QUANTIFYING UPWELLING AND FRESHENING IN NEARSHORE TROPICAL AMERICAN ENVIRONMENTS USING STABLE ISOTOPES IN MODERN GASTROPODS

Kai Tao, John A Robbins, Ethan L Grossman, and Aaron O’Dea

ABSTRACT

To identify and quantify upwelling and freshwater influences in contrasting tropical ecosystems, we performed stable isotope analyses (δ¹³C and δ¹⁸O) on 13 serially-sampled modern Conus shells collected from coastal waters in the southwestern Caribbean (SWC, non-upwelling) and gulfs of Chiriquí (non-upwelling) and Panama (upwelling) in the tropical eastern Pacific (TEP). Most shells reveal seasonal variations in temperature and/or seawater δ¹⁸O in their δ¹⁸O profiles. Unusually high or low seasonal δ¹⁸O values measure the intensity of seasonal upwelling or freshwater input, respectively. To quantify upwelling and freshening signals, baseline δ¹⁸O values free of seasonal upwelling and freshening have been calculated from average temperatures during rainy (non-upwelling) seasons and average salinities during dry (upwelling) seasons. Baseline-normalized δ¹⁸O profiles reveal little or no upwelling in the SWC and Gulf of Chiriquí, and strong upwelling in the Gulf of Panama, as well as strong freshwater input in most areas. Dry-season δ¹⁸O values for Gulf of Panama Conus can exceed the baseline by as much as 2‰, equivalent to seawater temperatures approximately 9 °C lower than normal. In contrast, rainy-season δ¹⁸O values can be as low as 1.8‰ below the baseline, equivalent to salinities approximately 7 units lower than dry-season values. We use shell δ¹⁸O range (Δ¹⁸O) and δ¹⁸O-δ¹³C (O-C) correlation to further identify upwelling and freshening environments and thus nutrient source and status. Eutrophic environments like the Gulf of Panama are characterized by high Δ¹⁸O (2.3‰–3.2‰) and little O-C correlation. In contrast, the oligotrophic environments of the SWC lead to low (0.4‰) to moderate (1.6‰) Δ¹⁸O and non-significant to positive O-C correlation. When applied to fossil shells, these methods can characterize the nutrient status of ancient ecosystems.

The formation of the Central American isthmus isolated the Pacific and Caribbean during the late Neogene and Pleistocene (Coates and Obando 1996, Jackson and O’Dea 2013), resulting in major oceanographic and biological changes in tropical America (Fuglister 1960, Glynn 1972, Keigwin 1978, D’Croz et al. 1991, O’Dea et al. 2007). Understanding the relationship between this environmental perturbation and the evolutionary and ecological origins of the modern tropical American marine fauna requires detailed environmental data from coastal waters during the formation of the isthmus (Schmidt 2007, Farris et al. 2011), which are currently lacking. Modern coastal waters around the isthmus show extreme hydrologic variability. This is principally caused by the presence of strong seasonal wind-jet driven upwelling in the tropical eastern Pacific (TEP) and the general absence of upwelling in the southwest Caribbean (SWC) (D’Croz and Robertson 1997, D’Croz and O’Dea 2007). Additionally, within each ocean there are substantial environmental differences, particularly in the origins of nutrient-rich waters critical for maintaining productivity.
In the present study, we explore novel approaches to distinguish and quantify seasonal upwelling and freshwater input preserved in the oxygen and carbon isotopic profiles of serially sampled gastropod shells from modern tropical American coastal environments. The aim is to provide high-resolution data to be used as reference points to help interpret the significance of isotopic variations in fossil mollusk shells. In doing so, the data will contribute to characterizing the changing environmental conditions associated with the uplift of the Isthmus of Panama.

**Modern Tropical American Hydrology.**—Trade winds blowing across the isthmus from late December to late March/April form wind jets where land elevation is <500 m (O’Dea et al. 2012). These wind jets push Pacific coastal waters offshore resulting in strong seasonal upwelling that brings cold, nutrient-rich water to the surface and greatly increases primary productivity (D’Croz and O’Dea 2007). The TEP is also affected by El Niño events, although the influence of El Niño on upwelling in the TEP remains unclear (O’Dea and Jackson 2002, Agujetas and Mitchelson-Jacob 2008, Okamura et al. 2013). In contrast, SWC waters generally do not experience seasonal upwelling, although there are three areas in the northern coast of Colombia and Venezuela that do experience Ekman-driven upwelling (Reuer et al. 2003). Consequently, the most striking difference across the isthmus is that upwelling in the TEP brings nutrients that drive a fervent planktonic productive system, whereas in the SWC productivity is shifted to the benthos because dissolved nutrient levels are considerably lower and principally supplied by terrigenous runoff (D’Croz et al. 2005, D’Croz and O’Dea 2007). The net movement of evaporative water by the trade winds from the Caribbean into the Pacific also results in the Caribbean being more saline (Fuglister 1960, Glynn 1972, Keigwin 1978, D’Croz et al. 1991).

In addition to inter-ocean differences, TEP and SWC environments are internally variable. In the TEP, the variation of upwelling is correlated with the altitude of the isthmus (O’Dea et al. 2012). During the boreal winter, the trade winds are built up by the high pressure in the SWC and Gulf of Mexico. Only where the isthmus is sufficiently low in elevation are trade winds able to push surface waters away from the Central American coast, where they are replaced by upwelled deep water (D’Croz and O’Dea 2007, 2009). This wind-driven upwelling occurs in the Gulf of Panama but not in the Gulf of Chiriquí, where the cordillera is much higher. In the SWC, in addition to the three Ekman-driven upwelling regions, the seasonal surface water run-off pattern also varies along the Caribbean coast resulting from the seasonal movement of the Intertropical Convergence Zone (ITCZ, Lachniet and Patterson 2002, 2006).

