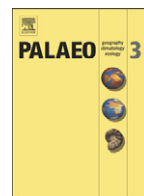




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History of upwelling in the Tropical Eastern Pacific and the paleogeography of the Isthmus of Panama

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ABSTRACT

Today there is a tight-knit relationship between the elevation of the Central American Isthmus and the oceanographic conditions of the Tropical Eastern Pacific. Where the elevation drops below 500 m low-level wind jets pass seasonally from the Atlantic to the Pacific driving coastal upwelling in the Tropical Eastern Pacific. This paper determines if seasonal upwelling was present in five Pliocene and Pleistocene fossiliferous sites on the Pacific coast of the Burica region of the Isthmus of Panama using two independent approaches that compare bryozoan morphology and whole community composition of fossiliferous localities with material from upwelling and non-upwelling modern localities. No definitive evidence of seasonal upwelling exists in the Pliocene, implying non-analogous oceanographic conditions because of continued interoceanic connection prior to the closure of the Isthmus of Panama. Conversely, data from three mid-Pleistocene sites reveal robust evidence of strong seasonal upwelling suggesting that the elevation of the Isthmus must have been sufficiently low to permit wind-jets to form. A low-elevation Isthmus of Panama may have persisted until as recently as the mid-Pleistocene.

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1. Introduction

The formation of the Isthmus of Panama stands as a model in paleoceanographic and evolutionary studies (Coates and Obando, 1996; Jackson and Budd, 1996; Haug and Tiedemann, 1998; Lessios, 2008) yet there remain many uncertainties regarding the paleoclimate, paleogeography and the timing and rates of uplift of the Isthmus during its formation (Schmidt, 2007; Farris et al., 2011; Montes et al., 2012). Today, the topography of the Central American Isthmus strongly dictates the marine oceanic environments of the Tropical Eastern Pacific (TEP). Trade winds pass from the Caribbean over Central America on a seasonal basis, and where elevation is low, sea-level wind-jets form that drive strong coastal upwelling in certain regions along the Pacific coast (D'Croz and O'Dea, 2007). This seasonal upwelling is one of the most important drivers of large-scale ecological and biogeographical patterns in the TEP, yet the history of upwelling along the Pacific coast of the Isthmus during the Late Neogene remains little studied. This paper first explores the relationship between Isthmus elevation and upwelling today using topographic and satellite-derived oceanographic data. The presence or absence of upwelling is then determined for coastal seas of the Burica peninsula on the Pacific coast of the Isthmus of Panama during the Pliocene and Pleistocene using two independent paleoenvironmental approaches. Finally, the results are used to

speculate on the elevation of the Isthmus of Panama during the last 5 million years.

2. Sequence of events

The collision of Central America with the South American continent and the subsequent uplift of the Isthmus of Panama resulted in the unification of two continents and the severance of two great oceans. Terrestrial fauna and flora of each continent merged fully for the first time since the entire break up of Gondwana in the Cretaceous in what is dubbed the Great American Biotic Interchange (Marshall, 1988; Webb, 2006) with winners and losers shaping the modern day terrestrial communities of both continents. The marine history of the region is no less dynamic. The Central American Seaway (CAS) first opened in the Early Jurassic when the continents of South and North America parted (Smith and Tipper, 1986), forming the western opening of the pan-tropical Tethys Ocean, and throughout the latter half of the Mesozoic and almost the entire Cenozoic providing a crucial gateway for the movement of equatorial water (and therefore marine organisms) between the Pacific and the Atlantic oceans. Consequently, when the Isthmus severed the marine connection in the Neogene, oceanic circulation on a global scale was fundamentally altered with equally global effects. These included major shifts in the salinity patterns of equatorial waters (Haug et al., 2001), radical changes in latitudinal heat transport in the Atlantic, the initiation and intensification of northern hemisphere glaciation (Haug and Tiedemann, 1998) (but see subsequent interrogation of this theory by Klocker et al. (2005))

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and the desertification of Africa which may have been decisive in hominid evolution (Stanley, 1998).

Isolated populations of marine animals and plants began to follow discrete evolutionary trajectories in the newly split Tropical Western Atlantic (TWA) and the TEP (Knowlton and Weigt, 1998; Lessios, 2008) and the hydrological conditions of both began to shift dramatically (Keigwin, 1978, 1982; Ibaraki, 1997; Fiedler and Talley, 2006). Upwelling declined and primary productivity collapsed (Allmon, 2001; Todd et al., 2002; Jain and Collins, 2007; O'Dea et al., 2007a) driving widespread extinction across the TWA (Allmon, 1992; Budd et al., 1996; Jackson and D'Croz, 1999; Jackson et al., 1999; Jackson and Johnson, 2000; Todd et al., 2002; O'Dea et al., 2007a; Johnson et al., 2008; O'Dea and Jackson, 2009; Smith and Jackson, 2009).

