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Increased rainfall remarkably freshens estuarine and coastal waters on the Pacific coast of Panama: Magnitude and likely effects on upwelling and nutrient supply

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ABSTRACT

Increased intensity of rainfall events during late 2010 led to a remarkable freshening of estuarine, near- and off-shore waters in coastal Pacific Panama. The increased rain intensity during the wet season of 2010 lowered salinity of estuarine and coastal waters to levels unprecedented in previous years. Fresher conditions were most marked within estuaries, but even at 6 km from shore, salinities were 8–13‰ lower during the 2010 wet season, compared to a lowering of up to 2‰ during previous wet seasons. Freshwater added to surface waters by rain had major biological, hydrodynamic, and biogeochemical consequences, increasing stream erosion, uprooting stream-edge terrestrial and mangrove trees, increasing mortality of benthic fauna, damping upwelling of denser, nutrient-rich water that was expected given the contemporaneous most intense La Niña in decades, as well as by enriching surface seawater by direct deposition and by horizontal advection of nutrients from land. It appears that wet season rainfall is slowly increasing in the region, and if the level of rainfall reported here is a harbinger of future climate change effects on land–sea couplings in tropical coastal ecosystems, the resulting freshening could significantly shift biogeochemistry and coastal food webs in the region and elsewhere.

1. Introduction

During late 2010 and early 2011 Central and Northern South America suffered severe floods, resulting in national states of emergency, with deaths, widespread evacuations, loss of homes and resources, lack of potable water and diseases such as cholera (*El Espectador online edition*, 26 April 2011; http://www.medicalnewstoday.com/articles/211566.php). Global-scale increases in rainfall may be attributed to a 4% rise of water vapor content of the atmosphere since 1970 (Milly et al., 2002; Trenberth et al., 2005; Santer et al., 2007; Pall et al., 2011), but more locally, effects have been spatially patchy, with increased rain in Panama and Colombia, while Brazil suffered droughts (Malhi et al., 2008; Marengo et al., 2008; Lewis et al., 2011; Min et al., 2011). It has been suggested that such shifts in rainfall within this part of the world may be associated with climate-driven changes in El Niño Southern Oscillation (ENSO), and, particularly, the increases in rain may be linked to rainy seasons influenced by La Niña phases of the cycle (Mackey et al., 2010).

In this paper we first examine whether the unusual high-rainfall conditions could be related to large-scale ENSO effects, and whether, as noted in recent global-scale climate studies (Milly et al., 2002; Groisman et al., 2005; Trenberth et al., 2005; Santer et al., 2007; Malhi et al., 2008; Min et al., 2011; Pall et al., 2011), the larger-than-normal rainfall occurred as higher frequency of high-intensity events. We then present a first documentation of the remarkable lowering of salinity of estuarine and coastal waters that followed the unusually high precipitation, and might forecast the future fate of coastal waters in a climate with increased precipitation. We lastly suggest some of the biological and ecosystem-level consequences of the freshening of coastal waters that we document.

2. Methods

2.1. The region

The site of the study lies on the Pacific coast of Panama (Fig. 1), where we examined eight watersheds (Fig. 1 and Table 1) that

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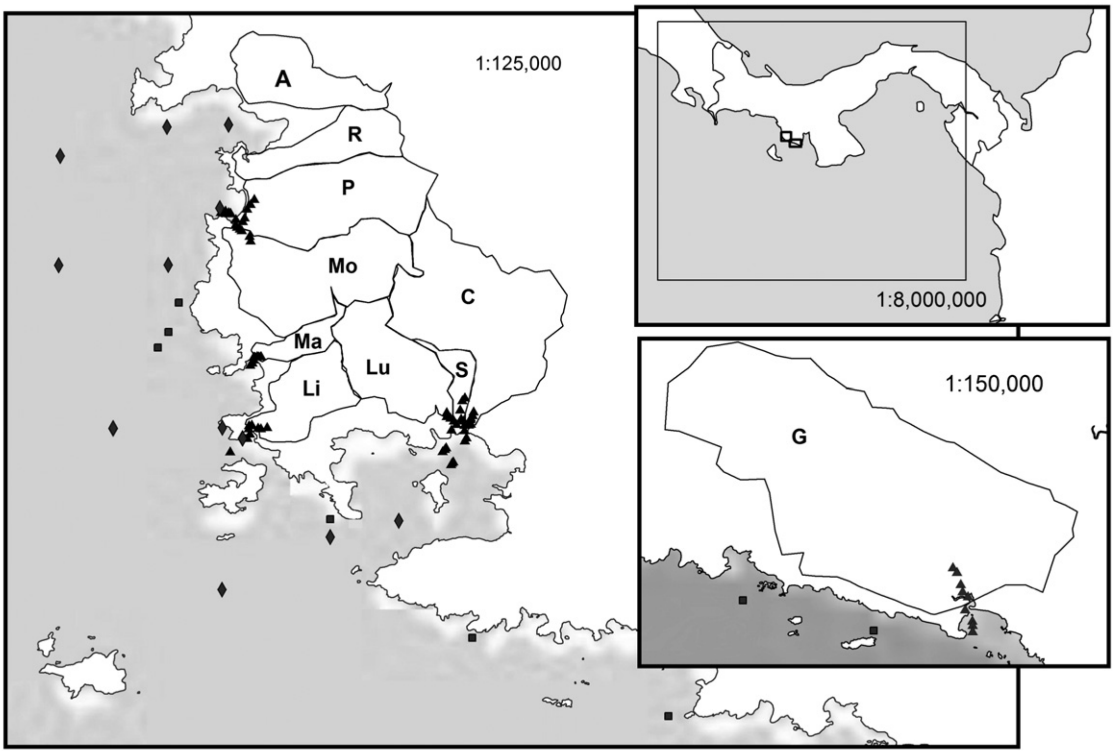