**Stable Isotope Profiles as Records of Environmental Conditions.**—Oxygen isotopes in serially sampled mollusk shells have been used as a proxy for seasonal variation in sea surface temperature (SST) for decades (e.g., Lowenstam and Epstein 1954, Killingley 1981, Krantz 1990, Jones and Allmon 1995, Kobashi and Grossman 2003, Surge and Walker 2006). Carbon isotopes, though influenced by vital effects (e.g., Lorrain et al. 2004, Gillikin et al. 2006), still provide an environmental record of the δ13C of ambient dissolved inorganic carbon (DIC; Mook 1971, Fritz and Poplawski 1974, Gentry et al. 2008, McConnaughey and Gillikin 2008, Beirne et al. 2012). The coupling of oxygen and carbon isotopic profiles can be used to detect seasonal upwelling (Killingley and Berger 1979) and freshwater input (Mook 1971). In the absence of other influences, shell accreted during times of upwelling should have higher δ18O and lower δ13C. This is because upwelled waters are cool, 18O-enriched,
and $^{13}$C-depleted, resulting in a negative $\delta^{18}$O-$\delta^{13}$C (O-C) correlation (Killingley and Berger 1979, Kroopnick 1980). This relationship, however, is not always simple as the $\delta^{13}$C minima and $\delta^{18}$O maxima are not always synchronous (Killingley and Berger 1979, Robbins 2010). Conversely, carbonate deposited during times of increased freshwater is typically depleted in both $\delta^{18}$O and $\delta^{13}$C, a reflection of the $^{18}$O-depletion of meteoric waters and $^{13}$C depletion of soil CO$_2$, resulting in a positive O-C correlation in the isotopic profiles of mollusks (Mook 1971, Surge et al. 2003).

Previous studies of modern mollusks from the TEP and SWC have successfully used oxygen isotopes to distinguish upwelling and non-upwelling environments (Geary et al. 1992, Bemis and Geary 1996). Geary et al. (1992) observed a significantly higher $\delta^{18}$O range for a strombid gastropod from the Gulf of Panama (4.5‰) vs one from a Caribbean non-upwelling area (1.5‰). Bemis and Geary (1996) obtained similar results for venerid bivalves. The present study builds upon the work by Bemis and Geary (1996), but rather than analyzing slow-growing bivalves, we analyze fast-growing gastropods to provide high-resolution isotopic profiles. The data are used for the first time to quantify upwelling and freshening, both critical factors in the delivery of nutrients. These data will then be used to develop a method for quantifying upwelling and freshwater influence in ancient tropical environments.

Samples and Study Area.—To help isotopically characterize the environmental variability in isthmian waters, we analyzed 13 modern gastropod shells, some collected live, from a variety of environmental settings. These include three non-upwelling areas in the Caribbean (Bocas del Toro, San Blas Archipelago, Golfo de los Mosquitos), and upwelling (Gulf of Panama) and non-upwelling (Gulf of Chiriquí) areas on the Pacific coast of Panama (Table 1, Fig. 1). Specimens were collected live from the following areas:

<table>
<thead>
<tr>
<th>Sample ID</th>
<th>Species</th>
<th>Locale</th>
<th>Collection date</th>
<th>Lat (°N)</th>
<th>Lon (°W)</th>
<th>Up</th>
<th>Depth (m)</th>
<th>SL (mm)</th>
<th>SW (mm)</th>
<th>WL (mm)</th>
<th>Sediment type</th>
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<tbody>
<tr>
<td>TA06-294A</td>
<td>Conus spp.</td>
<td>GM</td>
<td>20-08-2006</td>
<td>8.835</td>
<td>81.232</td>
<td>no</td>
<td>40.7</td>
<td>28.5</td>
<td>12.5</td>
<td>76.0</td>
<td>BSS</td>
</tr>
<tr>
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<td>GM</td>
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<td>8.835</td>
<td>81.232</td>
<td>no</td>
<td>40.7</td>
<td>16.3</td>
<td>8.9</td>
<td>23.5</td>
<td>BSS</td>
</tr>
<tr>
<td>SB95-1</td>
<td>C. mus</td>
<td>SB</td>
<td>14-10-1995</td>
<td>9.440</td>
<td>78.585</td>
<td>no</td>
<td>11.0</td>
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<td>13.4</td>
<td>57.5</td>
<td>BMT</td>
</tr>
<tr>
<td>TA04-10A</td>
<td>C. jaspideus</td>
<td>IC</td>
<td>30-09-2004</td>
<td>9.446</td>
<td>82.325</td>
<td>no</td>
<td>15.9</td>
<td>21.3</td>
<td>12.2</td>
<td>52.5</td>
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<tr>
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<td>11.9</td>
<td>52.0</td>
<td>MSC</td>
</tr>
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<td>79.250</td>
<td>yes</td>
<td>&lt;17.0</td>
<td>52.3</td>
<td>23.2</td>
<td>162.4</td>
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</tr>
<tr>
<td>GP97-17B</td>
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<td>GP</td>
<td>16-02-1997</td>
<td>7.988</td>
<td>79.250</td>
<td>yes</td>
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<td>16.4</td>
<td>72.7</td>
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<td>18-03-2000</td>
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<td>78.895</td>
<td>yes</td>
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<td>46.2</td>
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<td>140.2</td>
<td>na</td>
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<tr>
<td>301490A</td>
<td>C. ximenes</td>
<td>GP</td>
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<td>78.913</td>
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<tr>
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<td>15-03-2000</td>
<td>8.269</td>
<td>78.913</td>
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<td>GC</td>
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<td>123.0</td>
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<tr>
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<td>C. arcuatus</td>
<td>GC</td>
<td>21-03-1997</td>
<td>7.865</td>
<td>82.180</td>
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<td>61.0</td>
<td>30.1</td>
<td>13.8</td>
<td>69.0</td>
<td>MS</td>
</tr>
</tbody>
</table>

