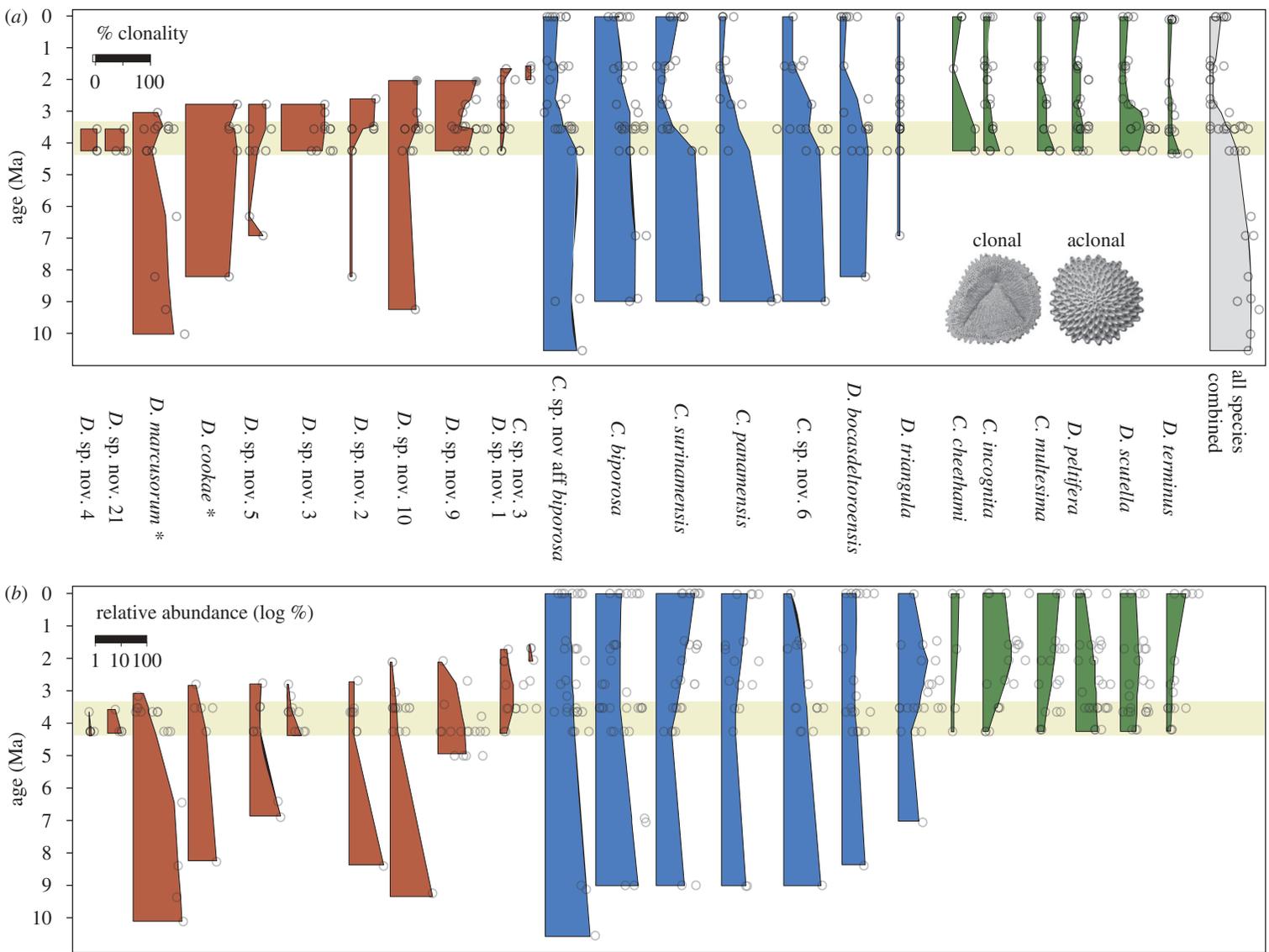


Figure 2. (a) Life histories and (b) relative abundances of 24 common cupuladriid bryozoan species responded dramatically to environmental change (horizontal yellow bar) in the SWC. As planktonic primary productivity collapsed, species that survived significantly reduced their levels of clonality and maintained steady abundances (blue), while newly originated species were all predominantly asexual and showed progressive increases in abundance (green). In contrast, species that failed to reduce levels of clonality showed synchronous reductions in abundance leading up to their final extinction 1–2 Myr after the environment changed (red). Thickness of the vertical range bar for each species represents the percentage of (a) clonal colonies and (b) percentage abundance derived from LOWESS from individual faunules (represented by circles). Data for all species combined (grey) were calculated as the percentage of all clonal colonies irrespective of species. Two closed circles are estimated data. Note that 0 per cent clonality is shifted slightly to the right to give entirely asexual values some thickness, and percentage abundance is log-scaled.