Fig. 1. Maps of the study areas. Inset on top right: Map of Panama, including a larger box showing the area used to estimate TRMM regional rainfall, smaller boxes indicating the position of the main area of our study, with seven of the watershed-estuary systems (P: Rio Pixvae, Mo: Rio de la Mona, Ma: Rio Manglarito, Li: Rio Limon, Lu: Rio Luis, S: Rio Salmonete, and C: Rio Chamuscado), and the position of Rio Grande, the remaining watershed-estuary system, shown in inset on bottom right. Sampling locations for 2010 in and off estuaries are shown as triangles, near-shore stations as squares, off-shore stations as diamonds. Selected features of the watershed-estuary systems are included in Table 1.

drain into estuaries that in turn empty into the Pacific. The land cover on the watersheds consisted largely of seasonal rainforest, with some pastures created by artisanal-level burning (Table 1 and Valiela et al., submitted for publication-a, submitted for publication-b). There were minimal bare surfaces or agricultural land covers in the region.

2.2. Analysis of the precipitation record

To examine the precipitation regime that led to the flooding events, we used precipitation estimates for the Eastern Tropical Pacific coast of Panama, based on satellite data and modeling, obtained from the Tropical Rainfall Measuring Mission (TRMM 3B42(v6); http://trmm.gsfc.nasa.gov/). We analyzed cumulative predicted rainfall over an area of 363,000 km^2 on latitude 5–10°N and from longitude 78°W to 84°W for the years 2004 through 2010 (Fig. 1, larger box in top right inset). These data are available as rectangles with a minimum pixel size of 0.5° (about 55 × 55 km or 3025 km^2). We considered a region of 363,000 km^2, which amounts to ~120 pixels—perhaps a minimum to be useful as regionally representative data. From these regional data, we compared rainfall during 2010 with the record for the previous six years. To assess whether the intensity of rainfall events differed in 2010 relative to earlier years, we also determined the frequency distribution of daily rainfall events from the TRMM record.

2.3. Freshening of estuarine and coastal waters

To assess the effect of rainfall during 2010 on the salinity regime of estuarine and coastal waters of the Pacific coast of Panama, we used data from surveys we conducted during December 2010; this sampling period was selected so as to capture cumulative effects of rain during the just-concluded 2010 rainy season. To determine the salinity regime within estuaries, we sampled 6 stations during ebbing to low tides, when water columns were shallower and reasonably

Table 1
Selected properties of the watershed-estuary systems included in this study, including area, land covers, maximum watershed elevations and lengths. Values derived from the remote sensing sources cited in text and Valiela et al. (submitted for publication-a, submitted for publication-b).

Watershed-estuary	Area of watershed	Land cover (% of area)					Max. elev.	Max. length
		Forest	Pasture	Burned	Bare	Mangrove		
	(ha)						(m)	(m)
Pixvae	1429	73	23	2	1.4	1.4	629	6410
de la Mona	1575	47	47	4.7	0.1	1.5	462	6468
Manglarito	239	91	6	1.8	0	0.4	340	3626
Limon	665	92	5	0	0	3	382	4220
Luis	1007	73	18	5.2	0.3	3.5	382	5109
Salmonete	195	29	52	2	0	18	330	3814
Chamuscado	2229	66	28	0.3	0.3	1.6	599	8229
Grande	9639	23	43	31	0	2	–	–

well-mixed vertically. These within-estuary stations span the fresh-to-seawater gradient within the estuaries (Fig. 1). The exact location of the stations differed among sampling times and among estuaries (longitude and latitude data for the stations are provided in Table S1 in Supplementary Information). The differences in location were influenced by contrasting area and horizontal reach among the different watershed–estuary systems (Table 1), and by having to adjust sampling locations to tidal variations that span well over 4 m.

To assess the salinity regimes just outside the mouth of the estuaries, we also sampled water during ebb tides at additional stations at approximately 50, 100, and 300 m off each estuary (Fig. 1). These off-estuary stations were deeper than the within-estuary stations, so we collected water samples in profiles down to 5 m.

To define whether freshening effects of the 2010 wet season extended beyond 300 m from estuary mouths, we carried out two additional sets of measurements. First, we measured seawater salinity profiles in the upper 5 m in 8 near-shore stations located about 0.5–1 km away from shore (Fig. 1). All stations within estuaries, off-estuary mouths, and near-shore, were sampled using a dissolved oxygen and conductivity meter YSI 85–10. To assess whether the high rainfall during the 2010 wet season resulted in unusual conditions in within-estuary, off-estuary, and near-shore stations, we compared salinity measurements taken in Dec 2010, a period representative of the cumulative effects of the wet season, to salinities we measured in previous dry (Dec–Apr) and wet (May–Nov) seasons.

