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Spatiotemporal variability in Terminos Lagoon (Mexico) waters during the 2009–2010 drought reveals upcoming trophic status shift in response to climate change

Renaud Fichez¹ · Carlos Linares² · Sandrine Chifflet¹ · Pascal Conan³ · Adolfo Contreras Ruiz Esparza⁴ · Lionel Denis⁵ · Pascal Douillet¹ · Christian Grenz¹ · Jean-François Ghiglione³ · Francisco Gutiérrez Mendieta⁶ · Montserrat Origel-Moreno¹ · Alain Muñoz Caravaca⁷ · Mireille Pujo-Pay³ · Jorge Zavala-Hidalgo⁴

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Abstract

The 2009–2010 El Niño was accompanied by a severe drought strongly impacting Mexico as well as Central America, the Caribbean, and the southern USA. The present work aims at assessing how such a major climatic event impacted the hydrological typology of transitional waters in Terminos Lagoon, one of the largest shallow tropical lagoons fringing the Gulf of Mexico. Spatiotemporal inter-comparison of hydrological conditions was conducted by pairing a reference multiparametric dataset (14 hydrological parameters versus 34 sampling stations) averaged over the October 2008 to July 2010 period with each sampling occurrence dataset and running Principal Component Analyses (PCA), setting the reference-survey dataset as active variables and each sampling occurrence dataset as non-active (supplementary) variables. It revealed that the exceptional deficit in freshwater supply to the lagoon during the 2009–2010 El Niño drastically reduced hydrological diversity and lowered the trophic status of the lagoon. Short-term shifts in environmental status are common in transitional waters and responsible for temporary shifts in community structure but climate change projections show a significant long-term decrease in the freshwater discharge at the regional scale that will impact Terminos Lagoon as well as other coastal lagoons of Mexico and Central America. When combined with sea level rise, such a decrease will result in a long-term shift in hydrological conditions with a subsequent increase in salinity and a decrease in the diversity of environmental conditions affecting trophic status, will have a long-term impact on the biota.

Keywords Coastal lagoon · Hydrology · Trophic status · El Niño · Global change · Climate change, Mexico

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Introduction

Littoral regions accommodate a broad range of coastal systems with heterogeneous water bodies often referred to as “transitional waters” characterized by strong variability in salinity as well as in most environmental parameters of natural or anthropogenic origin which are driven by the balance between marine and freshwater inputs (Elliott and McLusky 2002; McLusky and Elliott 2007). Response of transitional waters to ongoing climate change has risen to the highest level of economic and political priority, resulting in a growing demand for the accurate scientific expertise essential for the definition; implementation; and control of ecologically, socially, and economically effective management plans. This is especially true in the Terminos Lagoon area, on the southern Gulf coast of Mexico, which has been singled out as being vulnerable to climate change (Magrin et al. 2007), potentially exposed by the end of the twenty-first century to a drastic decrease in river discharge from the Usumacinta-Grijalva River (Kemp et al. 2016), and subject to general sea level rise in the range 0.5 to 1 m (Magrin et al. 2007; Rahmstorf 2012). Here, as in all other transitional water systems, a proper assessment of spatiotemporal variability must be considered as a prerequisite to the scientific establishment of cause to effect relationships between global change and shifts in environmental conditions. However, spatiotemporal variability issues have often been overlooked in environmental studies, raising the risk of drawing insufficiently supported scientific interpretation and of misguiding environmental policies toward inefficient management action plans (Lucena-Moya et al. 2012). Extracting comprehensive information from multiparametric environmental databases remains a challenge and environmetric approaches based on multivariate data ordination have been proven to be a rigorous and integrative way of assessing spatial and temporal variability of transitional waters (Fichez et al. 2010; Shin et al. 2013). The approach developed in the present study specifically focuses on the physico-chemical and biogeochemical indicators of water quality that are commonly measured in environmental status assessments. Establishing a multiparametric characterization of transitional waters has been identified as a key integrative diagnostic approach that is still strongly lacking in environmental management (Poikane et al. 2014). Recent concerns about delineating environmental status categories for transitional waters have largely focused on intercomparison between distinct systems, to the detriment of the preliminary assessment of internal spatiotemporal variability (Larned 1998; Liston et al. 1992; Muslim and Jones 2003; Lucena-Moya et al. 2012), with the most in-depth studies often being circumscribed to gray literature reports (Haynes et al. 2001; Furnas 2003). As a consequence, and due to the complex synergistic impacts of ongoing changes in climate conditions and local anthropogenic drivers, there is a strong risk of hastily drawing cause-and-

effect relationship, regardless of what spatiotemporal variability has to teach us about the flexibility of tropical transitional systems and about the most probable scenarios at stake in terms of environmental response to global change. Such a lack of information on the distribution and temporal variability of environmental parameters is especially critical for coastal tropical systems of emerging and developing countries where the potential threat of global change is increasingly acknowledged as a key parameter detrimentally impacting sustainable development. This is even more salient for the Mesoamerican region (Central America and Southern Mexico), which is considered to be the most prominent tropical climate change hotspot worldwide (Giorgi 2006) and which is increasingly vulnerable to extreme climatic events (Hidalgo et al. 2013; Vázquez-González et al. 2014).

The present study was conducted on the very large and shallow coastal Terminos Lagoon during a time period including the 2009–2010 El Niño Southern Oscillation positive anomaly when Mexico experienced the most severe drought since 1941 (Baringer et al. 2010). Its objectives, based on a 2-year hydrological survey, aimed to (i) apply a data treatment allowing for temporal intercomparison of typology approaches; (ii) analyze what such an intercomparison could reveal in terms of seasonal cycling and climate change in the specific context of the severe 2009–2010 El Niño-related drought period; and (iii) assess potential long-term environmental alteration in Terminos Lagoon in the context of climate change projection scenarios.