On land, a few small-bodied animals had managed to traverse from continent to continent in the Late Miocene as observed in the fossil (Webb, 1985) and molecular (e.g. Pinto-Sanchez et al., 2012) records via rafting helped by the formation of an ephemeral near-complete land bridge around 10 Ma (Roth et al., 2000; Coates et al., 2003; Coates et al., 2004). Likewise, the effects of deeper water shut-off occurred long before those of shallow water as observed in the timings of separation of different organisms with different life histories (O'Dea et al., 2007a; Landau et al., 2009; Smith and Jackson, 2009) and the earlier molecular divergences of deep-water vs. shallow-water organisms (Knowlton and Weigt, 1998; Naro-Maciel et al., 2008). Terrestrial evidence points to a 'final' closure date of ~2.8 Ma when an exodus of larger bodied organisms took place longitudinally, whereas most maritime evidence places final closure slightly earlier at ~3.5–3 Ma (reviewed by Schmidt, 2007), a discrepancy nevertheless expected given that an effective oceanic barrier would have appeared before the formation of an intact land bridge that would have permitted the large-scale emigration of large mammals and flightless birds into their respective new habitats.

Although a Late Pliocene date for final closure is now well constrained and strongly supported by several lines of independent evidence, the form, elevation and degree of subaerial emergence of the southern tip of Central America after it collided with South America approximately 24 Ma (Farris et al., 2011) remains unresolved (Kirby and MacFadden, 2005; Retallack and Kirby, 2007; Schmidt, 2007; Molnar, 2008). Uplift rates based on paleobathymetries of marine sediments from across the Isthmus suggest that the majority of the volcanic arc was submerged up until very recently with bathyal sediments of latest Miocene age present in the Caribbean and Pacific of western Panama, the Caribbean of central Panama and eastern Panama (Coates et al., 1992; Collins, 1992, 1993, 1996; Coates, 1999; Coates et al., 2000, 2003, 2004, 2005). Strong similarities between Pacific and Caribbean Mio-Pliocene biota (Chaisson and Ravelo, 2000; O'Dea et al., 2007b) and near-identical environmental conditions on either side of the Isthmus (Keigwin, 1978, 1982; Keller et al., 1989; Haug and Tiedemann, 1998; Haug et al., 2001) in the Early Pliocene imply the CAS was maintained in some form until the mid-Pliocene. Nevertheless, well-studied and extensive lacustrine sediments, shallow water reefs and mangroves, plus a continental-like mammal fauna in the Canal Zone of Panama demonstrate the presence of substantial subaerial land(s) in the middle Miocene (Whitmore and Stewart, 1965; Kirby and MacFadden, 2005; Johnson and Kirby, 2006; Retallack and Kirby, 2007; Kirby et al., 2008). Accordingly, Coates and Obando (1996) proposed a semi-submerged archipelago of islands from the Miocene up to final closure. Subsequently however, Kirby and MacFadden (2005) demonstrated that mammals in Panama in the middle Miocene were no smaller than coeval conspecifics from mainland North America, thus strongly implying free gene flow amongst them. As such, rather than an archipelago the proto-Isthmus must have been an entirely subaerial peninsula unconnected to south America until final closure, a conclusion supported by geological evidence (Montes et al., 2012). However, the mammal size-peninsula evidence is only pertinent to the middle Miocene, from when there exists questionable evidence of

high mountainous regions in central Panama (Retallack and Kirby, 2007) and the paleogeography of the Isthmus in the critical times of the Late Miocene and Pliocene remains to be defined.

3. Present day Isthmus elevation and oceanographic conditions in the Pacific

Modern marine conditions along the Pacific coast of Central America are typically dominated by strongly-layered bodies of water capped by the eastern Pacific warm pool with sea surface temperatures (SST) of 27 °C or more (Fiedler and Talley, 2006). This structured water column breaks down during the boreal winter by the action of high-pressure systems in the TWA and the Gulf of Mexico that induce strong wind-jets that pass over the cordillera of Central America (aka trade-winds). Where the isthmus is sufficiently low, these wind jets are sufficiently intense and remain at low enough altitudes to push surface waters in the TEP away from the coast of Central America. Deeper, nutrient rich and cool waters are then upwelled to replace this expelled surface water. This process of wind-jet driven seasonal upwelling occurs in three regions: The Gulf of Tehuantepec in Mexico, the Gulf of Papagayo, Nicaragua and the Gulf of Panama, central Panama (Legeckis, 1988; McCreary et al., 1989; Xie et al., 2005; D'Croz and O'Dea, 2007, 2009), and each are adjacent to areas to the North or Northeast where the land drops to around 500 m (Figs. 1,2).