Second, to see if the effects of the unusual rainfall during late 2010 extended even farther out from shore, beyond what we are calling the near-shore stations, we made high-resolution casts at 1, 3, and 6 km from shore (Fig. 1), in four transects perpendicular to the coast, and compared salinity profiles to similar data collected in wet and dry seasons (April and September, 2009, and February 2010). In each station, we measured depth, conductivity, and temperature with a RBR XR620 multichannel conductivity–temperature–pressure CTD coupled with a Seapoint fluorometer and turbidity sensor.

3. Results and discussion

3.1. Amount and intensity of rain in 2010 relative to previous years

Floods and unusual rainfall in 2010 coincided with the strongest recent La Niña phase (Fig. 2 left), made evident during late 2010 and early 2011 as the lowest reported ENSO index within recent decades (Wolter, 1987; Wolter and Timlin, 1993, 1998, http://www.esrl.noaa.gov/psd/enso/enso.mei_index.html).

Cumulative rainfall reported for the region (encompassed by large box within top right inset of Fig. 1) through 2010 was consistently but modestly larger than the average for 2004–2009 (Fig. 2 right). Annual rainfall on various parts of the Pacific coast of Panama normally reaches about 3000 mm yr^{-1} (Candanedo and Fábrega, 1999), an estimate similar to TRMM values (Table 2). By pooling the monthly data of the TRMM record, we calculated that wet season rainfall during 2010 reached 2984 mm. This value was 17% larger than the mean of 2561 mm that fell during the wet seasons of 2004–2009 (Table 2). These seem to be modest increases in total precipitation, so the question rises whether these increases could lead to the intense floods and other effects widely reported during late 2010.

Table 2
Dry, wet season, and annual rainfall during 2004–2011, for Western Panama (for area shown as large box in Fig. 1 (top right inset). Data from Tropical Rainfall Monitoring Mission.

Year	Rainfall (mm)		
	Dry season	Wet season	Annual
2004	233	2723	2956
2005	489	2141	2656
2006	555	2519	3074
2007	360	2857	3217
2008	343	2614	2957
2009	443	2510	2953
2010	343	2984	3327
2011	445	3316[a]	3761[a]
Mean	*401*	*2708*	*3113*

[a] 2011 wet season data provided by TRMM 3B42(v6) only extends to June. The 2011 wet season and annual rainfall data were extrapolated by using the ratio of May and June rainfall to total wet season rainfall from 2004 to 2010.

One answer to that question may be that TRMM estimates (Fig. 2) are averages over large areas (Fig. 1 top right inset), but rain is spatially highly heterogeneous: mean estimates for large regions may mask quite high (or low) amounts of rain falling at local sites (Javanmard et al., 2010). For example, highest *mean regional* rainfall values only reached 50 mm d^{-1} (Fig. 3 top), when, in fact, some localities, including the area where we carried out our measurements, experienced daily rainfall > 400 mm more than once during the 2010 wet season [SERVIR, the Mesoamerican Regional Climate Monitoring Center (http://www.nasa.gov/mission_pages/servir/index.html), and personal observations]. Since rainfall is spatially patchy, a 17% overall region-wide increase could have feasibly led to local high rainfall that led to flooding in Panama and elsewhere, as well as the remarkable freshening of coastal water we report below.

A second reason for the flooding of 2010 might involve the increased frequency of more intense rainfall events (> 30 mm d^{-1}, Fig. 3). To evaluate the frequency of intensity of rain events during 2010, we ran contingency χ^2 tests on the % difference between 2004 and 2009 and 2010 in frequency of rain events with different

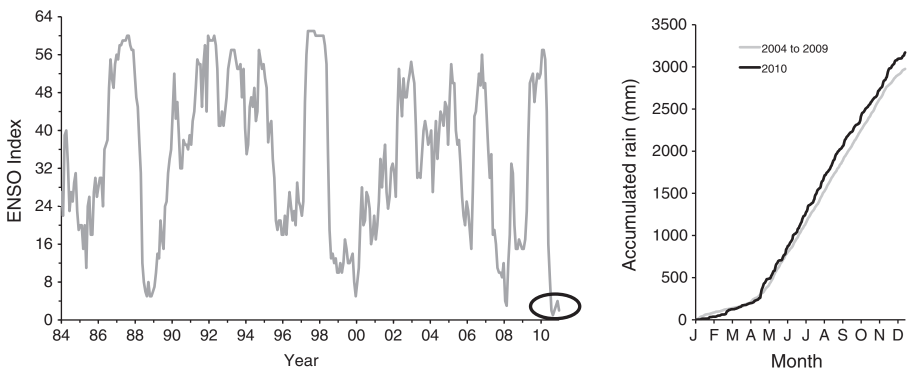

Fig. 2. Left: Multivariate El Niño–Southern Oscillation index, 1984–2011, data from http://www.esrl.noaa.gov/psd/enso/enso.mei_index.html. The oval highlights the 2010 La Niña period, the most intense in decades. Right: Running 2-day average of daily accumulated amount of rain, for Jan–Dec, for 2010, and for means of similar data for the years 2004–2009. Data obtained by remote sensing and modeling, from http://trmm.gsfc.nasa.gov/, for an area of 363,000 km^2 at 5° to 10°N latitude and 78° to 84°W longitude (see larger box, Fig. 1 inset on top right).