Material and methods

Study site and environmental conditions

The selection of Terminos Lagoon as a focus site for the study of tropical coastal lagoon transitional waters arose logically from its exceptional status as one of the largest shallow systems in the Gulf of Mexico, where conservation policies conflicted with anthropogenic pressure (Grenz et al. 2017). Moreover, Terminos Lagoon benefited from a significant scientific background and has been the recent object of renewed interest from the scientific community leading to its selection as a “pilot site” within the framework of the Global Environment Facility (GEF) Program on the Gulf of Mexico-Large Marine Ecosystem (GoM-LME) (García-Ríos et al. 2013). Terminos Lagoon (Fig. 1) is located on the southern coast of the Gulf of Mexico in the Mexican state of Campeche and stretches over a surface of 1936 km² with an average depth of only 2.4 m yielding a total water volume of 4.65 km³ (Contreras Ruiz Esparza et al. 2014). Climate categories shift from tropical wet and dry in the lowlands to tropical rainforest in the highlands. There are three distinct seasonal periods throughout the year: a relatively dry season from

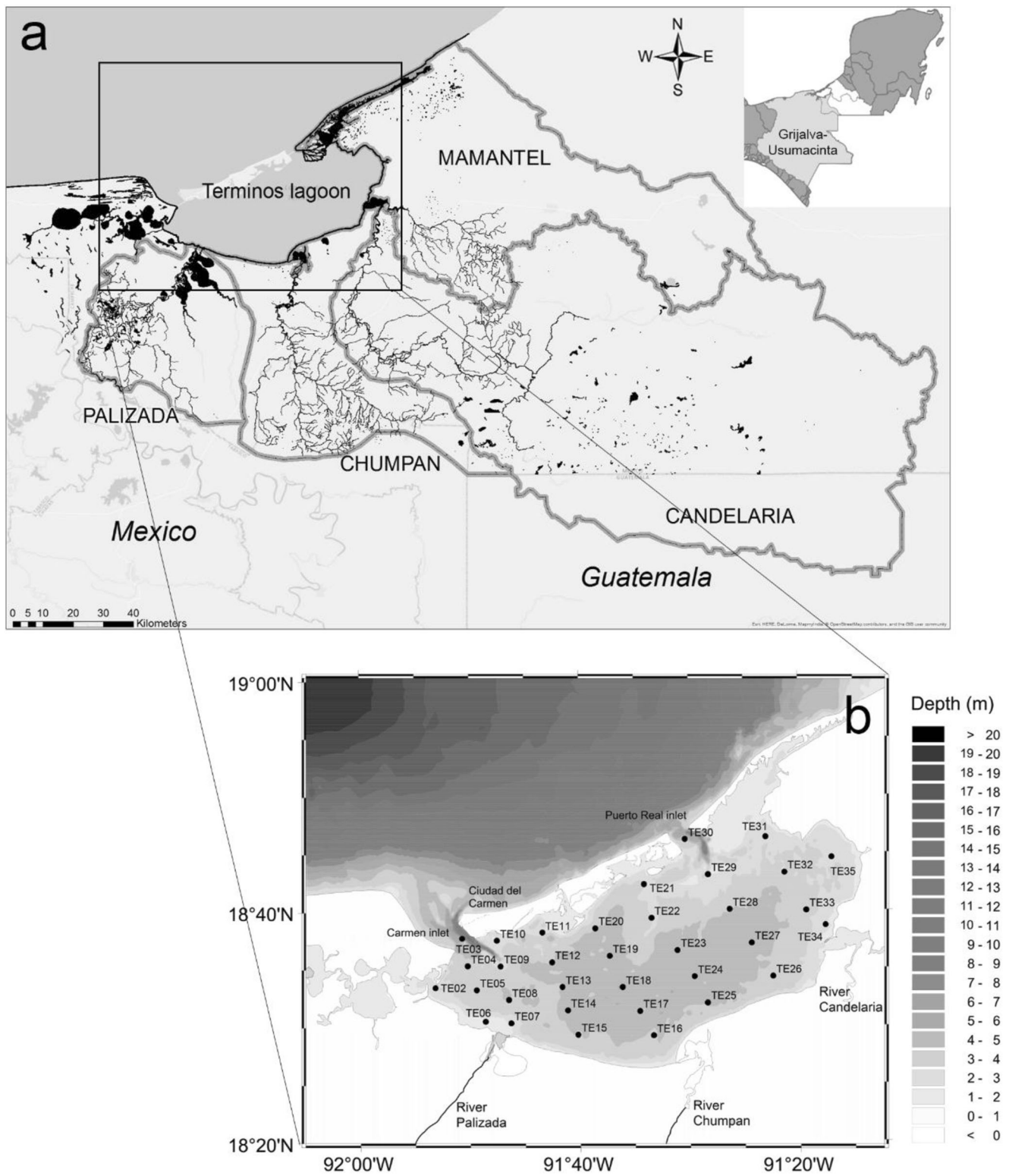


Fig. 1 **a** Terminos Lagoon location and surrounding watershed basins contributing to freshwater inputs keeping in mind that regardless of its watershed surface, roughly 10% of the Usumacinta River discharge flows

through the Palizada River contributing to circa 90% of the freshwater inputs to the lagoon; and **b** bathymetry of Terminos Lagoon with location of the 34 sampling stations

February to May, a rainy one from June to September, with a period of northern gales called “Nortes” between the two.