Upwelling is seasonal because wind-jets only form when the Inter-tropical Convergence Zone (ITCZ) lies to the south of the region in question. Upwelling is therefore governed by the north–south migration of the ITCZ and is consequently predictable. Another consequence is that the duration of upwelling becomes progressively shorter as one travels south. In the most northerly Gulf of Tehuantepec winds and upwelling persist for over eight months whilst at the most southerly range in the Gulf of Panama, the phenomenon lasts just three months (Legeckis, 1988; McCreary et al., 1989; Xie et al., 2005; D'Croz and O'Dea, 2007, 2009). Despite being ephemeral, upwelling in all regions is usually very intense, supporting large-scale commercially-valuable fisheries (Jackson and D'Croz, 1997, D'Croz and O'Dea, 2007).

Direct oceanographic measurements and long-term satellite data reveal that wind-jet induced upwelling results in rapid and extreme reductions in SST and increases in the abundance of photosynthetic plankton that then form the basis of highly productive ecosystems (D'Croz and O'Dea, 2009) (Fig. 2). In the Gulf of Panama upwelling tends to occur from January to March and involves the breaching of the thermocline resulting in a dramatic cooling of surface waters and an increase in levels of dissolved inorganic nutrients (NO_3 , PO_4 , and $\text{Si}(\text{OH})_4$) due to the emergence of deeper waters towards the surface (D'Croz and O'Dea, 2007).

4. Geological setting

Today western Panama and eastern Costa Rica is one of the most mountainous regions in Central America with peaks rising over 3000 m that are sufficient to prevent the formation of wind-jet induced upwelling (Figs. 1,2). They formed because of the regions complex tectonic geometry; the Cocos and Nazca plates subduct under the Panama microplate and are themselves separated by the Panama Fracture Zone (Farris et al., 2011). The Cocos ridge sits between them and being highly buoyant fails to subduct under the Panama microplate, which is hence uplifted (Corrigan et al., 1990; Sitchler et al., 2007). Collision of the Cocos ridge against the Panama microplate may have been a geologically recent event (Collins et al., 1995) given the rapid uplift rates of the Burica Peninsula estimated over the Late Pleistocene ($1\text{--}8\text{ m ka}^{-1}$) (Leon-Rodriguez, 2007) and Holocene ($2\text{--}3\text{ m ka}^{-1}$) (Davidson, 2010) derived from sea-level corrected ages of exposed marine sediments and radiocarbon dated wave cut platforms respectively.

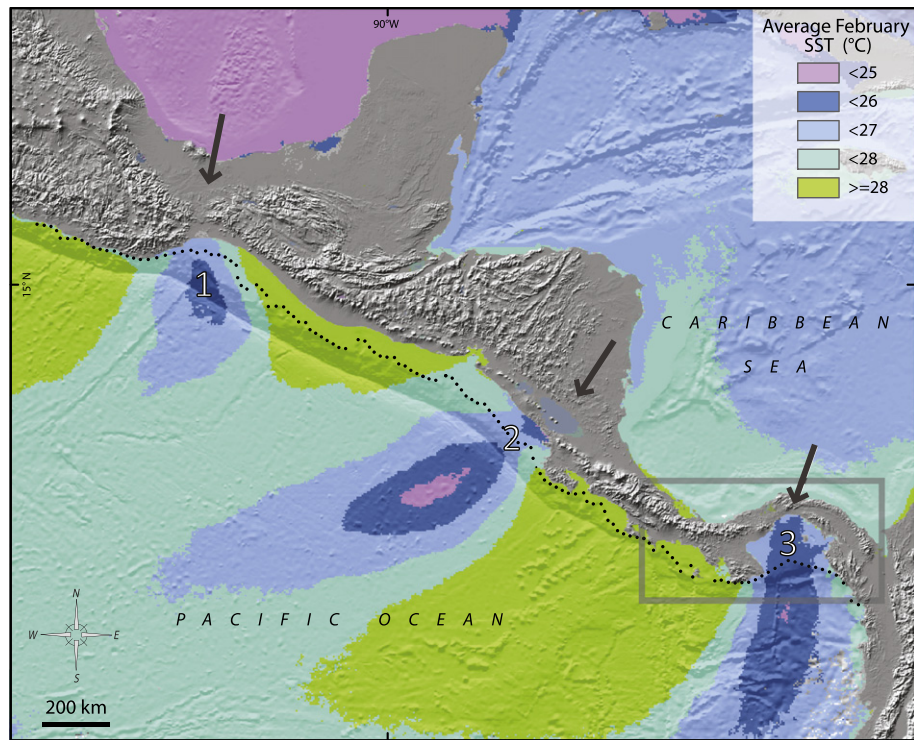


Fig. 1. Relief of the Central American Isthmus and mean February sea surface temperatures (SST) ($^{\circ}\text{C}$) averaged from Terra MODIS 4 km resolution dataset (11 μ daytime) between years 2001–2011 (not including 2009) (NASA, 2012a). Arrows represent the approximate location of low-level wind-jets and subsequent cooler upwelled waters are observable in the Gulfs of Tehuantepec (1), Papagayo (2) and Panama (3). Black dots represent location of NW–SE transect that follows the 200 m depth contour from which elevation and oceanographic data in Fig. 2 are derived. Inset over the Isthmus of Panama corresponds to area covered by Fig. 4. Elevation data from Shuttle Radar Topography Mission (SRTM), 1 km resolution (USGS, 2004). Bathymetry data from ETOPO1 dataset (Amante and Ekins, 2009).

