

Morphological response of planktic foraminifers to habitat modifications associated with the emergence of the Isthmus of Panama



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ABSTRACT

The impact of global change on marine ecosystems is a major concern for the future. Examples from the geological past may provide insight into how ecosystems respond to major shifts in environment. Here we use the progressive closure of the Central American Seaway over the last 10 Myrs, and the resulting new environmental conditions and niches on either side of the Panama Isthmus, as a time series documenting the reaction of planktic foraminifers to environmental change and vicariance. Our main finding is that the size and shape evolution of both investigated species is strongly influenced by temperature, despite their different ecology. The surface dweller *Trilobatus sacculifer* conserved the same shape on both sides of the Isthmus for most of the studied interval, and diverged only recently when the environment diverged on both sides of the Isthmus. The shape response is a combination of a change in mean shape and in percentage of morphotypes occurring within *T. sacculifer*. This suggests a minor role of vicariance and the potential to react to changes in the local environment through ecotypic or plastic variation. This interpretation is corroborated by extensive phenotypic variability in the absence of genetic differentiation today in this species. The shape of the deeper-living species *Gt. tumida*, in contrast, diverged on both sides of the Isthmus at a time that coincides with the cut-off of the connection of its habitat. This divergence combines a response to temperature and to location, suggesting local adaptation in response to vicariance. These different reactions highlight both a high potential for adaptation, but also sensitivity to temperature variations. The species-specific responses to environmental pressures indicate the difficulty in upscaling from one species to foraminifers in general.

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1. Introduction

The impacts of current global change have become a major issue in research fields as diverse as palaeoceanography, ecology, evolution and epidemiology (Dam, 2013; IPCC, 2014; Sanford and Kelly, 2011). Environmental conditions within this century are predicted to be outside of the ranges experienced by a large number of species in their evolutionary history (Pörtner et al., 2014; Ridgwell and Schmidt, 2010) posing a significant threat. The majority of studies have focused on the effects on terrestrial ecosystems (Austin and Rehfsch, 2005; Scholes et al., 2014); identifying coherent responses to global change in the marine environment has proven to be challenging (Poloczanska et al., 2013; Reusch, 2014). Marine plankton can be affected by drivers such

as warming either directly via metabolic rates or indirectly via increases in surface water stratification, limiting nutrient input (Pörtner et al., 2014). Seminal time series studies have documented distribution changes (e.g., Chavez et al., 2003; Edwards et al., 2004; Poloczanska et al., 2013), mismatches in phenologies across the components of the ecosystem (Beaugrand and Reid, 2003) and increased competition leading to a decline of specialist species (Clavel et al., 2010). However few studies assess the potential for evolutionary adaptation in response to climate change in marine species (Dam, 2013; Lohbeck et al., 2012), possibly because the marine ecosystem is often considered to be one of few barriers with limited opportunity for local adaptations (Norris, 2000). Vast population sizes and high dispersal potential in marine plankton are often suggested to limit spatial population structuring. Despite the postulated scarcity of barriers in the ocean, examples of geographic isolation (Casteleyn et al., 2010) and adaptation to local climate exist (Helmuth et al., 2006; Sanford and Kelly, 2011).

The emergence of the Panama Isthmus is an exemplary case of ecosystem reorganisation (Fig. 1). Classically, the focus has been put on the effect of the emerging physical barriers on marine organisms as a potential trigger to speciation (Chaisson, 2003; Knowlton et al., 1993; Miura

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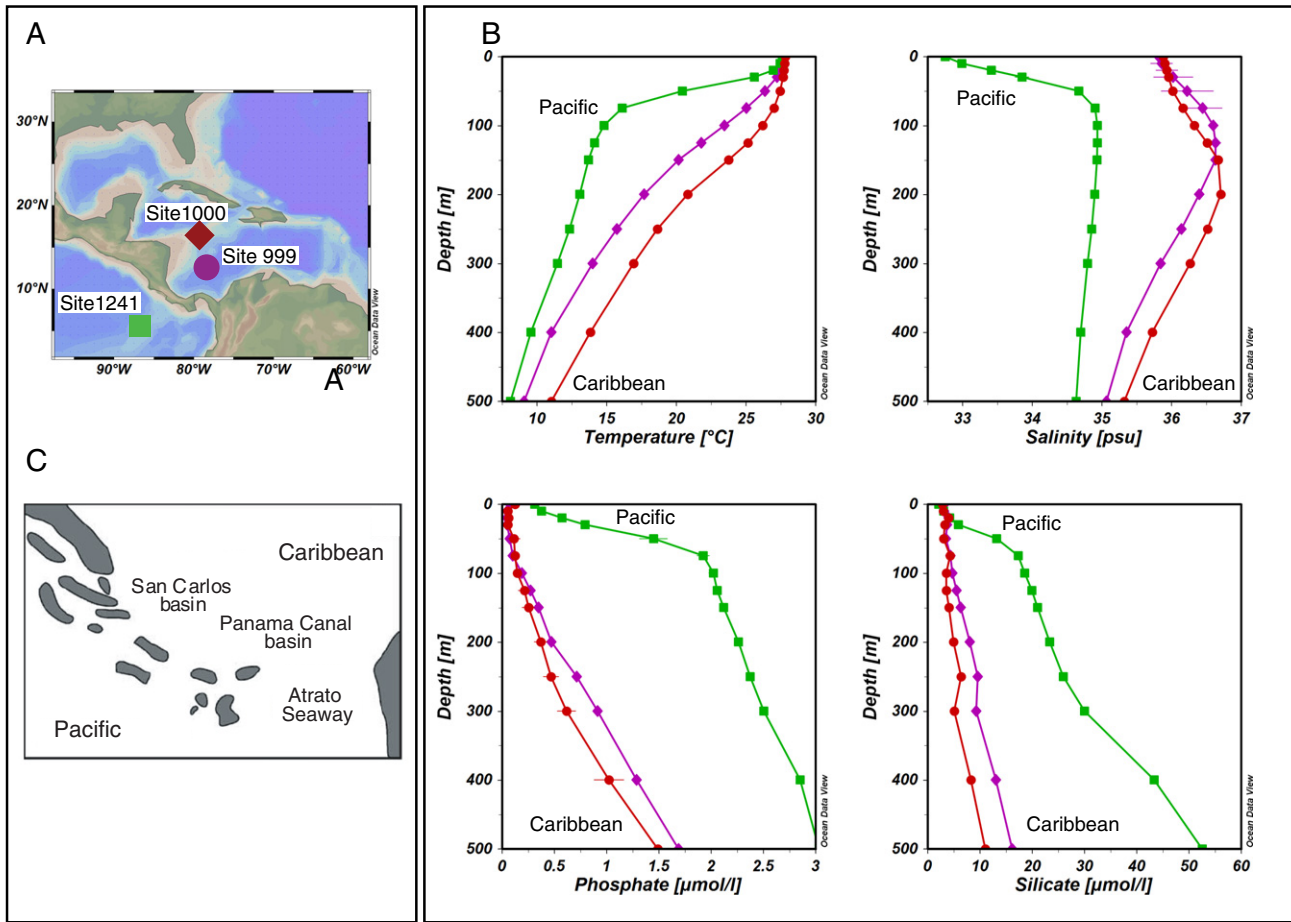