Inland, Terminos Lagoon is surrounded by two very distinct geologic provinces. Eastward stretches the Yucatan Peninsula,

characterized by low rainfall and a porous calcareous basement. This emerged carbonate platform has no river catchment so rainfall penetrates the porous basement, providing the water table with fresh water that finally seeps into the sea all along the coasts of the Peninsula. To the west and south of Terminos Lagoon are spread the lowlands of Tabasco and the highlands of Chiapas and Guatemala. Four river catchments directly discharge an average yearly volume of $11.96 \times 10^9 \text{ m}^3 \text{ yr}^{-1}$ of freshwater into Terminos Lagoon (Robadue Jr et al. 2004), roughly amounting to 2.6 times its volume. Average yearly precipitation and evaporation of 1805 mm yr^{-1} and 1512 mm yr^{-1} , respectively, result in a net rainfall of 293 mm yr^{-1} (David and Kjerfve 1998; Espinal et al. 2007) and freshwater groundwater inputs to Terminos Lagoon have been averaged at $4 \times 10^6 \text{ m}^3 \text{ yr}^{-1}$ (David 1999). The resulting freshwater input budget for Terminos Lagoon yielded a total net yearly input of $12.57 \times 10^9 \text{ m}^3 \text{ yr}^{-1}$, of which river discharge, precipitation net input, and groundwater seepage accounted for 95.44%, 4.53%, and 0.03%, respectively, river discharge, therefore, remaining by far the main source of freshwater inputs to Terminos Lagoon (Fichez et al. 2017). The Chumpán River is the lowest contributor, with an average annual freshwater discharge of $0.6 \times 10^9 \text{ m}^3 \text{ yr}^{-1}$ which passes through the Balchacah Lagoon before reaching Terminos Lagoon midway along its southern coast. The Candelaria River combines with the small Mamantel River to deliver a total of $2.26 \times 10^9 \text{ m}^3 \text{ yr}^{-1}$ of freshwater to the lagoon through the so-called Pargos Estuary. Finally, the Palizada River discharges an average of $9.1 \times 10^9 \text{ m}^3 \text{ yr}^{-1}$ of freshwater to Terminos Lagoon through the El Vapor, El Este, and Del Viento lagoons and the San Francisco and Chica openings, thereby accounting for more than two-thirds of the freshwater inputs to the lagoon. The Palizada is in fact a tributary of the Usumacinta River, which in turn is part of the intertwined Grijalva-Usumacinta basins that stretch over a total area of $112,550 \text{ km}^2$ (Hudson et al. 2005). Receiving an average annual rainfall of 1709 mm yr^{-1} , the Usumacinta River discharges an average annual freshwater volume of $69 \times 10^9 \text{ m}^3 \text{ yr}^{-1}$ to the Gulf of Mexico, of which a little less than one-tenth is diverted to the Terminos Lagoon through the Palizada River (Fichez et al. 2017). On its seaward side, the Terminos Lagoon is connected to the Gulf of Mexico by two straits — Carmen Strait on the western side (4 km long) and Puerto Real Strait on the eastern side (3.3 km long) — separated by Carmen Island, a carbonated sandbar 30 km long and 2.5 km wide. The lagoon's shallowness is disrupted only by channels located in the eastern part of each strait. Strong tidal currents generating lagoon inflow and outflow pass through those two straits that reach maximum depths of 19 m in Carmen Strait and 12 m in Puerto Real Strait.

Sampling

Sampling was conducted across a network of 34 stations (Fig. 1) during a total of nine sampling trips spanning a 2-year period from October 2008 to July 2010. Temperature, salinity (Sal), turbidity (Turb), oxygen saturation percentage ($\text{O}_2\%$), and in situ chlorophyll-a fluorescence (Fluo) profiles were obtained from a multiparametric profiler (SeaBird® SBE 19) equipped with additional sensors for turbidity (Seapoint® optical back scatter), dissolved oxygen (SeaBird® SBE 43), and chlorophyll-a in situ fluorescence (WETLabs® WETStar). Salinity was obtained with a precision of 0.001. Calibrated back scattering turbidity sensors set-up in high turbidity mode provided NTU or nephelometric turbidity unit values with a precision of 0.1 NTU. As a general rule, it has been reported that backscattering was linearly correlated to suspended particulate matter concentrations below 10 g l^{-1} with a general correspondence of 1 NTU for 1 mg, with negligible variability between individual nephelometers but significant inter-site variability due to the very diverse optical properties and multi-modal particle size distribution of suspended particles in coastal lagoons (Ouillon et al. 2004). Chlorophyll-a in situ fluorescence is reported as arbitrary fluorescence units with a precision of 0.01 units. The combination of in situ fluorescence and chlorophyll-a analysis permitted to establish positive correlations between chlorophyll-a concentrations and in situ fluorescence for each sampling period. But the relationship changed from one sampling period to the next as other pigments — as well as particulate and dissolved organic matter generally abundant in transitional waters — interfered with the 460/695 nm excitation/emission wavelengths used to detect in situ chlorophyll-a (Zeng and Li 2015), thus preventing the establishment of a generic conversion rule.

Water was sampled using 5-l Go-Flo bottles maintained horizontally at about 0.2 m below the surface. On board, water samples were treated following a three-step protocol: (1) as soon as the sampling bottle was retrieved, a 40-mL Schott® glass vial (previously washed with acid) was rinsed thrice with sampled water, filled, immediately injected with the reagent for ammonia (NH_4) determination, sealed, and stored in the dark for later fluorometric detection in the laboratory (Kérouel and Aminot 1997; Holmes et al. 1999); (2) two 30-mL and one 120-mL Nalgene® plastic vials, all previously acid-washed, were rinsed thrice with sampled water, filled, and stored in a specifically dedicated and refrigerated ice cooler, to be later deep-frozen in the laboratory while awaiting analysis of dissolved inorganic and organic nutrients; and (3) a previously acid-washed 4-L Nalgene® plastic container was rinsed thrice with sampled water, filled, and stored in a dedicated ice cooler. Back in the laboratory, water subsamples were filtered through 25 and 47 mm diameter Whatman® GF/F filters and immediately stored in the deep freeze for later analysis of suspended particulate material.