Uplift has resulted in the subaerial exposure of the Charco Azul Group on the Burica Peninsula of Panama and Costa Rica. The Charco Azul Group is split into three distinct sedimentary units or formations (Fig. 3). The oldest comprises sediments of the Pliocene Peñita

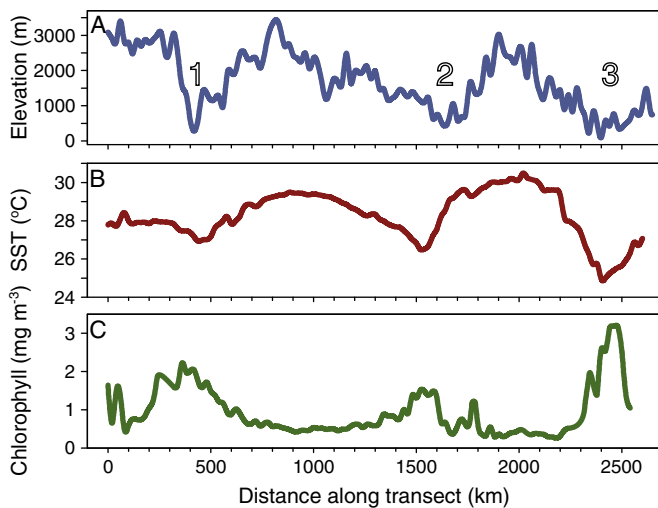


Fig. 2. The tight-knit relationship between elevation of the Central American Isthmus and oceanographic conditions in the Tropical Eastern Pacific, modelled along the NW–SE transect in Fig. 1. (A) Maximum elevation (masl) of isthmian land derived by taking the maximum elevation from perpendicular lines drawn every 20 km along the NW–SE transect. Marked are relative locations of the Gulfs of Tehuantepec (1), Papagayo (2) Panama (3). Elevation data from Shuttle Radar Topography Mission (SRTM), 1 km resolution (USGS, 2004). (B) Average February Sea Surface Temperature (SST) ($^{\circ}\text{C}$) along NW–SE transect in Fig. 1. from Terra MODIS 4 km resolution dataset (11 μ daytime) between years 2001–2011 (not including 2009) (NASA, 2012a). (C) Average February chlorophyll (mg m^{-3}) along NW–SE transect in Fig. 1 from SeaWiFS 9 km resolution dataset between years 2001 and 2010 (not including 2008) (NASA, 2012b).

Formation; around 1200 m of shallow marine silts and conglomerates. These are overlain by roughly 2800 m of volcanoclastic turbidites and siltstones that form the Burica Formation. Overlaying these, sometimes unconformably (pers. obs.), is the shallow marine siltstone and conglomerate deposits of the Armuelles Formation (Fig. 3).

Samples were collected from five localities in these three formations: (1) Quebrada la Peñita and (2) Punta la Peña in the Peñita formation, (3) Quebrada Calabazo in the upper part of the Burica formation, and (4) Rabo de Puerco and (5) Neily River both in the Armuelles formation (Fig. 3, Table 1). Estimates on the ages of localities are from Coates et al. (1992) and Cotton (1999) that have been recently updated by W. A. Berggren and M-P. Aubry reported in Leon-Rodriguez (2007) (Table 1). Paleodepths are estimated from benthic foraminiferal assemblages (Coates et al., 1992; Collins et al., 1995) combined with sedimentological observations in the field.

5. Establish the presence or absence of paleoupwelling

Two approaches are used to establish if upwelling was present in the fossiliferous marine sediments preserved in the Burica Peninsula. (1) The bryozoan zooid size approach to determining the mean annual range of temperature (MART) or zs-MART of ancient seas (O'Dea and Okamura, 2000b), (2) Comparison of the structure of fossil biological communities to modern day communities from both upwelling and non-upwelling regions.

5.1. Approach 1: zooid-size approach to MART

The zooid-size approach to MART (zs-MART) is a paleoenvironmental tool to estimate the MART of ancient seas (O'Dea and Okamura, 2000b). Variation in zooid size in modern day bryozoans is significantly related to the MART in which the colony grew due to the inverse relationship between zooid size and ambient temperature (Menon, 1972; Okamura,