1BSS = brown sediments with many shells, BMT = brown terrigenous mud, MWC = mud with sands and abundant cupuladriid bryozoans, CS = coarse sand, MS = muddy sand, na = not available,

2live-collected

GM = Golfo de los Mosquitos, SB = San Blas, IC = Isla Colón (Bocas del Toro), GP = Gulf of Panama, GC = Gulf of Chiriquí.
collected in muddy to coarse sands at depths of 10–61 m in the Pacific and 11–41 m in the Caribbean (Table 1).

Temperature and salinity profiles were obtained for each sample location at different depths from the World Ocean Atlas 2001 historical database (Fig. 2A; Conkright et al. 2002; henceforth referred to as “WOA 2001”). Figure 2B shows the expected shell δ\(^{18}\)O values based on estimates of seawater temperature and salinity at each sample location and depth (details for this calculation are discussed later). Note that both temperature and δ\(^{18}\)O profiles flatten in deep waters (100 m) because of little variation in temperature and salinity below the thermocline (approximately 60 m). Maximal temperature variations are found in water depths of 20–50 m, where strong seasonal upwelling occurs. Maximal salinity variations are found in surface waters due to the dominant influence of freshwater runoff in the rainy season.

For most of the Pacific coast, intense rainfall starts in May and lasts until December, while a dry season occurs from January to April (Fig. 3A). The Gulf of Panama experiences upwelling during the dry season when wind jets blow across the isthmus (D’Croz and Robertson 1997, D’Croz et al. 2001). Pacific upwelling is absent during the rainy season, which creates a strong contrast between the SWC and TEP seasonal temperature patterns as evident in temperature logger records from Smithsonian Tropical Research Institute (STRI) monitoring stations in Bocas del Toro and Gulf of Panama (Fig. 3B,C), as well as WOA 2001 data (Fig. 2A, Conkright et al. 2002). In the Gulf of Panama, SSTs can drop from approximately 28.5 °C during non-upwelling (rainy) periods to as low as 15.5 °C during upwelling (dry) intervals. In contrast, in Bocas del Toro the seasonal SST variations typically are within ±1 °C (2σ) of the mean (28.6 °C; Kaufmann and Thompson 2005). Though the Gulf of Chiriquí is characterized as non-upwelling, seasonal shoaling of the thermocline to nearly 30 m occurs in response to seasonal trade winds passing over the isthmus. The higher elevations north of Gulf of Chiriquí, however,
preclude the development of wind jets and strong upwelling (Fig. 2; D’Croz and O’Dea 2007, Liang et al. 2009).

Methods

Prior to sampling for stable isotopic analysis, all gastropod specimens were cleaned, polished, and ultrasonicated to remove extraneous materials from the surfaces. Serial sampling was applied at 2–3 mm intervals, starting from the apex of the shell spiral, to collect sample powders from shallow grooves perpendicular to growth direction using a 0.5 mm
Brassler carbide dental drill bit. Approximately 300 µg of powder was collected for each sample. For each analysis, about 100–150 µg of sample powder was reacted with “100%” phosphoric acid at 70 °C on a GasBench II gas handling system. The CO₂ gas generated was then analyzed on a DeltaPlusXP isotope ratio mass spectrometer. All results were calibrated to Vienna-PDB using NBS-19 standard. At least every fifth sample was analyzed in replicate to test for quality control. Maxima were replicated for specimen 301490A to confirm peaks defined by one point. Analytical precision averaged about 0.06‰ and 0.1‰ for δ¹³C and δ¹⁸O, respectively.

Shell chronologies were determined using comparisons with expected shell δ¹⁸O profiles for the appropriate sample location and depth. These profiles were estimated for analyzed specimens using modern temperatures and salinities obtained through Ocean Data View (ODV) software using the historical WOA 2001 database (Fig. 2, Conkright et al. 2002). For each sample location, at least two nearby WOA stations were chosen and averaged. Seawater δ¹⁸O values (δ¹⁸Ow; relative to VSMOW) can be calculated from salinity (S) data using relationships derived from natural waters. Robbins et al. (unpubl data) measured the δ¹⁸Ow and salinities of surface waters collected twice weekly from March 2011 to August 2012 from the Galeta Marine Laboratory (SWC, 9.4029 N, 79.8608 W) and Naos Island Marine Laboratory (Gulf of Panama, TEP, 8.9159 N, 79.5322 W) of the STRI (Fig. 4). The monthly averages of these data yielded the equations:

Figure 3. (A) Mean monthly rainfall for Panama City (Parque Natural Metropolitano) on the Pacific coast, and STRI’s Galeta Marine Laboratory (near Colon) and Bocas del Toro Research Station on the Caribbean coast. Panama City and Bocas del Toro data for 1971–2000 are from the World Meteorological Organization (WMO, http://worldweather.wmo.int/076/m076.htm) and Galeta data for 1974–2006 are from STRI’s Physical Monitoring Program (http://biogeodb.stri.si.edu/physical_monitoring/). (B,C). Temperature records from loggers from 4 m depth at Cayo Agua (Bocas del Toro) and 12 m depth at Pacheco watch station (Gulf of Panama) of STRI (gray curve) compared with World Ocean Atlas (WOA) temperature data (black curve plotted as 2001 but based on historic compilation) and shell δ¹⁸O (colored curves).
The $\delta^{18}O_w$-S slopes, y-intercepts, and correlation coefficients agree well with those of Fairbanks et al. (1992) for Pacific and Atlantic waters:

\[
\delta^{18}O_{w,\text{Pacific}} = 0.26 S - 8.77 \quad (\text{Eq. 3})
\]
\[
\delta^{18}O_{w,\text{Atlantic}} = 0.19 S - 5.97 \quad (\text{Eq. 4})
\]

