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ENVIRONMENTAL, ECOLOGICAL, AND EVOLUTIONARY CHANGE IN SEAS ACROSS THE ISTHMUS OF PANAMA

Aaron O'Dea and Laurel S Collins

ABSTRACT

This collection of 13 articles expands our knowledge of the historical and modern-day processes that have shaped tropical American seas. The articles deal with a wide range of topics and are brought together to stimulate collaborative research that breaks down the barriers among disciplines and time scales. Papers in this collection confront the recent challenge to the established age of the formation of the Isthmus of Panama, provide new methods that reveal marine paleoenvironments in the region, assess ecological and evolutionary events over deep time, and evaluate the pre-Columbian to modern-day influences of humans on Caribbean coasts of lower Central America.

Owing to the relentless efforts of paleobiologists, historical ecologists, and coastal archeologists, there is now a great appreciation among the marine biological community of the value of historical and fossil records to (1) place modern-day environmental conditions in context (e.g., Jackson and McClenachan 2009), (2) assess the factors most important in driving ecological and evolutionary change (e.g., Jackson and Erwin 2006), (3) produce baselines for setting conservation goals (e.g. Lotze et al. 2011), (4) expose the impacts of prehistoric human activities coastal marine ecosystems (Rick and Erlandson 2009), and (5) make predictions about uncertain futures (e.g., Harnik et al. 2012). Likewise, those who study the past now aim for the kind of quantitative, statistically rigorous sampling (within the chronological and taphonomic limits of the records available) that ecologists and evolutionary biologists have demonstrated is necessary to separate signal from noise.

The papers in this collection are set within this conceptual framework; a framework that has been central to the Panama Paleontology Project (PPP) spearheaded by JBC Jackson and AG Coates. The papers arise from a colloquium held at the Smithsonian Tropical Research Institute's Bocas del Toro Research Station. The aims of the meeting were to expand our understanding of key historical events around the Isthmus of Panama to help reveal processes of tropical evolution and ecology, describe ancient environmental conditions, better resolve the role human history has had on the seas of tropical America, and stimulate collaborative, multi-proxy research in the future.

The Isthmus of Panama, situated midway between two continents and two oceans, represents an ideal place to focus historical studies. Before the isthmus formed, a narrow seaway flowed between the Pacific and Atlantic oceans, controlling global climate and acting as a barrier to the mixing of terrestrial biotas from South and North America. Later, tectonic processes led to continental collision, the rise of new lands from the sea, and finally a true isthmus that separated the once connected tropical marine communities and formed a land bridge for the intercontinental exchange of terrestrial plants and animals. More recently, the Isthmus of Panama has served as the conduit for coastal exploitations and expansions of the earliest human arrivals in the Americas. Today the isthmus remains a focal point for marine and terrestrial biodiversity that is affected by increasingly intensive global mercantile interests such as shipping and mining as well as the local pressures of agriculture and over-harvesting driven by increasing human populations.

Following the above sequence of events, we have organized the thirteen articles of this issue into four principal themes:

Timing of Isthmus Formation

For most of the last 100 My, the Atlantic, Indian, and Pacific oceans were connected by low-latitude seaways. Only in the relatively recent geological past, as continents gradually took on their modern configuration, did these tropical seaways disappear. Africa and Eurasia collided, severing the western Tethys Ocean from the Atlantic Ocean, and the microplate between the two American continents cut the Tropical American Seaway in two. Australia and Eurasia are still colliding today, and will eventually sever the Indonesian seaways.

The consequences of continental collisions in the tropics are monumental in all respects. Ocean currents are deflected, redefining regional to global climate (e.g., Sarnthein 2013). Hotspots of high marine biodiversity first swell as shallow marine habitat accumulates (e.g., Renema et al. 2008, Jagadeeshan and O'Dea 2012), only to become split in two. Bounded to low latitudes by narrow thermal tolerances, they begin independent evolutionary trajectories (e.g., Jackson and Budd 1996). Finally, terrestrial animals and plants with limited ability to cross water are "suddenly" able to explore new lands with new opportunities, and equally new challenges (e.g., Leigh et al. 2013).

To understand fully the ecological and evolutionary processes involved it is crucial to resolve when the Panamanian isthmus completely severed the Tropical American Seaway. Global paleoclimate models are sensitive to how much water could pass from the tropical Pacific Ocean to the Atlantic Ocean and vice versa (e.g., Schneider and Schmittner 2006). Myriad theses on the evolutionary and biogeographical history of tropical American biotas are dependent on knowing until when significant marine connections existed and when dry land joined North and South America for the first time (see Leigh et al. 2013). In addition, the widely-applied molecular clock method is calibrated by the timing of seaway severance (see Lessios 2008).