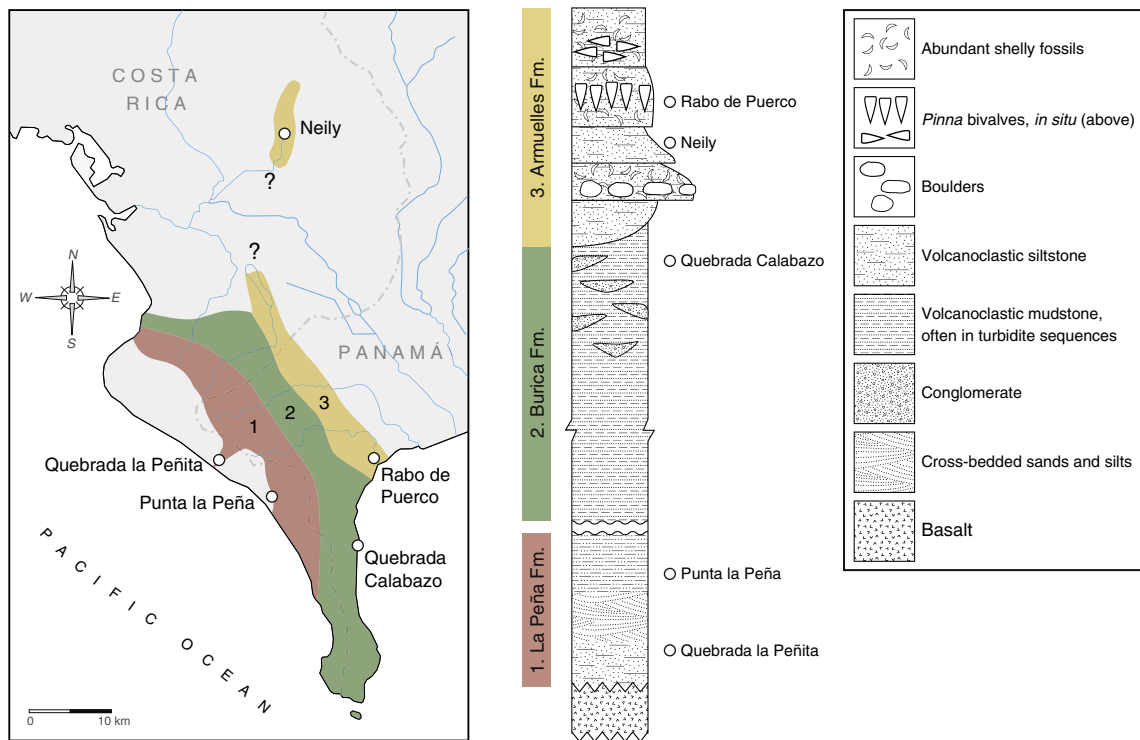


Fig. 3. Geological map of the Burica Peninsula with formations shaded (1 = La Peña, 2 = Burica, 3 = Armuelles) and stratigraphic section with location of fossil sites.

1987; Okamura and Bishop, 1988; Hunter and Hughes, 1994; O'Dea and Okamura, 1999, 2000a, 2000b, 2000c; O'Dea, 2005; Lombardi et al., 2006; Amui-Vedel et al., 2007). MART is estimated by measuring the amount of intracolony zoid size variation in fossil bryozoans and applying it to the following linear equation:

$$\text{MART} = -3 + 0.745(b) \quad (R^2 = 80.0\%),$$

where MART = the mean annual range of temperature experienced by the colony ($^{\circ}\text{C}$) and b = the mean intracolony coefficient of variance of zoid frontal area (zoid length \times zoid width) (O'Dea and Okamura, 2000b). Achieving reliable estimates of MART requires strict adherence to several rules described in O'Dea and Okamura (2000b) and Okamura et al. (2011). These aim to minimize the known effects of water current activity (Okamura and Partridge, 1999; Berning, 2007), food availability (O'Dea, 2005; Amui-Vedel et al., 2007; Hageman et al., 2009), surface irregularities (O'Dea and Okamura, 2000b) and disturbance and predation (Yagunova and Ostrovsky, 2008) on zoid size. If used appropriately and with sufficient replication, zs-MART provides accurate estimates of MART within a few degrees centigrade of error (O'Dea and Jackson, 2002; Okamura et al., 2011). This has proved adequate for (1) determining more equitable paleoclimates compared to the Recent in the Miocene and Pliocene of Europe (O'Dea and Okamura, 2000b), (2) discovering latitudinal gradients in seasonality among paleoenvironments across the

North Atlantic Ocean (Knowles et al., 2009; Williams et al., 2009), and (3) distinguishing rapid paleoenvironmental change in the SWC from an intense upwelling setting to no-upwelling when the Isthmus of Panama closed (O'Dea et al., 2007a).

For the present study, the zs-MART approach was applied to 24 colonies of fossil cupuladriid bryozoans following the methods described in O'Dea and Okamura (2000b) and O'Dea and Jackson (2002). Fossil colonies were available from each of five localities except La Peñita. Modern MARTs in the upwelling Gulf of Panama typically range from 6°C to $\sim 12^{\circ}\text{C}$ and are much lower in the non-upwelling Gulf of Chiriqui, typically ranging from ~ 2 – 6°C (D'Croz and Robertson, 1997; D'Croz and O'Dea, 2007).