Nitrate + nitrite concentrations (NO_3) were determined at micromolar concentrations (Raimbault et al. 1990), phosphate concentrations (PO_4) were determined according to Murphy and Riley (1962), and silicates (Si) were ascertained according to Fanning and Pilson (1973). All these analyses were conducted on a continuous flow Technicon® AutoAnalyzer II. Particulate and dissolved organic matter samples were subject to wet oxidation (Raimbault et al. 1990) and the resulting nitrate (PON and DON) and phosphate (POP and DOP) were analyzed as previously described. Active chlorophyll-a (Chl-a) and pheopigment (Pheo) concentrations were determined using the *in vivo* fluorometric technique (Lorenzen 1966).

Data treatment

Correlation matrix-based PCAs were conducted on the nine sampling datasets of 14 core variables (Sal, Turb, $\text{O}_2\%$, NH_4 , NO_3 , PO_4 , Si, DON, DOP, POP, PON, Fluo, Chl-a, Pheo) measured at 34 sampling stations (T02 to T35) and on a similar format matrix averaging data over the whole survey. Albeit of interest for the analysis of each sampling occurrence, the PCA data treatment, when conducted separately on each of the nine individual sampling datasets, allowed for no pertinent intercomparison, due to the absence of a common reference scale. Therefore, spatiotemporal intercomparison was obtained by pairing the averaged-survey dataset with each individual sampling occurrence dataset and running a PCA, setting the averaged-survey dataset as active (reference) variables and each sampling occurrence dataset as non-active (supplementary) variables (Abdi and Williams 2010). In the present work, the average data matrix (active variables) served as a common referential on which each sampling occasion (non-active variables) could be processed individually hence allowing for an objective multiparametric spatiotemporal intercomparison of hydrological conditions.

Results and discussion

Climate conditions during the sampling period

Climate conditions during the October 2008 to July 2010 survey were significantly altered by a period of ENSO instability (Table 1) corresponding to (i) a moderate La Niña period from

November 2008 to March 2009 with a minimum Oceanic Niño Index (ONI) of -0.8 ; (ii) a very short period of normal conditions; (iii) a period of relatively strong El Niño from July 2009 to April 2010 with a maximum ONI of $+1.6$; and finally (iv) a La Niña period starting at the very end of our survey in July 2010. Additionally, the 2009–2010 El Niño was categorized as a Modoki or Central-Equatorial Pacific (CP) El Niño, characterized by lower temperature anomalies than for an Eastern-Equatorial Pacific (EP) El Niño (Capotondi et al. 2015).

The January 2008 to December 2010 representation of Palizada River daily and monthly averaged flow rate (Fig. 2) evidenced a strong freshwater discharge deficit during the year 2009, mainly due to low river flow during the rainy and post-rainy seasons. Monthly averaged discharge peaked at $220 \text{ m}^3 \text{ s}^{-1}$ in November 2009, which was far below the 530 and $700 \text{ m}^3 \text{ s}^{-1}$ maxima recorded in October 2008 and September 2010, respectively. The yearly cumulated Palizada River discharge amounted to 8 and $8.7 \times 10^9 \text{ m}^3$ in 2008 (including contribution from Tropical Storm Marco) and 2010 (no such climatic event but sustained rainfall during the whole rainy period), respectively, whereas in 2009 it amounted to only $4.8 \times 10^9 \text{ m}^3$, corresponding to a deficit of 33% when compared to the average yearly discharge of $7.2 \times 10^9 \text{ m}^3$ calculated over the 1992 to 2011 time series (Fichez et al. 2017) and a deficit of 39% and 44% when compared to the years 2008 and 2010, respectively.

Survey averaged reference

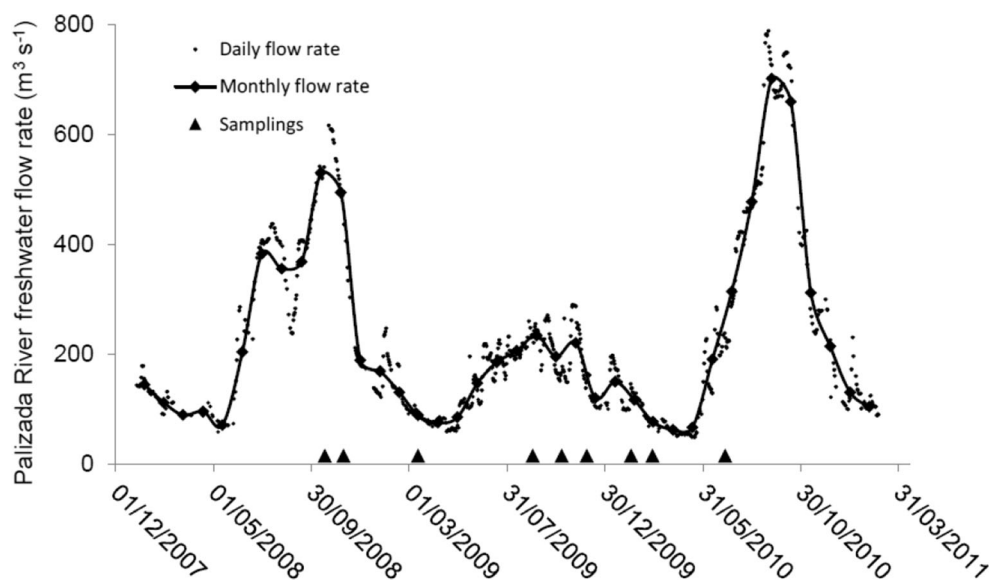
The PCA primarily yielded an ordination of the main factors accounting for the variability of Terminos Lagoon hydrology (Table 2). The cumulative 70% variance threshold identifying the main structuring factors (Afifi et al. 2011) was reached or exceeded when combining the first three factors with the exceptions of September 2009, when 77% of the variance was reached from the first two factors as opposed to March and July 2010, when the 70% threshold required a combination of the first four factors.