Camilo Montes and colleagues (2012a,b) proposed that the isthmus formed some 22–15 Ma. Dubbed the New Model, they presented detailed geophysical data to reconstruct the location of tectonic blocks in the region, leading them to suggest that by 15 Ma, the volcanic arc was in such a configuration that there could have been no space for seawater to pass from ocean to ocean, and that the Isthmus of Panama must have formed by this time. This conclusion is at great odds with a mass of independent data, not least the presence of abyssal sediments in the middle to Late Miocene of the Atrato basin (Duque-Caro 1990), abundant evidence of inter-oceanic seawater exchange into the Pliocene (Sarnthein 2013), and very young transisthmian species revealed by molecular phylogenies (Lessios 2008).

In the first paper of this special edition, Jackson and O'Dea (2013) confront the claims of Montes et al. (2012a,b) by reviewing a reservoir of evidence in three scientific arenas: (1) paleoceanographic evidence for when the divergence of oceanic conditions in the eastern Pacific and western Atlantic began and ended; (2) terrestrial biogeography and the timing of the Great American Biotic Interchange; and (3) marine biogeography and the timing of and divergence of marine biotas as observed in fossils and genes. The authors conclude that the evidence overwhelmingly points to closure approximately 4–3 Ma.

Coates and Stallard (2013) aim to reconcile this overwhelming evidence for formation of the isthmus at approximately 4–3 Ma with the new geophysical claims of Montes et al. (2012a,b). They agree that tectonic collision had occurred approximately 20 Ma, but reject the assertion that collision must equate with seaway closure. The key here is the definition of an isthmus as a fully emerged strip of land that joins two larger bodies of land and separates two bodies of water. Coates and Stallard (2013) consider that although many parts of the Isthmus were certainly emergent, a fully formed isthmus was not in place until about 3 Ma. To strengthen their argument, they turn to the Indonesian Archipelago as a modern-day analogue. Here, tectonic collision has occurred, volcanic arcs are emergent, and yet massive quantities of water still flow from the Pacific Ocean to the Indian Ocean through narrow gaps in the archipelago. These waters are sufficient to influence global climate and restrict the movement of terrestrial vertebrates from one continent to the other, otherwise known as the Wallace, Weber, and Lydekker biogeographic faunal boundaries.

Paleoenvironmental Reconstructions

Understanding the history of modern-day biogeography and interpreting macroevolutionary and ecological events in the past requires a rigorous paleoenvironmental context. Reconstructing the environmental conditions of many millions of years ago at a resolution that can contribute to deciphering ecological processes is challenging, especially in heterogeneous coastal settings (O'Dea et al. 2007). Three papers in this issue explore new approaches to extracting higher resolution paleoenvironmental information from ancient tropical American seas.

Across the tropics, the supply of dissolved nutrients plays a critical role in driving ecology and biogeography. There are two principal sources of nutrients: upwelling and rivers. Previous studies on nutrient flux in tropical American seas did not include river input despite its known role in limiting the extent of reefs in the region. Tao et al. (2013) address this using stable isotopes of oxygen and carbon serially profiled in marine gastropods. Using modern shells and oceanographic data, they develop a novel approach that uses the amount of variation in $\delta^{18}O$ and the correlation between oxygen and carbon isotope values in each shell to reveal the relative inputs of freshening and upwelling waters.

Key et al. (2013) explore the paleoenvironmental potential of annual profiles of oxygen and carbon isotopes in free-living cupuladriid bryozoans. They show that modern colonies faithfully preserve seasonal thermal changes. The authors emphasize that the great abundance of cupuladriids in shallow to deep shelf sediments throughout the Neogene and Pleistocene of tropical America makes them useful tools to reconstruct past upwellings.

Okamura et al. (2013) present an entirely new approach to determine the state of El Niño Southern Oscillation (ENSO) in the past. The model rests on the observation that seas experiencing ENSO exhibit a characteristic frequency distribution of thermal seasonality. The authors used the "zooid size approach to mean annual range of temperature" in bryozoa (O'Dea and Okamura 2000) to compile frequency distributions of seasonality from the Isthmus of Panama region through the Neogene and Pleistocene. Their observations suggest that ENSO conditions in the Miocene and Pliocene were similar to those present today, contradicting other studies suggesting a state of permanent El Niño in the Pliocene.