5.2. Approach 2: community structure

The second approach utilised to infer the presence or absence of upwelling takes advantage of differences in the relative abundances of fossilised organisms within communities from upwelling and non-upwelling regions today. Firstly, the structure of modern benthic communities from the upwelling Gulf of Panama and the non-upwelling Gulf of Chiriqui (Figs. 1,4) was assessed using dredge samples from the Pacific coast of Panama ($n = 49$) (O'Dea et al., 2007a). Twenty-one dredge samples were made in the upwelling Gulf of Panama and 28 in the non-upwelling Gulf of Chiriqui (Fig. 4). Dredge samples took roughly 3 min at a speed of between 1 and 2 knots. Samples

Table 1

Fossil localities used in this study. Ages and paleodepths from Coates et al. (1992), Collins et al. (1995), Cotton (1999), W. A. Berggren and M-P. Aubry reported in Leon-Rodriguez (2007), and field observations. Numbers of bulk samples are those used to examine ecological structure in Fig. 5. Number of bryozoan colonies applied to the zs-MART approach and the resultant estimated mean annual range of temperatures (MARTs). Lastly, the inference on the presence or absence of seasonal wind-jet driven upwelling.

Locality	Formation	Stage	Age (Ma)	Paleo-depth (m)	No. of bulks	No. of colonies	MART (SD)	Upwelling inferred?
Neily River	Armuelles	Gelasian (Pleistocene)	0.46–0.26	10	3	4	6.98 (1.56)	Yes
Rabo de Puerco	Armuelles			10	4	10	9.66 (1.42)	Yes
Quebrada Calabazo	Burica (upper)		25	25	2	3	7.99 (2.38)	Yes
Punta la Peña	Peñita	Piacenzian (Pliocene)	3.6–3.5	20	5	7	4.56 (1.12)	Inconclusive
Quebrada la Peñita				20	4	MART not estimated		No

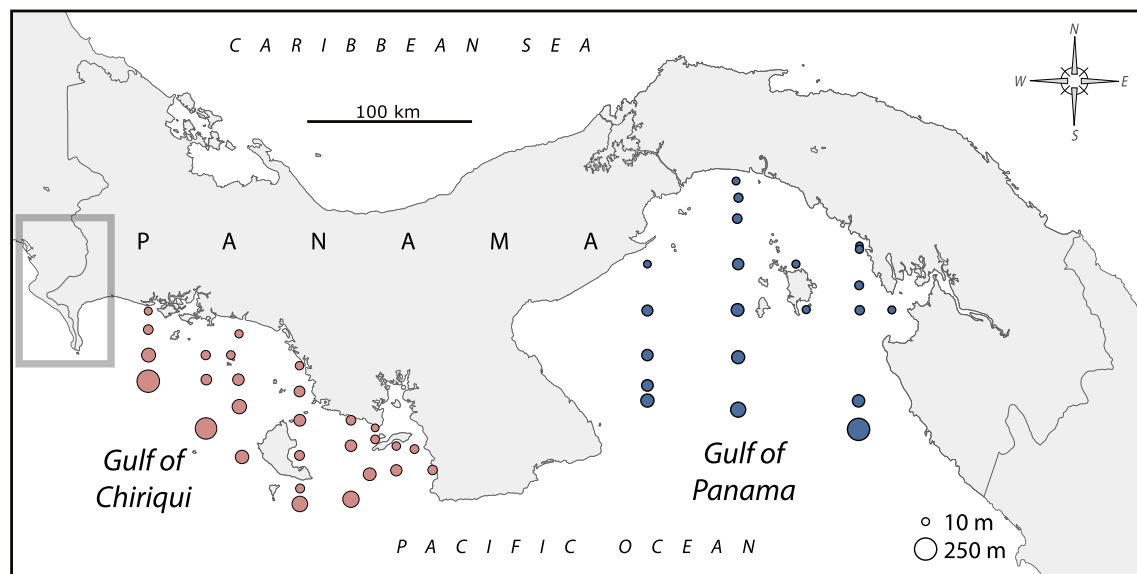


Fig. 4. The Isthmus of Panama with location of dredge samples in the Gulf of Chiriqui (red) and Gulf of Panama (blue). Size of points relates positively to depth of dredge sample. Inset over the Burica Peninsula corresponds to area covered by Fig. 3. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

retrieved were washed and dried on deck using a sieve with a mesh size of 2 mm. All skeletal remains >2 mm were sorted into one of five major taxonomic groups; 'bivalves', 'gastropods', 'scaphopods', 'bryozoans' and 'others', the latter typically forming only a small percentage of total sample and dominated in weight by fish teeth and bones. The weight of each group was recorded and the relative abundance by weight of each group calculated in each sample.

Fossil faunal data were obtained from bulk samples collected in the Pliocene and Pleistocene sites located onshore on the Burica Peninsula ($n=18$) (See Section 4; Fig. 3). A total of 188 kg of fossil sediments were processed by disaggregating and washing at 2 mm. Fossil skeletal remains were cleaned completely of sediment and sorted to the same taxonomic groups as modern samples and the relative weight calculated per bulk sample in the same way.