The first three factors computed from the averaged-survey dataset accounted for 78% of the variance (Table 2). The biplot representations of Factor 1 against Factor 2 (Fig. 3a) and Factor 3 against Factor 2 (Fig. 3b) showed that Factor 1 accounting for 51% of variance alone was strongly correlated positively with salinity (0.88) and negatively with most trophic status

Table 1 Oceanic Niño Index –ONI from January 2008 to December 2010. ONI negative values below -0.5 (La Niña) are shaded in light gray and ONI positive values over $+0.5$ (El Niño) are shaded in dark gray

Year	DJF	JFM	FMA	MAM	AMJ	MJJ	JJA	JAS	ASO	SON	OND	NDJ
2008	-1.5	-1.5	-1.2	-0.9	-0.7	-0.5	-0.3	-0.2	-0.1	-0.2	-0.5	-0.7
2009	-0.8	-0.7	-0.5	-0.2	0.2	0.4	0.5	0.6	0.8	1.1	1.4	1.6
2010	1.6	1.3	1.0	0.6	0.1	-0.4	-0.9	-1.2	-1.4	-1.5	-1.5	-1.5
2011	-1.4	-1.2	-0.9	-0.6	-0.3	-0.2	-0.2	-0.4	-0.6	-0.8	-1.0	-1.0

Fig. 2 Temporal variability of Palizada River daily and monthly averaged freshwater flow rates from January 2008 to March 2011. Sampling campaign occurrences are represented by dark triangles at the base of the *x*-axis. Hydrology data were downloaded on the 28th of April 2014 from the Mexican “Comisión Nacional de Agua” (CONAGUA) online hydrological surveys database. (<http://www.conagua.gob.mx/CONAGUA07/Contenido/Documentos/Portada%20BANDAS.htm>)



parameters such as POP (-0.93), pheopigments (-0.92), in situ fluorescence (-0.91), chlorophyll-*a* (-0.81), NO_3 (-0.78), PO_4 (-0.77), and Si (-0.73), or with turbidity (-0.73). Factor 2 accounting for 17% of variance was mainly positively correlated with DON (0.82), PON (0.63), and DOP (0.50) and negatively correlated with ammonium (-0.64). Factor 3 accounting for 9% of variance showed a weaker positive correlation with turbidity (0.49) and dissolved oxygen saturation (0.48) and a weaker negative correlation with Si (0.43).

The biplot representation of cases (i.e., sampling stations) for Factor 1 against Factor 2 (Fig. 3c) and Factor 3 against Factor 2 (Fig. 3d) provided a representation of environmental condition diversity. A strong distribution pattern could be observed on the Factor 1 against Factor 2 biplot that jointly accounted for 68% of the variance (Fig. 3c). A group of roughly 22 sampling stations located essentially in the central and eastern part of the lagoon was linearly ordinated along a diagonal line stretching from T18 to T35. A second group of ten stations (T02 to T10 and T15) located in the westernmost part of the lagoon diverged from that diagonal line and stretched toward the negative sides of Factors 1 and 2. Stations T16 and T14 stood between those two groups, while a final group of three eastern stations (T30, T29, T34) stretched in parallel to the first diagonal group and on its lower

side. The distribution along Factor 1 and Factor 3 was much more homogeneously spread with no strong specific pattern.

The signification of each of the first three PCA factors which cumulatively accounted for 78% of variance could also be inferred from the study of the few sampling stations that neared the extremity of each axis and/or that significantly departed from the scatterplot nucleus. Stations T06 and T07, located at the mouth of the Palizada River, stood on the negative far end of Factor 1, whereas stations T11, T12, and T20, located leeward of Carmen Island, stood on its positive end. Considering its tight relationship with salinity and trophic status parameters, that first factor of variability related to the estuarine influence essentially driven by the Palizada River that accounted for more than two-thirds of the freshwater inputs to the lagoon. That correlation with the Palizada River influence was further confirmed by the poor correlation with station T34, located directly downstream of Candelaria Estuary. Stations T35, T31, T33, and T32, confined to the easternmost part of the lagoon, stood on the far positive end of Factor 2 corresponding to organic-rich and NH_4 -depleted waters, whereas nearby station T30 stood on the very opposite end corresponding to water with lower organic load and higher NH_4 concentrations. Finally, stations T09 and T29, located in the alignment of the deep channels of Carmen

Table 2 Cumulative percentage of variance corresponding to the first four PCA factors for the nine sampling occasions and for the averaged datasets over the full survey. The dominant structuring factors defined as those cumulatively accounting for 70% or more (Afifi et al. 2011) are shaded in gray

Cumulative variance %	Oct-08	Nov-08	Mar-09	Sep-09	Oct-09	Dec-09	Feb-10	Mar-10	Jul-10	Full survey
Factor 1	38	41	46	51	36	41	32	27	33	51
Factor 2	59	61	64	77	55	58	53	50	54	68
Factor 3	70	71	76	86	73	72	70	67	63	78
Factor 4	78	79	83	91	81	81	77	79	71	84