Using Equations 1 and 2, we calculated $\delta^{18}O_w$ from local salinity measurements from WOA 2001 (Conkright et al. 2002). Expected shell $\delta^{18}O$ values were then determined from the WOA 2001 temperatures and calculated seawater $\delta^{18}O$ using the aragonite temperature equation of Grossman and Ku (1986, eq. 1 in that paper as modified by Hudson and Anderson 1989),

\[
T \,(^\circ\text{C}) = 19.7 - 4.34 (\delta^{18}O_{\text{aragonite}} - \delta^{18}O_{w}) \quad (\text{Eq. 5})
\]

which after substituting Equations 1 or 2 and rearranging terms yields:

\[
\delta^{18}O_{\text{TEP shell}} = (19.7 - T) / 4.34 + 0.25 S - 8.35 \quad (\text{Eq. 6})
\]
\[
\delta^{18}O_{\text{SWC shell}} = (19.7 - T) / 4.34 + 0.19 S - 5.75 \quad (\text{Eq. 7})
\]
When temperature logger data were available (e.g., Bocas del Toro and Gulf of Panama, both daily resolution), chronologies were easily established by comparing the measured δ¹⁸O with the seawater temperature profile (Fig. 3B,C). For the remainder of sample locations the relatively low-resolution (monthly) WOA 2001 data were used (Fig. 2). The sclerochronologies were established as follows. Firstly, the months with maximum and minimum expected δ¹⁸O were identified as reference points and assigned to the 15th day of that month. Next, the measured maximal, minimal, and last growth δ¹⁸O values of each annual cycle were assigned to the appropriate date (or day of the year for dead specimens) for that location. Lastly, a constant growth rate was assumed between reference points for the purpose of calculation, though in reality the shell growth rate varies intra-annually (e.g., Goodwin et al. 2001, Gentry et al. 2008).

Results

Oxygen Isotopes.—Overall, Gulf of Panama (TEP, upwelling) shells had larger δ¹⁸O ranges and lower δ¹⁸O averages than SWC shells, while the two deeper specimens (GC97-80A and B, 61 m) from the Gulf of Chiriquí (TEP, non-upwelling) had ranges between those of SWC and Gulf of Panama shells and the highest averages of all specimens in this study (Figs. 5, 6; Table 2).

Samples from the three nearshore localities in the SWC generally had little seasonal variation and small overall range, resulting in flat δ¹⁸O profiles (Fig. 5). Two specimens from Golfo de los Mosquitos (TA06-294A and B) averaged –0.9‰ and –0.6‰, and had ranges of 0.8‰ and 0.4‰, respectively. The larger shell (294A) had a whorl length of 76.0 mm and a δ¹⁸O profile indicative of approximately 1 yr of growth. The smaller shell (294B; whorl length = 23.5 mm) had a shorter record, which is likely responsible for its lower seasonality relative to 294A. Three specimens from Bocas del Toro (TA04-10A, B, and C) had average δ¹⁸O values of –0.8‰ to –1.3‰ and ranges of 0.7‰ to 1.0‰. The mean values were close to, but slighter lower than those of the Golfo de los Mosquitos shells. A single specimen from San Blas (SB95-1) had a significantly lower average δ¹⁸O value of –1.6‰ and a larger annual range of 1.6‰ with recognizable annual cycles (Fig. 5).

In contrast, Conus shells from the Gulf of Panama (TEP, upwelling) had δ¹⁸O profiles with substantial seasonal variations revealing 2–6 yrs of growth (Fig. 5). Maximal shell δ¹⁸O values (averaging –0.4‰) slightly exceeded those of SWC samples (averaging –0.6‰) despite TEP δ¹⁸O, being lower by 0.3‰ to 0.6‰ (Table 2). Mean shell δ¹⁸O values fell between –1.4‰ and –2.1‰ and annual ranges were between 2.3‰ and 3.2‰. Based on the chronology provided by the δ¹⁸O profiles, most shells grow faster during their juvenile years (first 1 or 2 yrs; Fig. 5) interpreted as a shift in energy allocation from growth to reproductive maturation by Perron (1983). Within each year, growth was faster mostly from maximum to minimum δ¹⁸O, thus creating an asymmetrical sawtooth pattern suggestive of enhanced growth during upwelling (see also Kobashi and Grossman 2003).

The Gulf of Chiriqui shells (GC97-80A and B) exhibited moderate seasonal variations and annual ranges with subdued cyclicity compared with the Gulf of Panama shells. The mean δ¹⁸O values of each specimen were 0.2‰ and 0.4‰, respectively, and the annual ranges were both 1.3‰. The annual range lies between those of shells growing in the upwelling environments of the Gulf of Panama and shells growing in the non-upwelling SWC. This is consistent with the seasonal
shoaling of the thermocline in the Gulf of Chiriqui (Fig. 2). Mean δ¹⁸O values were significantly higher (1.6–2.8‰; Mann-Whitney U test: \( P < 0.0001 \)) than those for the other two areas due to the greater depth (61 vs 10–15 m for shells from Gulf of Panama and 11–41 m for shells from SWC waters).