All samples, modern and fossil, were analysed together based upon the proportional weight of skeletal fractions in samples using Principal Components Analysis (PCA). Water depth or paleodepth of each sample was used as a covariable to remove variation explained by depth, which is often the most overriding driver of variation between benthic marine samples (Table 1).

6. Results

6.1. Modern community composition

The first three axes of PCA explain 85% of the variation in the data (Fig. 5). The first PC axis explains 48% of the variation and is primarily driven by changes in the relative weights of the group 'others' which principally constitutes fish remains. There is no clear separation of the two Gulfs along the first axis but in the second the ordination pulls samples from Gulf of Chiriqui and Gulf of Panama apart quite cleanly, although there remains some overlap (Fig. 5).

Given that the constituent species of the two gulfs are near-identical it is assumed that the proportional differences in abundance (as observed in the PCA) are driven by oceanographic differences, namely that seasonal upwelling occurs in the Gulf of Panama and is absent in the Gulf of Chiriqui. This conclusion is supported by the eigenvectors correlating with PC axis 2 which forms a trophic gradient that is driven principally by a variation between filter-feeding bivalves and bryozoans, that benefit from eutrophic conditions, and gastropods,

which are generally herbivorous. Samples from the highly productive Gulf of Panama fall into the former whereas samples from the Gulf of Chiriqui tend to fall into the latter, as predicted by their respective levels of planktonic primary productivity.

6.2. Pliocene

The community composition of the four bulk samples from Quebrada la Peñita clearly match the non-upwelling Gulf of Chiriqui using PCA (Fig. 5) strongly suggesting no upwelling in the Peñita section, although no bryozoan material was available to estimate MARTs (Table 1). Four out of five of the bulk samples from the Punta la Peña section are more similar in community composition to the upwelling Gulf of Panama, but one sample is more similar to the non-upwelling Gulf of Chiriqui and the estimates of MART suggest little to no upwelling. There is therefore no conclusive evidence on the presence or absence of upwelling at the time of deposition of Punta la Peña.

6.3. Pleistocene

The biological communities of the Quebrada Calabazo, Rabo de Puerco and Neily sites all reveal strong resemblances in the communities of the upwelling Gulf of Panama. Additionally, they each have high to very high estimated MARTs. These two independent lines of evidence combine to convincingly conclude that strong wind jet-driven seasonal upwelling occurred during the time of their deposition (Table 1).

7. Paleogeographic implications

Strong wind-jet driven seasonal upwelling probably did not occur during deposition of the Lower Pliocene Peñita succession, and neither during deposition of the slightly younger La Peña section – a conclusion that is supported by two isotope profiling studies of bivalve (Teranes et al., 1996) and gastropod (Kai Tao, personal communication) shells. The lack of evidence for strong seasonal upwelling in these shallow water, near-shore sites implies that either (1) mountains on the Isthmus were high enough to have blocked cross-isthmian winds in the Pliocene or (2) that wind patterns were different, or (3)

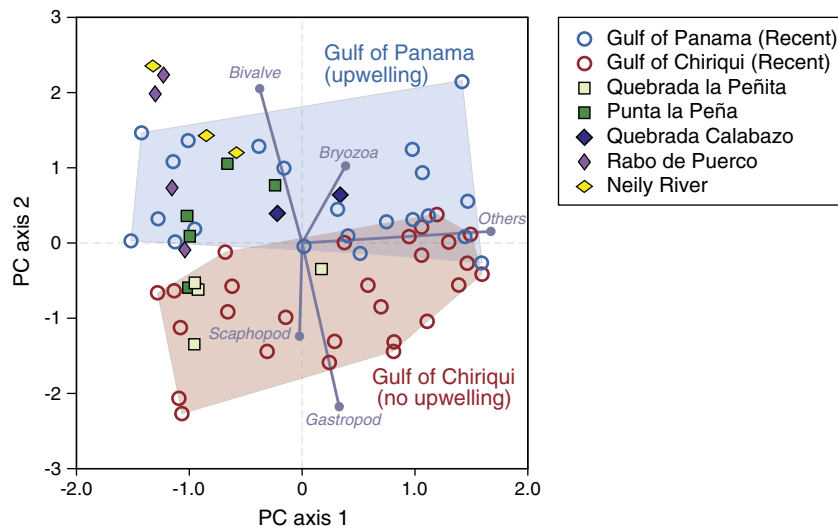


Fig. 5. Ecological structure of Recent dredge and fossil bulk samples based upon skeletal fractions using Principal Components Analysis. Recent samples from the Gulf of Chiriqui (red) and Gulf of Panama (blue) are bounded. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

oceanographic and environmental conditions existed that have no modern analogue.