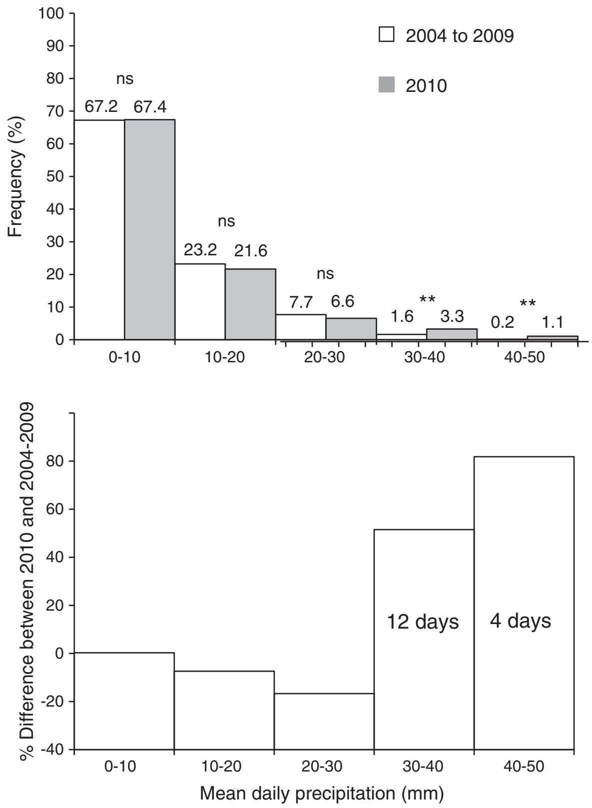

Fig. 3. Top: Frequency distribution of mean daily precipitation records, for the same data source in Fig. 2 right, for 2010 and for 2004–2009, pooled into bins of 10 mm of rain. Numbers on top of bars are the percentages per bin per the year; contingency $\chi^2 = 13.7$, comparing 2010 to pooled 2004–2009 data, significant at 0.01 for the entire data set; $\chi^2 = 0.31$ for bins 0–30, not significant; $\chi^2 = 18.1$ for bins 30–50, significant at 0.01. Bottom: % difference between 2010 and 2004–2009 per bin, from data in histogram on top panel. The % differences between 2010 and the period 2004–2009 were not different for rain events between 0 and 30 mm, but in 2010 there were 12 extra days with 30–40 mm rain, and 4 extra days with rain of 40–50 mm.

magnitude (in bins of 0–10, 10–20, 20–30, 30–40, and 40–50 mm of rain, Fig. 3). Frequency of rain events <30 mm did not differ between 2004 and 2005 and 2010, but there was a significant difference in rain events >30 mm (Fig. 3 top). In addition to more intense rains, there were significantly more days when more intense region-wide rain fell during 2010 compared to the mean of 2005–2009 (12 additional days with 30–40 mm of rain, 4 additional days with 40–50 mm rainfall, Fig. 3 bottom). The conclusion that more frequent high intensity rain events are key to increases in annual rainfall and its effects is in agreement with other studies (Milly et al., 2002; Groisman et al., 2005; Trenberth et al., 2005; Santer et al., 2007; Malhi et al., 2008; Min et al., 2011; Pall et al., 2011).

3.2. Reduction of salinity throughout the region

The watersheds in the study region drain into streams that deliver freshwater down the estuaries toward the sea. The estuaries we studied differ in length, so we first normalized station locations to % of the distance where each sample was collected relative to the mouth of the estuary, then calculated mean salinity for the data binned by 10% increments, both upstream and off the estuary mouth (Fig. 4).

The relative effect of the increased rain during 2010 is evident in comparisons of down-estuary gradients in salinity during dry and wet seasons, and among years (Fig. 4). During dry seasons, salinity of estuarine water ranged from 0 at upstream stations to the 31–34‰ typical of surface seawater in this region (Fig. 4, gray band). During the wet season of 2009, when rainfall was near average for previous years (Table 2), salinities were lower throughout the

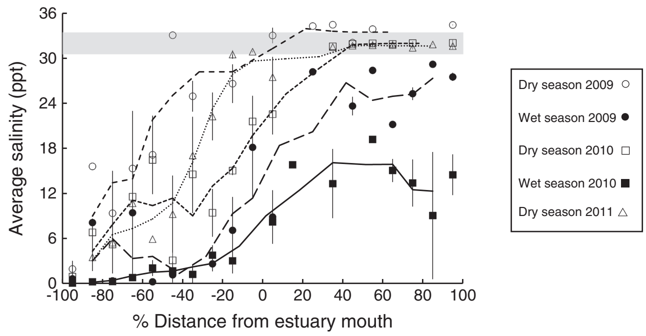

Fig. 4. Salinity (mean ± se) in water collected at sampling stations from fresh headwaters to 300 m from mouth of the eight estuaries included in Table 1 and Fig. 2, during wet and dry seasons for 2009 and 2010 and dry season of 2011. Station location is shown as the % of the distance (either upstream or off-estuary) between location of the station sampled relative to the mouth of the estuary. The % values were pooled into 10% bins. The lines are three-point running means included to guide the reader as to trends. The data for stations off the estuary mouths show surface salinity; vertical profiles of off-estuary stations are shown in Fig. 5. (left). The gray band represents the range of surface salinity for the region, from D'Croz and O'Dea (2007), and our own data.

estuaries, and only reached about 20‰ near estuary mouths (Fig. 4, black circles), compared to the more usual 31–34‰ recorded during dry seasons. In contrast, during the wet season of 2010 salinities through the estuaries became considerably freshened (Fig. 4), reaching surprisingly low values of about 10‰ at the estuary mouth.