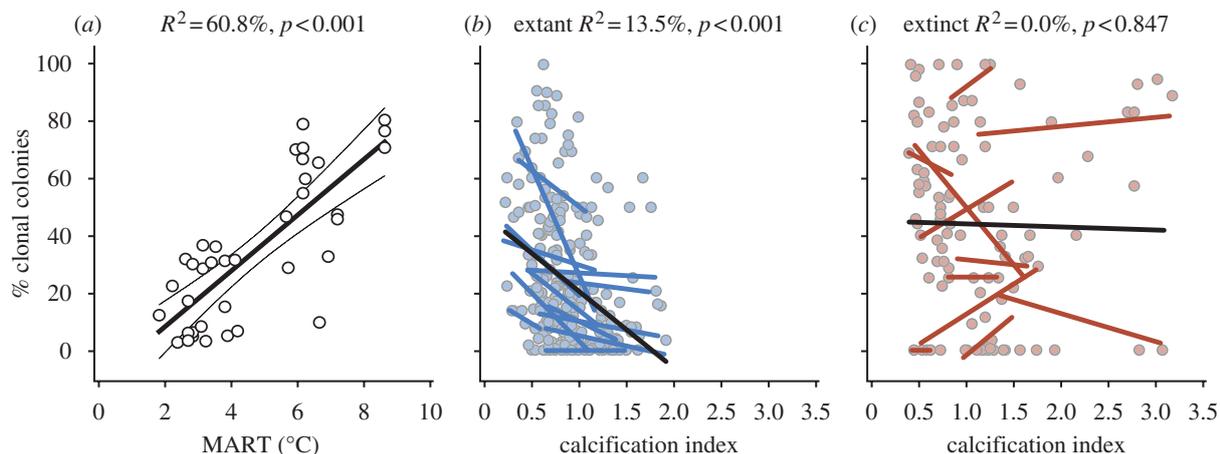


Figure 3. Mechanistic correlates of rates of clonal reproduction. (a) Rates of cloning for entire faunules (all species combined) are positively correlated with mean annual range of temperature (MART). (b,c) Rates of cloning decrease with increased calcification for (b) extant species but not for (c) extinct species. In (b) and (c), dots represent individual species in faunules and heavy black lines the regression of all species in all faunules. Coloured lines represent regressions for individual species.

exclusion would have resulted in a decrease in their stratigraphic range. In these two cases, percentage clonality and percentage relative abundance were estimated from the temporally closest faunules that are marked as filled circles in figure 2. The percentage clonality for the whole assemblage in figures 2 (grey) and 3a was calculated from all colonies irrespective of species or genera. For each species, trends in percentage clonality and percentage relative abundance through time (and the whole assemblage data patterns in % clonality) were constructed using locally weighted regression scatterplot smoothing (LOWESS) smoothing (Minitab).

Robustness of cupuladriid colonies was measured using the Calcification Index (Ci), calculated by measuring the height, diameter and weight of a maximum of 100 colonies of each species in each faunule following the methods described in O’Dea *et al.* (2004).

Majority of environmental change in the SWC was estimated to have occurred between 4.25 and 3.45 Ma based upon several lines of evidence, including (i) the timing of Isthmus closure (Coates *et al.* 1992, 2004; Coates & Obando 1996), (ii) the inferred end of Pacific seasonal upwelling, increase in carbonate-dominated habitats, and a shift to a coral-dominated benthos (O’Dea *et al.* 2007), and (iii) oceanographic shifts estimated from deep-sea cores (Haug & Tiedemann 1998).

3. RESULTS

Species richness increased to a maximum of 25 species in the Early Pliocene around 5–4 Ma and remained high until around 2 Ma (figure 1). High rates of origination around 10–8 Ma are an artefact of the beginning of the record in the region. Otherwise, rates of origination peaked around 5–4 Ma, an interval encompassing the onset of major environmental change around 4.25 Ma as the Isthmus closed (O’Dea *et al.* 2007). In contrast, extinction was nil from 10 to 5 Ma and low from 5 to 3 Ma, but peaked from 3 to 1 Ma.