**Carbon Isotopes.**—Unlike oxygen isotopes, carbon isotopes showed greater differences within than among localities (Figs. 5, 6). There were no distinct seasonal variations within some shell profiles and subdued seasonality in others. A
long-term decrease with ontogeny was sometimes present (e.g., GP97-17A, and 301474). The mean δ¹³C values of both SWC and TEP samples fell mostly between 1.3‰ and 2.3‰, with two exceptions (TA04-10C, 0.9‰, and GP97-17B, 0.8‰). Only three of 13 shells exhibited a significant correlation ($P < 0.05$) between δ¹³C and δ¹⁸O (Fig. 6). Gulf of Panama shells GP97-17B and 301474 had a positive correlation, whereas Gulf of Chiriquí shell GC91-80B exhibited a negative correlation (Table 2).

**Discussion**

**Expected vs Measured Oxygen Isotope Profiles.**—Nearshore marine environments proximal to freshwater sources can be highly variable, both spatially and temporally, complicating comparisons between shell isotopic profiles and environmental data collected kilometers to tens of kilometers from the shell recovery site. As discussed earlier, environmental temperature and salinity data were available from offshore oceanographic sites (WOA 2001) and in certain cases from nearshore temperature logger sites. WOA 2001 data from Bocas del Toro (SWC) are generally consistent with logger data (within ±1 °C). For the Gulf of Panama (TEP) sites, the WOA 2001 data are consistent with high (rainy-season) temperatures, but do not capture the lowest temperatures during the upwelling season. This is likely because upwelling is patchy, sporadic, and ephemeral (D’Croz and O’Dea 2009), and the WOA 2001 data set represents monthly averages (Conkright et al. 2002) that moderate extreme values.

Most of the average SWC shell δ¹⁸O values are statistically identical to the expected δ¹⁸O values, while the average TEP shell δ¹⁸O values are lighter (0.2‰–1.2‰). The ranges of measured shell δ¹⁸O values from the SWC and TEP waters are 0.2‰–1.7‰ lower and 0.1‰–1.0‰ higher, respectively, than expected ranges. For the Bocas del Toro and Gulf of Panama shells, the measured δ¹⁸O profiles match well with the logger temperature profiles, though with slightly lower resolution (weekly to fortnightly for the stable isotopic analyses compared with daily for the logger data) and with time-averaging of 3–7 d in each sample hole (calculated
Table 2. Specimen information and environment, and stable isotope values and correlations. $T_{rec}$ and $S_{rec}$ are averages for temperature and salinity measurements in nearby hydrographic stations (Fig. 1). Bold numbers represent significant correlations ($P < 0.05$). Italicized numbers represent values for the dry season only (values higher than the baseline). GM = Golfo de los Mosquitos, SB = San Blas, BT = Bocas del Toro, GP = Gulf of Panama, GC = Gulf of Chiriquí.

| Sample ID   | Species       | Location | Depth (m) | $T_{rec}$ ($^\circ$C) | $S_{rec}$ | $\delta^{18}O_w$ | $\delta^{13}C$ | $\delta^{18}O_{min}$ | $\delta^{18}O_{max}$ | $\delta^{18}O_{mean}$ | $sd$ $\delta^{18}O_{mean}$ | $\delta^{18}O_{measured-expected}$ | $\Delta^{18}O$ | $\delta^{18}O-\delta^{13}C$ | $R$ | $P$-value |
|-------------|---------------|----------|-----------|------------------------|-----------|------------------|-----------------|-----------------------|-----------------------|--------------------------|-------------------------------|-------------------|------------------------|-----|----------|
| TA06-294A   | Conus spp.    | GM       | 40.7      | 23.6                   | 33.6      | 0.41             | $-1.3$       | $-0.5$                | $-0.9$                | 0.2                      | $-0.2$                        | 0.8                            | $2.3$             | $-0.43$                | $0.03$ | $0.12$   |
| TA06-294B   | Conus spp.    | GM       | 40.7      | 23.6                   | 33.6      | 0.41             | $-0.9$       | $-0.5$                | $-0.6$                | 0.1                      | $-0.1$                        | 0.4                            | 1.8               | $0.34$                | $0.02$ | $0.56$   |
| SB95-1      | Conus mus     | SB       | 11.0      | 27.5                   | 35.6      | 0.79             | $-2.5$       | $-0.9$                | $-1.6$                | 0.3                      | $-0.4$                        | 1.6                            | 1.8               | 0.01                | $0.96$ | $0.96$   |
| TA04-10A    | Conus jaspidea| BT       | 15.9      | 27.1                   | 35.1      | 0.70             | $-1.4$       | $-0.5$                | $-0.8$                | 0.2                      | 0.2                           | 0.9                            | 1.3               | $-0.06$              | $0.74$ | $0.74$   |
| TA04-10B    | Conus jaspidea| BT       | 15.9      | 27.1                   | 35.1      | 0.70             | $-1.2$       | $-0.5$                | $-0.9$                | 0.2                      | 0.1                           | 0.7                            | 1.5               | 0.28                | $0.16$ | $0.16$   |
| TA04-10C    | Conus jaspidea| BT       | 15.9      | 27.1                   | 35.1      | 0.70             | $-2.0$       | $-0.9$                | $-1.3$                | 0.2                      | $-0.3$                        | 1.0                            | 0.9               | $-0.20$              | $0.32$ | $0.32$   |
| Pacific, upwelling |             |           |           |                        |           |                  |               |                      |                       |                          |                               |                                 |                   |                      |       |          |
| GP97-17A    | Conus recurvus| GP       | <17.0     | 26.5                   | 31.7      | $-0.53$          | $-3.5$       | $-0.3$                | $-2.1$                | 0.7                      | $-0.6$                        | 3.2                            | 2.2               | $-0.19$              | $0.12$ | $0.12$   |
| GP97-17B    | Conus mahogani| GP       | <17.0     | 26.5                   | 31.7      | $-0.53$          | $-3.4$       | $-1.1$                | $-2.0$                | 0.7                      | $-0.5$                        | 2.3                            | 0.8               | $0.42$              | $0.00$ | $0.00$   |
| 301474      | Conus patricius| GP      | 14.8      | 27.0                   | 34.2      | $0.12$           | $-3.4$       | $-0.5$                | $-2.4$                | 0.7                      | $-1.2$                        | 2.9                            | 2.0               | $0.42$              | $0.00$ | $0.00$   |
| 301490A     | Conus ximenes| GP       | 10.0      | 27.1                   | 33.8      | 0.02             | $-2.5$       | 0.2                   | $-1.4$                | 0.8                      | $-0.2$                        | 2.6                            | 1.9               | 0.08                | $0.57$ | $0.57$   |
| 301490B     | Conus ximenes| GP       | 10.0      | 27.1                   | 33.8      | 0.02             | $-2.9$       | $-0.5$                | $-1.8$                | 0.7                      | $-0.7$                        | 2.3                            | 1.4               | 0.25                | $0.18$ | $0.18$   |
| Pacific, non-upwelling |       |           |           |                        |           |                  |               |                      |                       |                          |                               |                                 |                   |                      |       |          |
| GC97-80A    | Conus arcatus| GC       | 61.0      | 18.3                   | 34.6      | $0.23$           | $-0.5$       | 0.8                   | 0.2                   | 0.3                      | $-0.5$                        | 1.3                            | 1.9               | $-0.25$             | $0.09$ | $0.09$   |
| GC97-80B    | Conus arcatus| GC       | 61.0      | 18.3                   | 34.6      | $0.23$           | $-0.2$       | 1.1                   | 0.4                   | 0.4                      | $-0.3$                        | 1.3                            | 1.7               | $-0.55$            | $0.00$ | $0.00$   |
using shell chronology). For the Bocas del Toro shells, differences between measured δ¹⁸O values and WOA 2001 data may be caused by inter-annual fluctuations (i.e., historical mean vs logger and isotopic data for the year 2004). For the Gulf of Panama shells, WOA 2001 data do not appear to record the temperature minima during the upwelling season, resulting in higher average temperatures and reduced annual range. This could explain the range difference in the TEP shells mentioned above. However, WOA 2001 average temperatures are already higher than logger temperatures and δ¹⁸O-derived mean temperatures are even higher [i.e., δ¹⁸O values lighter (e.g., specimen 301474) Fig. 5]. The likely explanation is that the salinity, and thus δ¹⁸O_w at the nearshore localities is lower than that modeled by the WOA 2001.