The freshening during the 2010 wet season extended to waters off the estuary mouths, where salinities were about 12‰ (Fig. 4), the lowest found during the three years of study. Moreover, the unusual 2010 wet season freshening extended, in sites off the mouth of the estuaries, from a maximum of 8–10‰ at the surface, and the freshening was still notable as far as 5 m down the water column (Fig. 5 left). For comparison, during the more-normal rain of the 2009 wet season (Table 2), surface seawater salinities at stations off estuaries decreased, but only to 24–27‰ (Fig. 5 left).

The degree of freshening measured during wet seasons, and particularly during the unusually rainy 2010 wet season, should be compared to conditions during dry seasons, when salinities in surface samples beyond the estuaries (Fig. 5 left) reached—and in 2009 even exceeded—the 31–33‰ values typical of oceanic surface water in the region (Takesue et al., 2004; D'Croz and O'Dea, 2007). The saltier water during the 2009 dry season (Fig. 5 left) indicated significant upwelling, since water with salinity >32‰ likely rose from depths below 30 m or so (Takesue et al., 2004; D'Croz and O'Dea, 2007). During the 2010 dry season salinity in stations beyond estuary mouths was vertically uniform (Fig. 6 left), with no hint of effects of upwelling or freshening owing to rainfall.

The substantial freshening we observed in and near estuaries during wet season 2010 extended well into the coastal marine environment, judging from salinity profiles taken at stations 0.5–1 km from shore (Fig. 5 right) and at 1–6 km from shore (Fig. 6). The upper 5 m of the water column at distances 0.5–1 km from shore were, on average, 13‰ lower than mean seawater (Fig. 5 right), far fresher than the 1–3‰ lowering reported during more-normal wet seasons (D'Croz and O'Dea, 2007). At the peak of the 2010 wet season, sea water salinity of seawater was reduced to 20‰ in the upper 5 m in stations 0.5–1 km from the coast (Fig. 5 right). By April 2011, late in the dry season, salinity profiles in these same stations had returned to the usual 31–33‰ (Fig. 5 right). Freshening during the unusually wet season of 2010 was therefore unusually large following the wet season, but was a transient phenomenon that disappeared during the next dry season.

During the wet season of 2010 considerable freshening of surface waters was detectable even farther offshore. In CTD profiles (Fig. 6) obtained at 1, 3, and 6 km from land during the 2009 dry season,

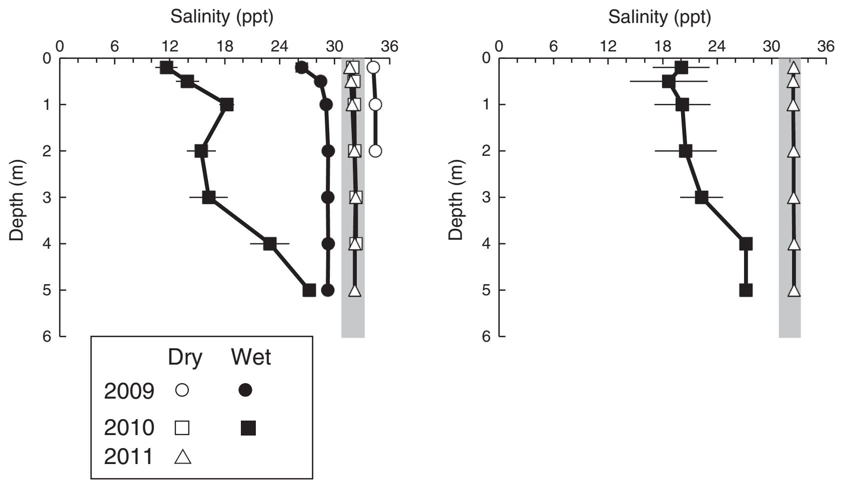

Fig. 5. Left: Salinity (mean ± se) profiles from stations located 50–300 m off the mouth of the estuaries. Right: Salinity profiles (mean ± se) for 8 additional stations (Fig. 2) located between 500 and 1000 m from shore, taken during wet season, Dec. 2010 and dry season, April 2011. Gray bands show the range of 31–33‰ characteristic of salinity of ocean water in the region.

salinity of the upper 20 m remained within the 31–33‰ range, regardless of distance away from shore (Fig. 6). As heavy rain started through September 2010, surface salinity became lower, and by December 2010—the end of the wet season—near-surface salinity reached about 10‰ at 1 km and 22‰ at 6 km from shore. The freshening of surface water we found in estuarine areas therefore surprisingly extended to more than 6 km from shore, and extended vertically to 30–40 m (Fig. 6). By February 2010, rains diminished, and salinity increased.