The proportion of colonies derived from clonal reproduction for all species combined declined significantly from a median of 70 per cent between 10 and 4.25 Ma to just 11 per cent over the last 3.45 Myr (figure 2a, grey; Mann–Whitney *U*-test, $U=404$, $p < 0.001$).

Among extant species only, those species that originated before 4.25 Ma (figure 2, blue) had higher rates of clonality (median = 39%) compared with those that originated more recently (figure 2a, green; median = 11%; Mann–Whitney *U*-test, $U=64.0$, $p < 0.05$). Moreover, rates of clonal reproduction for the six oldest extant species were higher before 4.25 Ma than after 3.25 Ma (two-way ANOVA, $F = 107$, d.f. = 1, $p < 0.001$). In contrast, none of the 11 species that went extinct showed a decrease in clonal reproduction (figure 2a, red). Thus, the overall trend in reduced clonal reproduction resulted from a combination of increased origination of predominantly aclonal species, increased extinction of species that maintained consistently high rates of clonal reproduction and strong reduction in the incidence of clonality among surviving species.

Patterns of relative abundance in species were also significantly related to their final evolutionary outcome (figure 2b). Nine out of the ten extinct species declined in abundance during the environmental transition from 4.25 to 3.45 Ma (figure 2b, red), whereas only four of thirteen extant species (figure 2b, blue and green) declined with the remainder holding steady or increasing ($p < 0.01$; Fisher’s exact test of independence).

4. DISCUSSION

The striking decrease in clonal reproduction coincided with the decline in upwelling as the Isthmus of Panama closed (figure 3a; O’Dea *et al.* 2007). This strongly supports the hypothesis that origination, extinction and decreases in clonal reproduction were all the result of decreased planktonic productivity as expected from predictions of how growth and reproduction responds to increasing oligotrophy based upon modern-day studies and models (Winston 1977; Hakansson & Thomsen 2001; O’Dea *et al.* 2004; O’Dea 2006). Three additional lines of morphological evidence support the hypothesis that collapse in productivity was the causal mechanism. First, the shift from predominantly clonal to predominantly aclonal reproduction was associated with the production of more robust colonies across all extant species (figure 3b) but not extinct species (figure 3c). Second, two of the species

that disappeared from the SWC are common today in the tropical eastern Pacific where food levels remain high, and both species sustain high levels of clonal reproduction (O'Dea *et al.* 2004). Third, the only two species in the SWC that possessed specialized methods for cloning (colony budding and peripheral fragmentation) both became extinct (asterisked in figure 2).

Data therefore present a robust mechanism of cause and effect. The question remains as to why extinction lagged for as long as 1–2 Myr beyond the decline in productivity—a pattern also observed for reef corals and gastropods (Budd & Johnson 1999; Todd *et al.* 2002; O'Dea *et al.* 2007). Significant differences in the patterns of abundances between those species that went extinct and those that survived provide an important clue. Extant species maintained or increased their relative abundances during the environmental transition from 4.25 to 3.45 Ma, while most extinct species declined dramatically at this time (figure 2*b*). It appears, therefore, that species that failed to adjust their reproductive life histories and morphologies (as extant species did) to the new environmental conditions suffered immediately despite then lingering on for a further 1–2 Myr. Progressive decline in population in response to stress, leading to eventual extinction, is consistent with metapopulation models (Levins 1969; Gaggiotti & Hanski 2004), and presents one explanation for the observation that survivorship during times of extinction does not necessarily secure subsequent evolutionary success (Jablonski 2002).

Felix Rodriguez, Brigida DeGracia and Yadixa DelValle identified, counted and measured most of the cupuladriids. Anthony Coates, Helena Fortunato, Amalia Herrera and many more helped collect, process and analyse material. Egbert Leigh, Beth Okamura, Walton Green and Katie Cramer made useful comments to the manuscript. The Panamanian Recursos Minerales kindly gave permission to collect material. Funding was provided by the National Science Foundation (EAR03-45471), the Smithsonian Marine Science Network, the Smithsonian Tropical Research Institutes' Tupper Fellowship and Scholarly Studies programmes, SENACYT and the National Geographic Society Exploration Grants.