Neogene Caribbean Paleoecology and Evolution

The stratigraphic, environmental and spatial framework provided by the PPP (Collins and Coates 1999; http://www.fiu.edu/~collinsl) has provided unique opportunities to observe evolutionary and ecological processes in the highly biodiverse tropics over deep time with a relatively high level of rigor and resolution.

Todd and Johnson (2013) take advantage of the groundwork laid by the PPP to rigorously analyze 12 My of macroevolution in the hyper-diverse gastropod genera *Polystira* within which they identify more than 100 species. Unlike most carnivores that experienced high rates of extinction in the Caribbean after isthmus formation, *Polystira* underwent an extraordinary radiation. The authors propose that as food levels fell, non-specialized carnivores failed, but the *Polystira* clade excelled because it partitioned into highly specialized feeding modes.

Leonard-Pingel and Jackson (2013) use a large collection of fossil bivalves accrued by the PPP to explore how shell morphology and mode of life influenced the frequency of predatory drilling. Their results confirm the prediction that bivalves that burrow deep into seafloor sediments and/or have larger shells are more likely to avoid being drilled. Contrary to predictions, their data reveal that heavy ornamentation appears to do little to reduce the rates of predation. Their work sets the stage for a much-needed, in-depth study that uses the PPP's stratigraphic and environmental framework to reveal the ecological and macroevolutionary patterns of predation through time.

Smith et al. (2013) explore the biogeographical patterns of benthic foraminifera in the tropical eastern Pacific Ocean and Caribbean Sea as their biotas diverged over the last 20 My. They calculate biogeographic similarity indices from newer Venezuela collections and PPP collections from Panama, Costa Rica, and Ecuador, and find that inner neritic assemblages of Venezuela, Panama, and Ecuador were still relatively similar during the late Miocene, demonstrating an open seaway to a depth of at least 30 m. As the Central American Seaway constricted in the late Miocene to early Pliocene, progressively cutting off Pacific influence, inner neritic Caribbean faunas increased in similarity as the characteristic modern shallow-water Caribbean fauna was formed.

Klaus et al. (2013) analyze stable isotopes of carbon and oxygen in free-living flabello-meandroid (FSFM) corals to try to explain why they were hardest hit during the Caribbean Plio-Pleistocene extinction. By comparing isotope values to modern corals with known resource usage, they uncover evidence that although FSFM corals were utilizing algal symbionts, they were much more reliant upon heterotrophic feeding, and probably more sensitive to the decline in primary productivity following Pliocene closure of the seaway.

Human Influences

Historical overfishing of the Caribbean, followed by post-Colombian intensification of large tetrapod harvesting and the industrialization of fishing practices, have irrevocably altered Caribbean marine ecosystems (Jackson 1997, Jackson et al. 2001, Myers and Worm 2003). Cramer (2013) reveals, in her comprehensive narrative of human history, that the waxing and waning of human populations along the Caribbean slopes of the Isthmus of Panama, shifting agricultural practices, development, and overfishing have had significant impacts upon coastal ecosystems. It has long been recognized that the earliest arrivals to lower Central America preferred the drier, seasonal, and more agreeable Pacific slopes (Cooke 2005), but Cramer's research reveals a sequence of relentless human impacts upon Caribbean coastal ecosystems that are so pervasive that little of modern-day Caribbean Panama makes sense without this historical context.

Fredston-Hermann et al. (2013) take advantage of newly-discovered mid-Holocene (about 7 ka) coral reef and seagrass sediments in Bocas del Toro, Panama, that expose conditions from a time before humans began to have an appreciable impact. Focusing on the diverse communities of gastropods and bivalves, they find twice the relative proportion of filter-feeding molluscs as in modern reefs, a result consistent with the hypothesis that coastal waters have become more eutrophic. They highlight the vital functional roles molluscs play in reef communities and recommend their inclusion in future reconstructions of "pristine" states.

Schlöder et al. (2013) explore anthropogenic impacts on a much shorter time scale. Simulating the effect that boat anchorage and grounding has on a reef, the team clear-felled small patches of four reefs in Bocas del Toro, Panama, and observed the community composition of the reef over the subsequent 2 yrs. They discovered that only one of the reefs showed unambiguous recovery to pre-clear-felling conditions. Another reef showed almost no recovery, while the final two moved toward being dominated by macro-algae, suggesting that even small-scale disturbances such as those caused by careless anchorage may be sufficient to tip reef communities into alternative stable states (Knowlton 2004).