The lowered salinities recorded during the peak of the 2010 wet season in the CTD surveys (Fig. 6) could result from direct deposition of fresh rainwater. To test this conjecture, we roughly estimated the volumes of freshwater that fell directly on the sea surface, and compared these to estimates of volumes of freshwater that were responsible for the seawater dilution we measured. We estimated these freshwater volumes by back-calculation from salinity measurements taken during the CTD surveys (Table 3). Direct rain deposition amounted to about half the volume of freshwater that had to be present in the water column of 1–6 km from shore (Fig. 6). This suggests that there had to be considerable horizontal advection of freshwater, presumably derived from rain water that fell on land and was transported seaward (Takesue et al., 2004). The land-to-sea gradient in % of the water column volume that was contributed by freshwater (Table 3) was additional evidence that some advection from the land may have taken place. An abundance of mangrove leaves floating on the sea surface in most

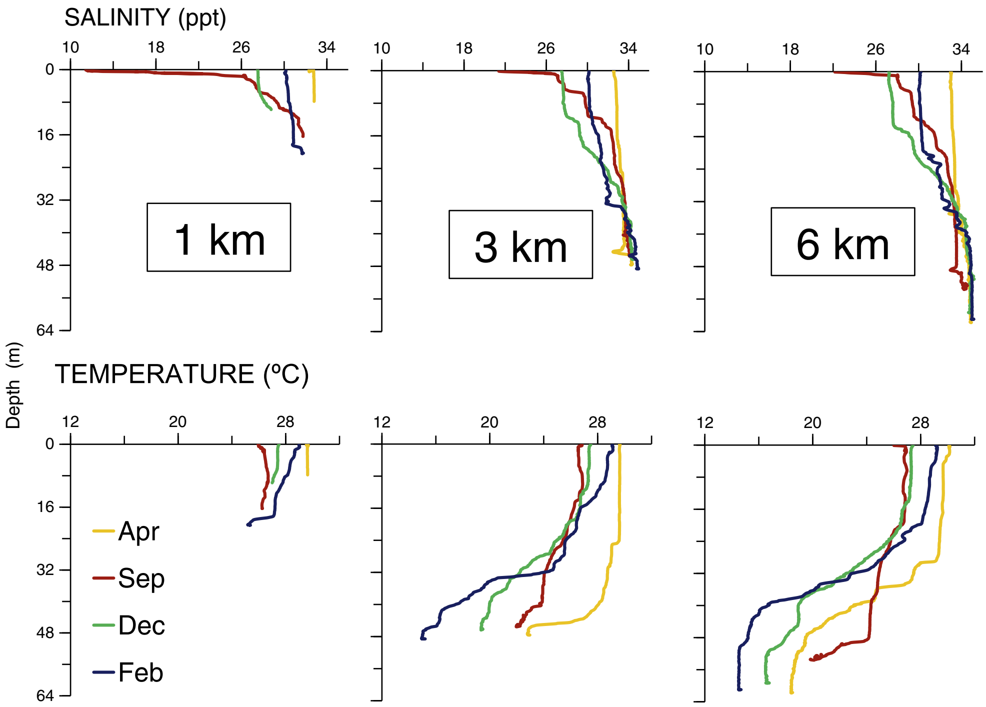

Fig. 6. Profiles of salinity and temperature taken during CTD casts done in April, September, December 2010, and February 2011, in stations located at 1, 3, and 6 km away from shore.

Table 3
Approximate assessments of the relative contributions of freshwater to a 1 m^2 of the water column, at three different distances away from shore, wet season 2010.

Distance from shore (km)	Down to depth[a] of	% of water column that was freshwater[b]	Volume of freshwater in water column (m^3)[c]	Volume of freshwater directly contributed by rainfall (m^3)[d]	% freshwater in the water column derived from direct deposition
1	20 m	21.4	4.3	2.7	63
3	30 m	16.7	5.0	2.7	54
6	50 m	11.3	5.7	2.7	47
				Mean	*55*

[a] Depths selected from the CTD profiles in Fig. 7.
[b] Back-calculated as volume fraction in freshwater = [1 − (salinity in sample / salinity in seawater end-member), for depth bins of 10 m each, and summing the bins to the depths shown in the second column. A value of 35.01‰ was taken as the salinity end member, from CTD profiles shown in Fig. 7. The procedure was repeated, and results averaged across CTD stations shown as diamonds in Fig. 2.
[c] Values calculated refer to an area of 1 m^2 of sea surface.
[d] For the wet season of 2010, Apr–Nov, TRMM data shows that about 2719 mm of rain fell on the region shown as the larger box in the top right inset of Fig. 2.

stations provided additional visual evidence of horizontal export from the estuaries to the offshore.

3.3. Some biological consequences of the increased freshwater influx

The unusual weather in Panama during 2010 increased flow of freshwater to estuaries and to the sea, and the consequent lowering of estuarine and coastal salinities—documented above—could have had significant biological consequences. We have some hints that major biological effects were a result of the higher-than-normal freshwater flows during the wet season of 2010.

In the estuaries on the Pacific coast of Panama, there was widespread uprooting and stranding of large terrestrial trees (Fig. 7a), and abundant branch and leaf fragments moving in tidal waters. Studies elsewhere in tropical estuaries have demonstrated large storm-related fluxes, particularly of organic materials, with significant biological effects on the receiving marine environments (Hilton et al., 2008; West et al., 2011). Erosion of stream banks and re-deposition of sediments down-stream were responsible for removal of many seedlings of the endemic mangrove tree, *Pelliciera rhizophorae*, a species whose seedlings colonize new stream-banks, which were eroded; erosion also undermined and collapsed long-established larger trees of this species (Fig. 7b, c).

There was also near-complete mortality of dense populations of oysters (*Saccostrea palmula*) settled on intertidal rocks in estuaries (Fig. 7d). The lowering of salinity associated with the higher rainfall of 2010 apparently was large enough to overwhelm the tolerance of estuarine oysters to lowered salinities (Bardach et al., 1972).