Isotope Proxies—Baseline Approach.—Here we propose a method for using oxygen isotope profiles in tropical Conus shells to quantify seasonal upwelling and freshening signals. To separate the two signals in a δ¹⁸O profile, we first calculated the expected aragonite isotope value of waters unaffected by upwelling or freshening. This was accomplished by inserting average rainy-season (non-upwelling) water temperatures and dry-season δ¹⁸O_w values (calculated from WOA 2001 and STRI logger data using Equations 1 and 2) into the aragonite paleotemperature equation (Eq. 5).

We can assume that shell δ¹⁸O values plotting below the baseline in Figure 7 are caused only by cooler temperatures as the normal salinity of upwelled water fixes the upper limit of seawater δ¹⁸O. Because tropical SSTs are relatively stable in the absence of upwelling, unusually cool temperatures undoubtedly reflect upward water mass transport. Shell δ¹⁸O values plotting significantly above the baseline (Fig. 7) no longer represent temperature variations, but salinity variations caused by freshening. Salinities can be calculated from Equations 1 and 2 and the Grossman and Ku (1986) equation:

\[
S_{\text{TEP}} = \frac{((\delta^{18}O_{\text{shell}} + 8.35) - (19.7 - T) / 4.34) / 0.25}{\text{(Eq. 8)}}
\]

\[
S_{\text{SWC}} = \frac{((\delta^{18}O_{\text{shell}} + 5.75) - (19.7 - T) / 4.34) / 0.19}{\text{(Eq. 9)}}
\]

Based on this approach, Gulf of Panama specimen GP97-17A recorded temperatures of upwelled seawaters as low as 23 °C and salinities of freshened seawaters as low as 31, compared with a dry-season salinity of 35.

When the shell δ¹⁸O values are normalized to their respective baselines, 75% of the SWC δ¹⁸O values lie below (to the left of) the baselines (Fig. 8), with salinities up to 7 below baseline, indicating strong freshening and little or no upwelling (Fig. 8). This is consistent with freshwater input being the primary driver for productivity along the Caribbean coast of Panama, especially in Bocas del Toro (D’Croz et al. 2005). The Gulf of Panama shell profiles (TEP, upwelling area) fluctuate across the baseline, suggesting both freshening and upwelling. Samples 301490A and GP97-17A in this area show the clearest record of upwelling, with temperatures up to 9 °C below baseline. This suggests upward movement of nutrient-rich waters of >60 m (D’Croz and O’Dea 2007). In addition, the isotopic profiles document rainy-season salinities as low as 28 in the Gulf of Panama. The Gulf of Chiriquí (TEP non-upwelling) profiles lie largely within the error of the baseline, but do
Figure 7. δ¹⁸O profiles of specimen 301490A with shell δ¹⁸O baseline. δ¹⁸O values lower than the baseline values are calibrated to salinity change while those higher than the baseline values are calibrated to temperature change. The error bar is calculated based on the standard deviation of the environmental data (salinity and temperature) and the error in Equations 1 and 2.