REFERENCES

- Barnosky, A. D. 2001 Distinguishing the effects of the Red Queen and Court Jester on Miocene mammal evolution in the northern Rocky Mountains. *J. Vertebr. Paleontol.* **21**, 172–185. (doi:10.1671/0272-4634(2001)021[0172:DTEOTR]2.0.CO;2)
- Budd, A. F. & Johnson, K. G. 1999 Origination preceding extinction during late Cenozoic turnover of Caribbean reefs. *Paleobiology* **25**, 188–200.
- Coates, A. G. & Obando, J. A. 1996 The geologic evolution of the Central American Isthmus. In *Evolution and environment in tropical America* (eds J. Jackson, B. C. A. Budd & F. A. G. Coates), pp. 21–56. Chicago, IL: The University of Chicago Press.
- Coates, A. G., Jackson, J. B. C., Collins, L. S., Cronin, T. M., Dowsett, H. J., Bybell, L. M., Jung, P. & Obando, J. A. 1992 Closure of the Isthmus of Panama—the near-shore marine record of Costa Rica and western Panama. *Geol. Soc. Am. Bull.* **104**, 814–828. (doi:10.1130/0016-7606(1992)104<0814:COTIOP>2.3.CO;2)
- Coates, A. G., Collins, L. S., Aubry, M. P. & Berggren, W. A. 2004 The geology of the Darien, Panama, and the late Miocene–Pliocene collision of the Panama arc with north-western South America. *Geol. Soc. Am. Bull.* **116**, 1327–1344. (doi:10.1130/B25275.1)
- Cook, P. L. & Chimonides, P. J. 1983 A short history of the Lunulite Bryozoa. *Bull. Mar. Sci.* **33**, 566–581.
- D'Croz, L. & O'Dea, A. 2007 Variability in upwelling along the Pacific shelf of Panama and implications for the distribution of nutrients and chlorophyll. *Estuar. Coast. Shelf Sci.* **73**, 325–340. (doi:10.1016/j.ecss.2007.01.013)
- Dick, M. H., Herrera-Cubilla, A. & Jackson, J. B. C. 2003 Molecular phylogeny and phylogeography of free-living Bryozoa (Cupuladriidae) from both sides of the Isthmus of Panama. *Mol. Phylogenet. Evol.* **27**, 355–371. (doi:10.1016/S1055-7903(03)00025-3)
- Gaggiotti, O. E. & Hanski, I. 2004 Mechanisms of population extinction. In *Ecology, genetics, and evolution of metapopulations* (eds I. Hanski & O. E. Gaggiotti), pp. 337–366. San Diego, CA: Academic Press.
- Gould, S. J. 1985 The paradox of the 1st tier—an agenda for paleobiology. *Paleobiology* **11**, 2–12.
- Grey, M., Haggart, J. W. & Smith, P. L. 2008 Variation in evolutionary patterns across the geographic range of a fossil bivalve. *Science* **322**, 1238–1241. (doi:10.1126/science.1162046)
- Hakansson, E. & Thomsen, E. 2001 Asexual propagation in cheilostome Bryozoa: evolutionary trends in a major group of colonial animals. In *Evolutionary patterns: growth, form and tempo in the fossil record* (eds J. B. C. Jackson, S. Lidgard & F. K. McKinney), pp. 326–347. Chicago, IL: University of Chicago Press.
- Haug, G. H. & Tiedemann, R. 1998 Effect of the formation of the Isthmus of Panama on Atlantic Ocean thermohaline circulation. *Nature* **393**, 673–676. (doi:10.1038/31447)
- Herrera-Cubilla, A., Dick, M. H., Sanner, J. & Jackson, J. B. C. 2006 Neogene Cupuladriidae of tropical America. I: Taxonomy of recent *Cupuladria* from opposite sides of the Isthmus of Panama. *J. Paleontol.* **80**, 245–263. (doi:10.1666/0022-3360(2006)080[0245:NCOTAI]2.0.CO;2)
- Herrera-Cubilla, A., Dick, M. H., Sanner, J. & Jackson, J. B. C. 2008 Neogene Cupuladriidae of tropical America. II: Taxonomy of recent *Discoporella* from opposite sides of the Isthmus of Panama. *J. Paleontol.* **82**, 279–298. (doi:10.1666/06-034.1)
- Jablonski, D. 2002 Survival without recovery after mass extinctions. *Proc. Natl Acad. Sci. USA* **99**, 8139–8144. (doi:10.1073/pnas.102163299)
- Jablonski, D. 2008 Extinction and the spatial dynamics of biodiversity. *Proc. Natl Acad. Sci. USA* **105**, 11 528–11 535. (doi:10.1073/pnas.0801919105)
- Jackson, J. B. C. & Erwin, D. H. 2006 What can we learn about ecology and evolution from the fossil record? *Trends Ecol. Evol.* **21**, 322–328. (doi:10.1016/j.tree.2006.03.017)
- Jackson, J. B. C., Todd, J. A., Fortunato, H. & Jung, P. 1999 Diversity and assemblages of Neogene Caribbean Mollusca of lower Central America. In *A paleobiotic survey of Caribbean faunas from the Neogene of the Isthmus of Panama*, vol. 357 (eds L. S. Collins & A. G. Coates), pp. 193–230. Lawrence, KS: Allen Press.
- Knoll, A. H., Bambach, R. K., Canfield, D. E. & Grotzinger, J. P. 1996 Comparative earth history and Late Permian mass extinction. *Science* **273**, 452–457. (doi:10.1126/science.273.5274.452)
- Levins, R. 1969 Some demographic and genetic consequences of environmental heterogeneity for biological control. *Bull. Entomol. Soc. Am.* **15**, 237–240.
- Marcus, E. & Marcus, E. 1962 On some lunulitiform Bryozoa. *Universidade de São Paulo Boletins da Faculdade de Filosofia, Ciências e Letras, Zoologia* **3**, 111–353.