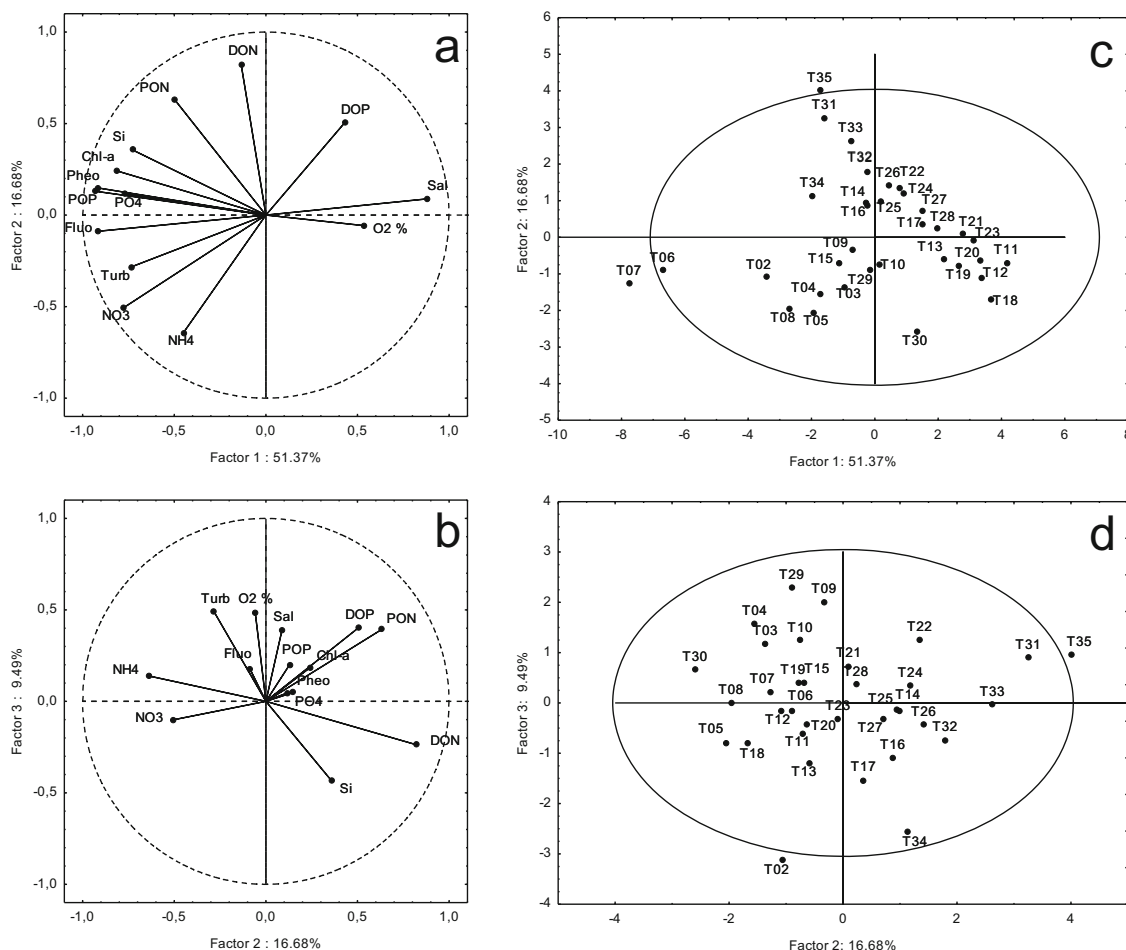


Fig. 3 Biplot representation of the principal component analysis conducted on a reference matrix gathering data averaged over the whole survey (34 stations by 14 parameters). Projection of the 14 variables (water parameters) **a** along factor 1 (51.4% of variance) showing the essential influence of estuarine (trophic status variables) versus marine (salinity) sources and factor 2 (16.7% of variance) oppositely linked to DON and NH_4 ; and **b** along factors 2 and 3 (9.5% of variance) oppositely

linked to $\text{O}_2\%$ and Si. Projection of the 34 cases (stations) along **c** factors 1 and 2, and **d** factors 2 and 3. Sal = salinity, Turb = turbidity, $\text{O}_2\%$ = oxygen saturation percentage, NH_4 = ammonia, NO_3 = nitrate + nitrite, PO_4 = phosphates, Si = silicates, DON = dissolved organic nitrogen, DOP = dissolved organic phosphorus, POP = particulate organic phosphorus, PON = particulate organic nitrogen, Fluo = in situ chlorophyll-a fluorescence, Chl-a = Chlorophyll-a, Pheo = pheopigments

Inlet and Puerto Real Inlet, respectively, stood on the positive end of Factor 3 correlated with high salinity, oxygen saturation, and turbidity, whereas stations T02 and T34 stood on its negative end.

Spatiotemporal intercomparison

Results from PCAs using the survey-averaged dataset as active variables and each sampling dataset as non-active (or supplementary) variables allowed to graphically represent the hydrological heterogeneity of each sampling occurrence according to a common referential, hence yielding a statistically supported multiparametric spatiotemporal intercomparison approach. Results from such a combined PCA plotted according to factors 1 and 2 (Fig. 4) and factors 2 and 3 (Fig. 5) showed the most widespread distribution to occur in

October 2008, close to the peak of the rainy season, with coordinates ranging from -25.5 to -1.3 , -5.9 to 11.5 , and -9.2 to 4.7 for Factors 1, 2, and 3, respectively, when the survey-averaged distribution only ranged from -7.8 to 4.2 , -2.6 to 4.0 , and -3.1 to 2.3 for the same respective factors. Additionally, all coordinates in October 2008 were negative for Factor 1 and mostly positive for Factor 2 or negative for Factor 3. This strong dispersion constricted slightly in November 2008 with values ranging from -14.4 to -4.0 , -3.6 to 7.9 , and -8.1 to 2.5 for Factors 1, 2, and 3, respectively, thus still significantly more widespread than for the survey-averaged distribution and still exclusively on the negative side for Factor 1 and mainly on the positive side for Factor 2. The scattering then narrowed strongly in March 2009, as the usual dry period conditions prevailed, with coordinate values ranging close to the survey-averaged ones. It then spread slightly