The unusual freshening seems likely to have affected subtidal biota: circumstantial evidence of such effects comes from increased mortality we recorded in two experiments with benthic bivalves

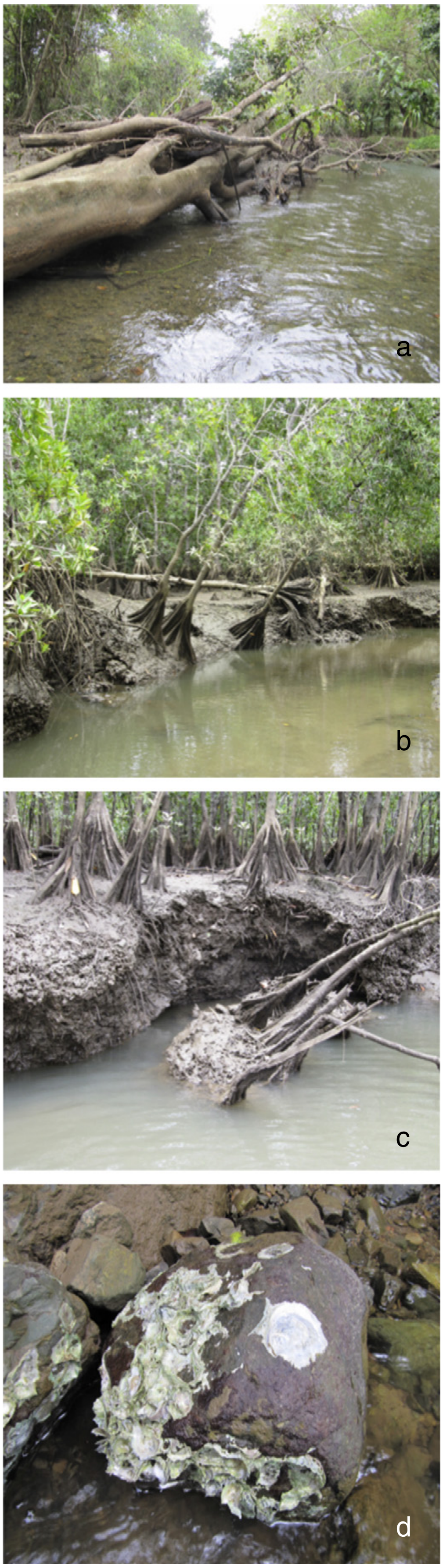

Fig. 7. Some effects of higher-than-usual discharges of freshwater down-stream in the estuaries. a: Large terrestrial trees were commonly swept into headwater streams of estuaries during wet season, 2010. b: Undermining of estuarine stream banks by the increased freshwater flows of late 2010. Specimens of the endemic mangrove tree, *Pelliciera rhizophorae*, originally growing upright on the mangrove platform near the edge of estuarine streams, were, after the intense rains, now tilting into the streams. The strong flows undermined mangrove stands by removing sediments below the upper 50 cm of sediment consolidated by a dense mat of mangrove roots. The upper layer still remained in this image, but now slopes steeply into the estuary. c: example where the freshwater flow more thoroughly eroded the shore, so that the *P. rhizophorae* tree roots could no longer hold the upper layer in place. d: Oysters killed by exposure to freshwater during wet season, 2010. The one largest specimen was about 8 cm in length.

that were designed with other aims, but were on-going during the 2010 wet season. In one, we had placed oysters (*Pinctada mazatlanica*) and sponges (*Aplysinia chiriquensis*) in cages at depths of 5 m at sites 100–300 m offshore from estuaries. Survival of oysters and sponges in these experimental cages was only 22 and 50%, respectively. In a second experiment, we had placed mangrove cockles (*Anadara tuberculosa*) in cages that were then installed in the mangrove sediment that is the natural habitat of the cockles. None of the cockles survived. These anecdotal observations lack appropriate controls, but the mortalities were suggestive of likely biological effects of the freshening. The loss of cockles might also have consequences for local peoples, because harvest of mangrove cockles makes a considerable contribution to sustenance diet of villages in the region (pers. obs., and MacKenzie, 2001).

3.4. Ecosystem-scale effects of freshening

The increased rainfall in the Pacific region of Panama is likely to have affected the ecology and biogeochemistry of coastal ecosystems. The larger-than-usual rainfall seems likely to have affected the action of external driving mechanisms such as upwelling of enriched deep waters, nutrient enrichment by increased rainfall, and also altered land-to-sea couplings.

One effect of the unusually high rainfall during the 2010 wet season might be to prevent nutrient enrichment by impeding upwelling of nutrients from deeper waters. Such upwelling has been an essential feature supporting coastal primary production in the region (Takesue et al., 2004; D'Croz and O'Dea, 2007). The large rainfall during 2010 created a 30 m-deep, less-dense surface layer (Fig. 6) that could certainly impair upwelling of deeper denser water bearing high nutrient concentrations.

A second, and countering effect, might have been that the unusual amount of rain could have enriched surface layers. We have shown that, for example, concentrations of nitrate and ammonium in local rain were considerably higher than those in surface seawater [on average, 5.3 vs. 0.02, and 3.7 vs. 0.5, all in μM, respectively, for nitrate and ammonium (Valiela et al., submitted for publication-a, submitted for publication-b)]. It therefore seems reasonable that the rainwater must have significantly enriched surface seawater, as found elsewhere (Duarte et al., 2006; Baker et al., 2007, 2010; Mackey et al., 2010; Zhang et al., 2010; Min et al., 2011; Pall et al., 2011). The enrichment had to be quantitatively important, since the rainfall of 2010 added freshwater volumes equivalent to one third of the volume of the surface layer, and the rain bore concentrations one to two orders of magnitude larger than those in the receiving seawater.