- McKinney, F. K. & Jackson, J. B. C. 1989 *Bryozoan evolution*. Special Topics in Palaeontology. Boston, MA: Unwin Hyman.
- O'Dea, A. 2006 Asexual propagation in the marine bryozoan *Cupuladria exfragminis*. *J. Exp. Mar. Biol. Ecol.* **335**, 312–322. (doi:10.1016/j.jembe.2006.04.002)
- O'Dea, A. In press. Relation of form to life habit in free-living cupuladriid bryozoans. *Aquat. Biol.*
- O'Dea, A., Herrera-Cubilla, A., Fortunato, H. & Jackson, J. B. C. 2004 Life history variation in cupuladriid bryozoans from either side of the Isthmus of Panama. *Mar. Ecol. Progr. Ser.* **280**, 145–161. (doi:10.3354/meps280145)
- O'Dea, A., Jackson, J. B. C., Fortunato, H., Smith, J. T., D'Croz, L., Johnson, K. G. & Todd, J. A. 2007 Environmental change preceded Caribbean extinction by 2 million years. *Proc. Natl Acad. Sci. USA* **104**, 5501–5506. (doi:10.1073/pnas.0610947104)
- O'Dea, A., Jackson, J. B. C., Taylor, P. D. & Rodriguez, F. 2008 Modes of reproduction in recent and fossil cupuladriid bryozoans. *Palaeontology* **51**, 847–864. (doi:10.1111/j.1475-4983.2008.00790.x)
- Simpson, G. G. 1953 *The major features of evolution*. Columbia Biological Series. New York, NY: Columbia University Press.
- Smith, J. T. & Jackson, J. B. C. 2009 Ecology of extreme faunal turnover of tropical American scallops. *Paleobiology* **35**, 77–93. (doi:10.1666/07054.1)
- Todd, J. A., Jackson, J. B. C., Johnson, K. G., Fortunato, H. M., Heitz, A., Alvarez, M. & Jung, P. 2002 The ecology of extinction: molluscan feeding and faunal turnover in the Caribbean Neogene. *Proc. R. Soc. Lond. B* **269**, 571–577. (doi:10.1098/rspb.2001.1923)
- Wing, S. L., Harrington, G. J., Smith, F. A., Bloch, J. I., Boyer, D. M. & Freeman, K. H. 2005 Transient floral change and rapid global warming at the Paleocene-Eocene boundary. *Science* **310**, 993–996. (doi:10.1126/science.1116913)
- Winston, J. E. 1977 Feeding in marine bryozoans. In *Biology of bryozoans* (eds R. M. Woollacott & R. L. Zimmer), pp. 233–271. New York, NY: Academic Press.
- Winston, J. E. 1988 Life histories of free-living bryozoans. *Natl Geogr. Res.* **4**, 528–539.