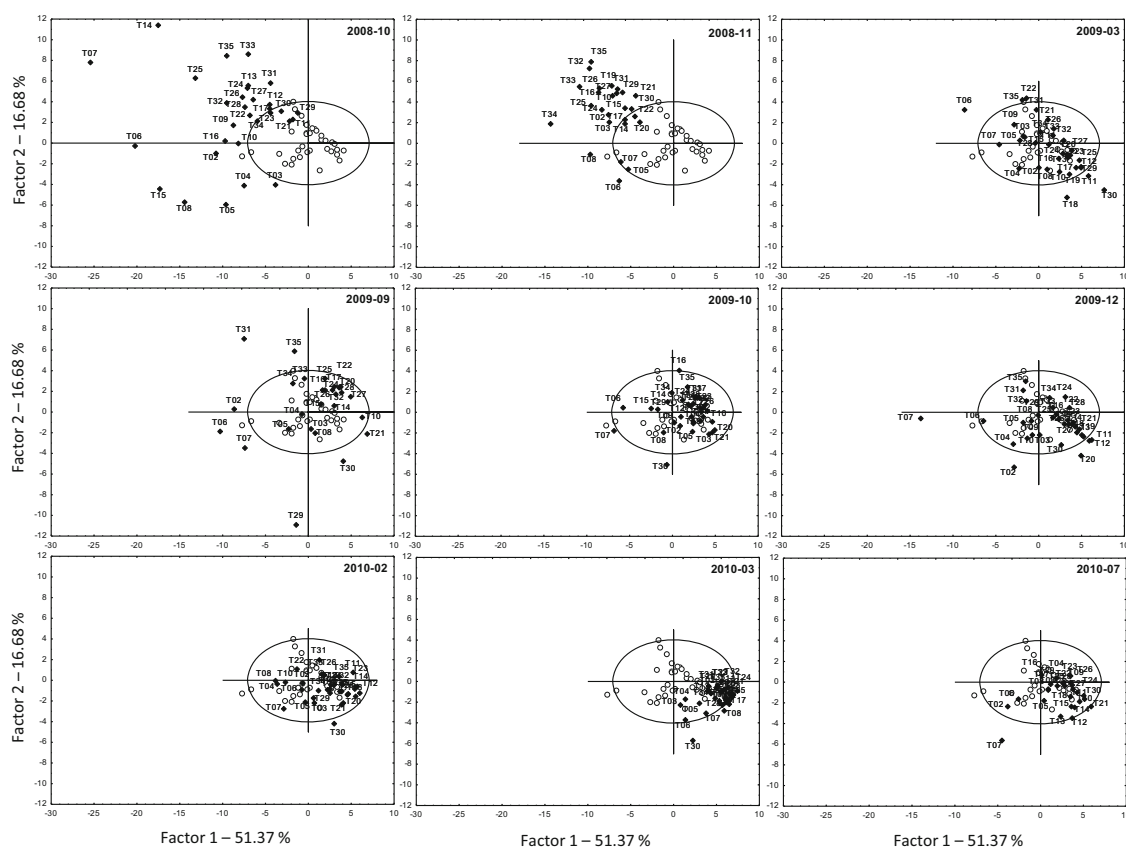


Fig. 4 Principal component analysis of the temporal variability driven by the 14 variables (water parameters) based on the projections along factors 1 and 2 (68% cumulated variability) of each of the nine sampling

again in September 2009, but instead of expanding to reach a situation identical to that of October 2008, it collapsed drastically in October 2009, at the beginning of the drought period, and shifted toward the positive end of Factors 1 and 3 and the negative end of Factor 2. This condensing and shifting trend built up during the following 6 months until March 2010 when coordinates ranged from 0.7 to 7.3, -5.7 to 0 , and -2.8 to 3.9 for Factors 1, 2, and 3, respectively, in parallel to the growing deficit in river discharge. In July 2010, as river discharge increased again with the end of the drought, a slightly more widespread distribution began to appear, especially along Factor 3.

The strong variance accounted for by the first factor and its positive correlation with salinity and negative correlation with trophic status and turbidity evidenced the primordial influence of estuarine versus marine sources. More surprisingly, the second factor appeared to be largely decoupled from salinity and mostly correlated with organic matter and even more specifically with dissolved organic matter on one side and with ammonium on the other side, hence most likely relating to heterotrophic degradation processes that led from organic-rich waters to waters enriched in recycled N-nutrients. Combined together, these two factors which accounted for 68%

campaigns against the matrix gathering data averaged over the whole survey (34 stations by 14 parameters) used as a common reference

variability evidenced a strong partitioning into two main subsystems with: (i) a first western subsystem covering approximately one third of the surface and strongly influenced by the balance between the inputs from the Palizada River and the exchanges through the El Carmen Strait, and (ii) a second subsystem covering approximately the remaining two thirds of the surface and extending over the central and eastern part of the lagoon, and organized along a gradient going from the central part to the easternmost embayment. Such a 1/3 western 2/3 eastern partitioning is consistent with previous works on water budget (Robadue et al. 2004) on the distribution of inorganic nutrients close to the main fresh water input sources (Medina-Gomez et al. 2015) or on the presence of maximal phytoplankton production in the western part due to Palizada River inputs of phosphates and organic matter and strong on-site bacterial mineralization that released additional nutrients (Conan et al. 2017).