The relative role in nutrient supply of the two countering processes—impaired upwelling of nutrients and enrichment by direct rain deposition—remains to be discerned, but the profiles shown in Fig. 6 provide hints as to the action of the competing large-scale forcings on coastal Panama water columns. First, the unusually strong La Niña (Fig. 2 left) phase of ENSO has usually been associated with marked upwelling of deeper waters (D'Croz and O'Dea, 2007). Second, high rainfall—perhaps also associated with the La Niña condition (Mackey et al., 2010)—significantly increased freshwater discharge from land, reducing salinity of the upper layer of the water column. The net result of these countering forces can be seen in temperature profiles measured in the offshore stations (Fig. 6). Temperatures were nearly 29–30 °C in the upper layers of water and only varied a few degrees through the seasons (Fig. 6). La Niña conditions might have been expected to allow colder, deeper water to shoal toward the surface, but this did not take place in late 2010, even though this was the strongest La Niña in decades (Fig. 2). We cannot be sure of the specific mechanisms that prevented upwelling, but we conjecture that the freshening of the upper layer was involved in preventing upwelling.

The freshening of surface waters of wet season 2010 therefore likely impaired upwelling in the region, and the rainfall added nutrients by direct deposition on the sea surface. Only half the diluting freshwater, however, came to the surface layers by direct rain deposition. The other half, as estimated above, arrived by horizontal advection, most probably from land. The freshwater that emerged from land contained nutrient concentrations larger than concentrations present in surface seawater of the region (Valiela et al., submitted for publication-a, submitted for publication-b). Assessment of magnitudes of such advective nutrient exports, and comparisons to upwelling fluxes, await adequate mass balance studies, but it certainly appears as if increased rainfall lowered potential upwelling nutrient supply while favoring direct deposition and advective nutrient delivery to Pacific Panama coastal waters.

On aggregate, therefore, the evidence shows that increased frequency of more intense rain events during late 2010 substantially freshened coastal waters in the Pacific coast of Panama, intensified land-sea coupling by horizontal transport from watersheds through estuaries, and uncoupled surface water ecosystem production from deeper waters by both direct rainfall onto the sea surface, and by impeding upwelling. These alterations might be transient (http://www.cpc.ncep.noaa.gov/products/predictions/, http://www.bom.gov.au/climate/ahead/ENSO-summary.shtml), but if future climate trends include larger precipitation, we might anticipate consequential changes in upwelling-based and rain-delivered nutrient supply to ecosystems in the region and elsewhere in the tropics.

Precipitation in the region is trending upwards (Fig. 8). A longer skein of data would be desirable, but while we might worry about further statistical confirmation of trends of increased rainfall, continued increased rainfall is quite real to the many people affected by continuing widespread floods, damage, evacuations, and other rain-related issues such as reported in the press during the wet season of 2011—the year *after* our detection of remarkable rainfall and freshening ("Central America floods and landslides leave 80 dead", BBC News 17 Oct. 2011; "Central America flood crisis only just beginning", UN News Centre 5 Nov. 2011; "Floods in Central America", New York Times 17 Oct. 2011).

It may very well be that in coming decades Central America will have to increasingly deal with larger rainfall. Much will depend on the relative strength of future ENSO phases, but if rainfall continues to increase, coastal ecosystems may be subject to a new dynamic that may change the nature of land-sea couplings, perhaps in part by interfering with upwelling transport of marine-derived nutrients, and by advective and direct increased delivery of rain-borne nutrients. Anticipated changes in temperature and precipitation predicted by climate models could significantly increase freshwater inputs to the Pacific (http://trmm.gsfc.nasa.gov/), and altered ENSO events

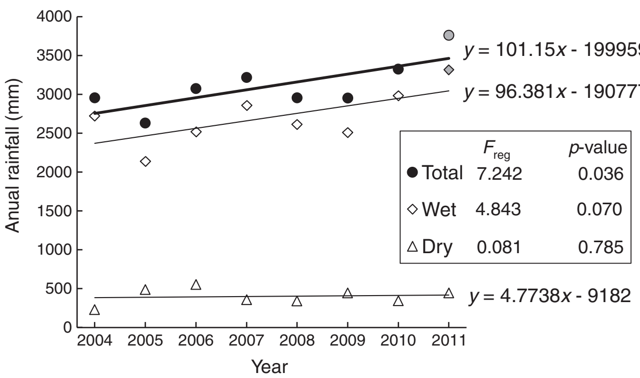

Fig. 8. Multiannual trend in total annual rainfall, and in wet season and dry season rainfall, 2004–2011. Data from TRMM. Linear regression equations. F_{reg} values, and *P* values are displayed on the graph. The grey points are extrapolated from May and June rain data values, as explained in Table 2.

may further shift upwelling rates. If the freshening we report here is a harbinger of the future, climate change may make fresher conditions more frequent, which would pose increasing problems for the human population, force major shifts in coastal food webs of this and similar regions elsewhere, as well as alter biogeochemical exchanges that mediate land-sea couplings in tropical coastal ecosystems.

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.gloplacha.2012.05.006.

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