In the final paper of this special issue, Wake et al. (2013) use a suite of archeological remains from a new site in Bocas del Toro, Panama, to help uncover the interactions between pre-Colombian peoples and the myriad local marine ecosystems. Their excavations and quantitative analyses reveal a higher-density and more complex society than was previously thought to have existed, in which people traded across lower Central America with a heavy utilization of fish, shellfish, sea turtle, and manatee collected from the diverse local reef, mangrove, and lagoonal ecosystems. By quantitatively cataloguing the use of food resources through time, the authors reveal shifts in diets that appear to have been driven by the local depletion of more desirable resources, which demonstrate lasting historical impacts on the seas of the region.

Summary

Irrespective of the time-scales of interest, there are two steps necessary to resolve the biological and environmental history of a region. First, reliable context must be provided. This might include establishing past tectonic and land-sea configurations, reconstructing ancient environments to a high resolution with multiple proxies, and constructing reliable chronologies with geological methods or historical records. Second, a high level of sampling rigor must be applied that can statistically resolve fundamental patterns and processes, and spatial and temporal variation.

The PPP, inspired by the large-scale, collaborative success of the Deep Sea Drilling Project, established that quantitative, rigorous, multidisciplinary, and systematic sampling and analysis of the fossil record can reveal fundamental ecological and evolutionary processes that mold the history of life in biodiverse tropical seas (Jackson and Budd 1996). In the future we anticipate more such collaborative and integrated projects with greater geographic scope as the fossil record of the tropics becomes more resolved stratigraphically, and taxonomic identification catches up with collecting (e.g., Sánchez-Villagra et al. 2010, Gower et al. 2012). Novel and independent approaches to high-resolution paleoenvironmental reconstruction, when allied with more traditional approaches, are critical to resolve questions about local, regional, and global climatic stability. They also reveal the drivers and dynamics of extinction and rapid speciation and explain large-scale biogeographical changes. Revealing how processes such as ENSO affect biological marine communities has relevance for making future predictions for life in the sea (e.g., Dowsett et al. 2013).

The PPP model of context, framework, and rigor can also be applied to the Holocene fossil record to reconstruct biological communities and environments from before and during the extensive modification of marine ecosystems by humans. Applying the paleobiologists' "tool-kit" of morphological taxonomy, morphometrics, stable isotope and trace element geochemistry, sedimentology, and taphonomy is a powerful way to use the Recent fossil record to ask questions about the functional ecology and environmental condition of "pristine" marine ecosystems and the growth and life histories of the animals that lived within them (Jackson and McClenachan 2009). Rather than focus on a single group of organisms, entire communities should be studied, ideally from a functional and not just taxonomic perspective. The reefs of tropical America preserve in great abundance many biological components, including the skeletons of corals, molluscs, bryozoans, and algae, the spicules of sponges, and the teeth and otoliths of fish. With an appropriate understanding of taphonomy and time-averaging these can faithfully resolve the structure of ancient biological communities. Microfossils are powerful proxies of water quality (Cheng et al. 2012), and stable isotopes and trace elements resolve temperatures, nutrient fluxes, rainfall, land use changes, and human population levels. The Holocene fossil record represents an extraordinary opportunity to determine conservation baselines, reveal natural variability within which modern changes can be placed, and pinpoint when changes in the seas began and why.

One exciting future direction is to unite the data from these paleobiological approaches with the fresh vision of coastal archeologists (Rick and Erlandson 2009). Shell middens provide a direct way to observe what humans were taking from the seas and how the animals that were harvested responded, but the record is ecologically limited because samples have been filtered by humans and pertain to a time *after* humans began interacting with the seas. The benefit of the fossil record is the ability to reveal pre-human states with an ecologically-rigorous approach and how sea life that was not being harvested responded over time. Alliances among archeologists, historians, and paleobiologists working toward the common goal of revealing past conditions in the seas should be particularly productive.

Collectively, the papers in this issue demonstrate that rigorous, quantitative, and replicated studies of the past are crucial to enrich our understanding of evolution, ecology, and anthropogenic effects on a wide variety of time scales. It has been a privilege to be given the opportunity to call upon researchers with such a wide spectrum of interests to contribute, and we hope their research will stimulate a new chapter of multidisciplinary and collaborative study of tropical American seas that breaks down the barriers amongst disciplines and time scales.

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Addresses: (AO) *Smithsonian Tropical Research Institute, PO Box 0843-03092, Panama, Republic of Panama.* (LSC) *1. Department of Earth and Environment, Florida International University, Miami, Florida 33199. 2. Smithsonian Tropical Research Institute, PO Box 0843-03092, Panama, Republic of Panama.* Corresponding Author: (AO) *Telephone: +507 2128065, Email: <odeaa@si.edu>.*