Figure 8. Box and whisker plot of shell δ¹⁸O values normalized to baseline values for all specimens. Gray bars represent analytical error (1σ) for each sample location. δ¹⁸O values the baseline are calibrated to salinity change while those plotting to the right of the baseline are calibrated to temperature change.
show some evidence for cooling, especially in GP97-80B, consistent with observed seasonal shallowing of the thermocline. Thus, the baseline approach applied to Conus $\delta^{18}O$ profiles provides proxy data for upwelling and freshening in coastal Panama, correctly showing (1) seasonal freshening in the shallow waters of both coasts, (2) little or no upwelling in the SWC, and (3) seasonal shallowing of the thermocline (Gulf of Chiriquí) to strong upwelling (Gulf of Panama) in the TEP.

Isotope Proxies—$\delta^{18}O$ Range and $\delta^{18}O$-$\delta^{13}C$ Correlation Approach.—The relative importance of upwelling and freshening can also be identified by combining $\delta^{18}O$ range ($\Delta^{18}O$) with O-C correlations within shell isotopic profiles (Fig. 9A). Upwelling brings cold, saline, deep water ($^{18}O$ enriched, but $^{13}C$-depleted) to the surface, resulting in $^{18}O$ enrichment and $^{13}C$ depletion in shell carbonate (e.g., Killingley and Berger 1979, Jones and Allmon 1995). In contrast, freshwater input decreases both $\delta^{18}O$ and $\delta^{13}C$ values, resulting in a positive correlation (e.g., Mook 1971, Surge et al. 2003). WOA 2001 20-m temperature and salinity data for the SWC and TEP coasts of Panama (Fig. 10) provide reference values for fields in Figure 9A. In the SWC, the vast majority (>80%) of data for temperature and salinity range ($\Delta T$ and $\Delta S$, respectively) fall within $2.1 \pm 0.9$ °C and $1.2 \pm 0.6$, which equates to a maximum $\delta^{18}O$ range of 1.0‰ ($3 \times 0.23$‰ per °C $+ 1.8 \times 0.19$‰ per salinity unit). Thus, $\Delta^{18}O$ values <1‰ are interpreted to represent environments with minimal upwelling and freshening, like that of Golfo de los Mosquitos. The TEP $\Delta T$ data show a bimodal distribution with the second mode at 5.1 ± 0.3 °C (Fig. 10B). This equates to $\Delta^{14}O$ of approximately 1‰, so $\Delta^{18}O > 1$‰ can serve as a threshold for significant upwelling. In contrast to SWC water, TEP waters show a large seasonal $\Delta S$, with a mode of 3.0 ± 0.4 for 20 m (Fig. 10B). Significant freshening equates to $\Delta^{18}O$ of 0.6‰ ($2.6 \times 0.26$‰ per salinity unit). Thus, significant upwelling and freshening can yield $\Delta^{18}O$ data of approximately 1.5‰. We set $\Delta^{18}O > 2$‰ as the threshold for strong upwelling and freshening, which would equate to an additional $\Delta T$ of 2.5 °C or $\Delta S$ of 1.9–2.6. Because seasonal freshening and upwelling impart opposite O-C correlations on the data, data fields in Figure 9A that represent a combination of these processes fall within $|R| < 0.3$, with 0.3 being the approximate value above which our correlations are significant ($P \leq 0.05$;
Table 2). Upwelling without freshening will result in a less extreme Δ^{18}O and an $R < -0.3$, and freshening without upwelling will yield a less extreme Δ^{18}O and an $R > +0.3$ (Fig. 9A).

Most modern SWC specimens fall into the area of minimal upwelling and freshening, while most TEP specimens fall into the area of strong upwelling and freshening (Fig. 9B), both consistent with environmental measurements. With minor exception, the inverse O-C correlations are not apparent in the Gulf of Panama samples. As mentioned earlier, only three out of 13 specimens show significant correlations ($P < 0.05$), with the two specimens from TEP upwelling area (GP97-17B and 301474) showing positive O-C correlations indicative of strong freshening, and the one from TEP non-upwelling area (GC97-80B) showing a negative correlation indicative of upwelling. This upwelling signal recorded in the baseline and correlation methods likely results from the seasonal shoaling of the thermocline, combined with the greater depth (61 m) that limits freshwater influence (Fig. 9C).
No inverse O-C correlation was found in the bivalve and gastropod shells from the TEP upwelling areas studied by Geary et al. (1992) and Bemis and Geary (1996). Geary et al. (1992) attributed the absence of negative O-C correlations in this upwelling area to intense freshwater input during the rainy season, the interpretation adopted here. Matthews et al. (2008) found no significant difference in marine DIC δ¹³C between upwelling and non-upwelling times in the Gulf of Panama, confirming this interpretation.

**Isotope Profiles and Nutrients.**—As a proxy for seasonal upwelling and freshwater input, the isotopic results provide insight into nutrient delivery and status in ancient environments. Freshwater input and upwelling differ in their capability to bring phosphate, nitrate, and silica to the photic zone, resulting in different impacts on productivity (e.g., Falkowski et al. 1998). In Panama Bay, seasonal upwelling brings waters rich in P, N, and Si during the dry season, whereas freshwater discharge brings waters relatively low in P, N, and Si during the rainy season (D’Croz and O’Dea 2007). This observation has led researchers to propose that freshwater has little effect on nutrient input and productivity in the Gulf of Panama (Forsbergh 1969, D’Croz and O’Dea 2007). However, where upwelling is not a factor, such as in the SWC, nutrient delivery by freshwater input can play a significant role in the distribution of nutrients and productivity. For example, D’Croz et al. (2005) found “high” concentrations of nutrients, chlorophyll a, and zooplankton biomass during periods of heavy rainfall in the Bocas del Toro archipelago. Furthermore, lower-salinity Chiriquí Lagoon waters in the archipelago (not to be confused with Gulf of Chiriquí) had higher N and Si, and slightly higher P concentrations during periods of high rainfall, compared with Almirante Bay which has a smaller catchment area, and open ocean exposed areas. Admittedly, the influence of anthropogenic nutrients associated with modern freshwater input is uncertain. Such an inverse relationship between nutrients and salinity was not evident at San Blas, with its lower agricultural impact; however, the San Blas area is also more exposed to the open ocean and has a smaller watershed (D’Croz and Robertson 1997, D’Croz et al. 2005).