Fig. 1. Overview of the core locations and their environmental conditions. (A) core locations and (B) environmental characteristics: temperature, salinity, phosphate and silicate. Note the strong modern differences in water column structure and nutrient distribution between the two regions. Green circles – Pacific Site 1241, Red squares – Caribbean Site 1000, purple diamond – Caribbean Site 999; same colour coding is used through the figures. The map was generated with Ocean Data View (Schlitzer, 2006). The environmental data is from World Ocean Atlas (Garcia et al., 2006).

et al., 2011). However, the closure of the Central American Seaway also led to a reorganisation of ocean circulation that significantly changed the physico-chemical conditions on both sides of the Isthmus (Haug and Tiedemann, 1998; Haug et al., 2001; Keigwin, 1982; Schmidt, 2007). The exchange between Pacific and northwest Atlantic waters gradually declined between 8 and 5 Ma (Frank et al., 1999), resulting in a shoaling of the Central American Seaway to <100 m by 4.7 Ma and restricting surface water exchange (Haug et al., 2001). By 4.2 Ma, the seaway was generally closed, though Pacific waters episodically breached into the Caribbean across a still-submerged sill or by short-lasting re-openings (Haug et al., 2001). The closure created a habitat separation, both, physically through the Isthmus but also via a separation of the physio-chemical environment (Fig. 1c). Today, surface water temperatures are not much different in both environments (Fig. 1b), but the Caribbean has a much larger mixed layer thickness and higher salinity than the Pacific. The surface waters of the eastern equatorial Pacific are influenced by upwelling of nutrient and CO_2 -rich waters, leading to a shallow nutri- and thermocline and a lower pH (Fig. 1b) (Schmidt, 2007; Zhang et al., 2012).

Planktic foraminifers have an excellent fossil record, which allows us to assess the impact of environmental change and habitat separation. Their morphology has been shown on a geographical scale to reflect environmental preferences (Schmidt et al., 2004a) and genetic diversity (André et al., 2014; e.g., Darling and Wade, 2008; e.g., de Vargas et al., 2001), and temporally to reflect environmental changes (e.g., Malmgren et al., 1983; Norris et al., 1994; Renaud and Schmidt, 2003) and evolution (Malmgren and Kennett, 1981; Norris et al., 1996). We

focused on two morphospecies with contrasting ecologies: the deep-dwelling lineage *Globorotalia plesiotumida-tumida*, and the shallow-dwelling *Trilobatus sacculifer*. The deep-dweller should have been affected prior to the surface dweller by the progressive closure of the seaway, as the habitat separation at depth would be expected to predate the surface water separation.

There are a number of competing hypotheses about the response of planktic foraminifers to the physical separation and alteration of their environments: (1) No divergence may occur, because of world-wide gene flow. (2) Divergence could occur due to the physical separation of populations via the simple break down of gene flow, known as vicariance (Guarnizo et al., 2009). (3) The divergence of the environment itself could select for different adaptation. Here we construct long-term records of planktic foraminifer size and shape and sea surface temperature from either side of the Isthmus to test these hypotheses.

2. Materials and methods

2.1. Background on the investigated species

Trilobatus sacculifer (Brady, 1877, Fig. 2 top) is widespread in subtropical and tropical waters (Bé and Tolderlund, 1971). Its stratigraphic range extends from the early Miocene to the present day (Kennett and Srinivasan, 1983). The species' photosynthetic symbionts (Bé et al., 1982) restrict its habitat to the photic zone with a maximum habitat depth at the base of the mixed layer (Bé, 1965; Hecht and Savin, 1972). Its final chamber may take on different shapes: typically it is

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