It is unlikely that wind patterns were markedly different at the time of deposition of all the localities because (1) the ITCZ (whose seasonal movement drives the formation of wind-jets) reached its modern position around 4.4 Ma (Billups et al., 1999), and (2) the obliquity of the earth away from the sun, although less in the Pliocene than it is today (Naish et al., 2009), would have been enough to ensure that the ITCZ passed seasonally over the Burica region. We also reject that mountains were high enough to have blocked wind-jet formation because Cocos Ridge subduction (Corrigan et al., 1990) did not begin until the Pleistocene (Collins et al., 1995; Leon-Rodriguez, 2007). We therefore conclude that non-analogous oceanographic conditions existed in the Pliocene TEP. Such conditions are easily envisioned given that the CAS still maintained a connection to the Caribbean in the east in the Atrato Strait (Duque-Caro, 1990; Coates et al., 2004).

Evidence of strong seasonal upwelling from the Quebrada Calabazo, Rabo de Puerco and Neily River sections imply that during the Pleistocene, after the Isthmus of Panama closed, the Burica region of the Isthmus experienced strong wind-jet driven upwelling that was persistent and similar to that seen in the Gulf of Panama today (D'croz and O'Dea, 2007). This conclusion is supported by the wide variations in intrashell oxygen isotope values found in fossil bivalves from two sites in the Pleistocene Armuelles formation (Teranes et al., 1996). We therefore conclude, based upon our examination of the relationship between modern elevation and Pacific coastal upwelling, that the elevation of the Isthmus to the North of the Burica region during the mid-Pleistocene must have been lower than ~500 m (interpreting Figs. 1, 2).

Today this region stands at an average of 2311 m above sea level (as measured along a straight profile between the peaks of Cerro Chirripó in Costa Rica and Volcán Barú in Panama). This suggests there has been a combined uplift and volcanic accretion rate of around 3.2 m ka^{-1} as estimated by the median age of the Rabo de Puerco section deposited at close to sea-level (1600 m \div 500 ka), corroborating previous estimated uplift rates in the region of 1 to 8 m ka^{-1} over the Late Pleistocene (Leon-Rodriguez, 2007) and 2 to 3 m ka^{-1} during the Holocene (Davidson, 2010). Our data therefore support the following conclusions. (1) Elevation of the Isthmus of western Panama – eastern Costa Rica during the Plio-Pleistocene was considerably lower than at present. (2) The topography of the region is a recent consequence of rapid uplift driven by Cocos ridge subduction (Collins et al., 1995; Leon-Rodriguez, 2007). (3) This rapid uplift dramatically altered the environmental and biotic conditions of the Pacific coast of the Isthmus of Panama.

The conclusion that the Isthmus was entirely emerged yet generally low-lying up until around half a million years ago is corroborated by genetic data from oceanic seabirds. Today even the lowest passes of the Isthmus appear to act as effective barriers to Pacific and Caribbean populations of most oceanic sea birds, yet genetic data suggest that Pacific and Caribbean populations of the masked booby (*Sula dactylatra*) only began to diverge around 640 ka (Steeves et al., 2005a,b), thus supporting the hypothesis that before this time there existed much lower passes across the Isthmus than today (Schmidt, 2007). Keller et al. (1989) and Cronin and Dowsett (1996) both present evidence that the Isthmus of Panama was ephemerally breached after closure as late as 2–1.8 Ma, similarly suggesting a low topographic prominence into the Pleistocene.

8. Future work

This study uses two approaches to provide information on the marine environmental conditions of the region where the Burica peninsula is today during the Pliocene and Pleistocene which help speculate on the elevation of the Isthmus during its formation. Being the first such estimates the data should be corroborated by independent methods. Estimating the relief of ancient mountain ranges is however notoriously difficult (Poulsen et al., 2010). One approach is to estimate mean annual temperatures and rainfall patterns from preserved paleofloras (assuming uniformitarianism with modern floras), the isotopic or mineral composition of soils (e.g. Quade et al., 2011), or the clumped-isotopes in the carbonates of ancient lake sediments (e.g. Huntington et al., 2010), and use the tight correlations between temperature and elevation and precipitation and elevation to estimate paleoaltitude corrected for latitude, but these approaches require paleosols or lake sediments to be preserved from a variety of different elevations and ages; a rare occurrence in a highly volcanic zone like the Isthmus of Panama. Alternatively one may observe the types and amount of sediments reaching coastal basins which is highly dependent upon several factors including rainfall and the amount of rock exposed to weathering, both of which are possible proxies for elevation, but depositional basins around the Isthmus of Panama are perhaps too heterogeneous to permit great success with such an approach. Finally, one may estimate rates of uplift from which paleoelevation can be derived but one needs to either assume that no erosion or intrusive deposition has taken place, or estimate both. Erosion rates can probably be estimated with sufficient certainty to be constructive, especially if one incorporates changes in climate (chiefly temperature and rainfall)

over geological time. Estimating rates of accumulation of volcanic rock over millions of years, will require more care given that the rate of magmatic activity on the Isthmus has been far from constant because Pacific subduction slowed when the Panama block was formed as the Farallon plate split into the Cocos and Nazca Plates (Farris et al., 2011).

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