Based on previous oceanographic observations we have labeled our isotopic fields in terms of shallow-water nutrient status (Fig. 9C). As expected, Bocas del Toro and Golfo de los Mosquitos (SWC) samples fall within the oligotrophic zone and Gulf of Panama (TEP) samples fall within the eutrophic zone. Gulf of Chiriquí samples (TEP) are mesotrophic, reflective of the moderate shoaling of the thermocline and greater sample depth that limits the influence of low salinity waters. The one San Blas sample is an enigma, which falls within the mesotrophic facies yet comes from the oligotrophic SWC. The juvenile portion of this shell (first 24 of 40 samples), however, shows a strong positive O-C correlation ($R = 0.85$). This relationship and the low average and baseline-normalized δ¹⁸O values for the sample are all consistent with a strong influence of freshening, and placement in an oligotrophic zone.

**Application to Neogene Fossils.**—Successful application of the isotopic baseline method to quantify upwelling and freshening in ancient environments requires accurate paleodepth and baseline determinations. With increasing depth, seasonal temperature and salinity ranges and consequently Δ¹⁸O$_{shell}$ decrease. This effect is seen in the low Δ¹⁸O$_{shell}$ of specimens from the Golfo de los Mosquitos (41
m) and Gulf of Chiriquí (61 m). Deeper waters have a higher nutrient content, but bottom productivity is limited by light availability. Surface productivity is also limited by the upward penetration of deeper waters. Hydrographic measurements and the isotopic profiles of Gulf of Chiriquí sample GC97-80B at 61 m reveal seasonal shoaling of the thermocline, but these vertically advected waters do not penetrate the surface ocean and thus do not produce the high productivity seen in the Gulf of Panama.

Paleodepth can be constrained with faunal depth indicators such as benthic foraminifera, ostracods, fish, and scleractinian corals (Aguilera and Aguilera 1999, Collins et al. 1999). Using benthic foraminifera, Collins (1993) was able to determine the paleobathymetry of Neogene deposits from Bocas del Toro Basin into relatively precise ranges of 20–40, 40–80, 100–150, 150–200, and 300–500 m. Preliminary oxygen isotope data for serially sampled fossil gastropods corroborate the depth assignations of these Neogene deposits (Robbins et al. 2011).

With estimates of paleodepth and planktonic foraminiferal δ¹⁸O data from proximal deep-sea drill cores, it is possible to determine open-ocean baseline values for δ¹⁸O in the geological past. Seasonal deviation in gastropod δ¹⁸O profiles from these baseline values can then used to quantify the relative amounts of upwelling and freshening. Depending on paleodepth and availability, isotopic baselines can be established with data from *Globigerinoides ruber* (d’Orbigny, 1839) (<30 m), *Globigerinoides sacculifer* (Brady, 1877) (approximately 20–40 m), or *Neogloboquadrina dutertrei* (d’Orbigny, 1839) (approximately 60–150 m; Farmer et al. 2007). To correct for cross-isthmian temperature and salinity differences, these baseline data should be collected for samples on the Caribbean and Pacific sides of the isthmus.

In conclusion, oxygen isotope profiles of *Conus* shells collected from modern Panamanian seas typically follow the expected δ¹⁸O pattern estimated from temperature and salinity. It is therefore possible to determine shell chronologies based on seasonal variations in upwelling and rainfall when present. Upwelling intensity and freshwater input can be quantified by referencing seasonal variations in δ¹⁸O profiles to open-ocean baselines free of freshwater and upwelling effects. Shell profiles reveal little upwelling in the southwest Caribbean but strong upwelling in the Gulf of Panama, consistent with hydrological observations. In the Gulf of Panama, seasonal δ¹⁸O maxima yield isotopic temperatures as much as 9 °C lower than non-upwelling temperatures, suggesting upward movement of nutrient-rich waters of 60 m or more; seasonal δ¹⁸O minima document rainy-season salinities as low as 28. Correlation between δ¹⁸O and δ¹³C also serves as an indicator of upwelling (negative correlation) and freshening (positive correlation), and when plotted vs δ¹⁸O range provides a graphic representation of an environment’s nutrient status and sources. These techniques, combined with paleodepth information and baseline δ¹⁸O values defined from analyses of deep-sea planktonic foraminifera, can be used to characterize the nutrient status of ancient tropical coastal ecosystems.
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Literature Cited


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Addresses: (KT) Department of Geology and Geophysics, Texas A&M University, College Station, Texas 77843-3115. (JAR) Department of Geology and Geophysics, Texas A&M University, College Station, Texas 77843-3115. (ELG) Department of Geology and Geophysics, Texas A&M University, College Station, Texas 77843-3115. (AO’D) Smithsonian Tropical Research Institute, P.O. Box 0843-03092, Balboa, Republic of Panama. Corresponding Author: (ELG) Email: <e-grossman@tamu.edu>.