Finally, the third major environmental factor correlated with turbidity, oxygen saturation, and salinity related mostly to stations located close to El Carmen and Puerto Real Straits and could be interpreted as being driven by entering well-mixed marine surface waters loaded with particles resuspended from the shallow coastal banks (Contreras Ruiz Esparza

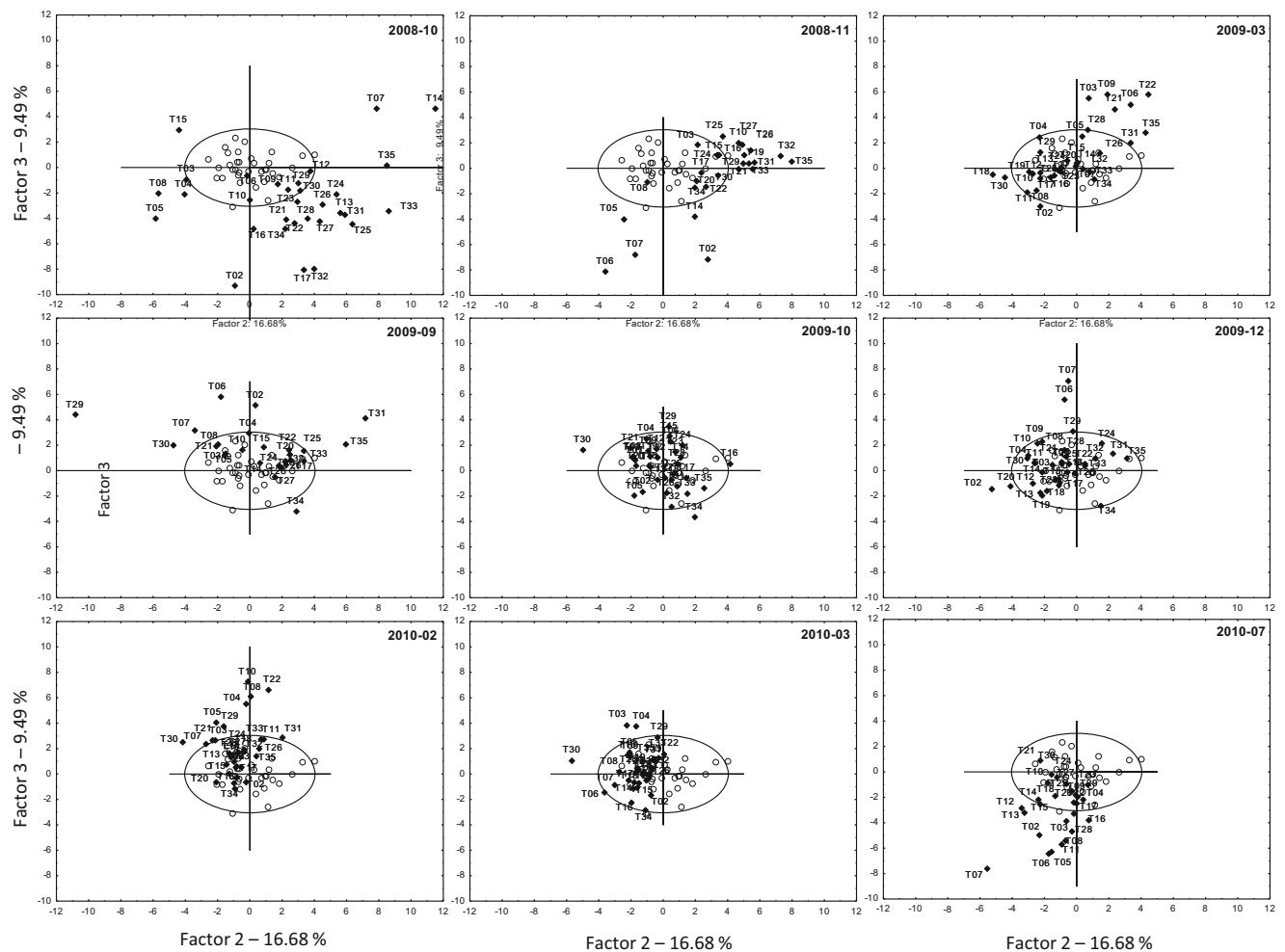


Fig. 5 Principal component analysis of the temporal variability driven by the 14 variables (water parameters) based on the projections along factors 2 and 3 (26% cumulated variability) of each of the nine sampling

campaigns against the matrix gathering data averaged over the whole survey (34 stations by 14 parameters) used as a common reference

et al. 2014). Despite the significant level of turbidity more generally generated by resuspension in such a shallow lagoon system, chlorophyll-*a* amounted to 70–80% of the sum of chlorophylls in most areas, a ratio range characteristic of relatively productive and non-senescent phytoplankton populations. That apparent paradox between light limitation and active primary production is consistent with recently reported results on phytoplankton dynamics in Terminos Lagoon (Conan et al. 2017) and is not uncommon in very shallow but hydrodynamically active systems where it has been demonstrated that even under very turbid conditions, turbulent water motion may cyclically expose phytoplankton to sufficient surface irradiance to allow for phytoplankton primary production to occur (Fichez et al. 1992).

The dispersion of stations as a function of the PCA factors accounted for the diversity in hydrological conditions, with the more widespread dispersion corresponding to more diverse environmental conditions, and the most compact dispersion corresponding to more homogeneous environmental

conditions. The strong variations observed between October 2008 and July 2010 matched with the recorded variability in river discharge driven by the combination of seasonal cycle (rainy versus dry season) and drought period related to the ENSO climate anomaly. The most widespread, and therefore, diverse hydrological conditions were recorded in October 2008, corresponding to a situation typical of the end of the wet season with yearly maximum river discharge. Lesser diverse hydrological conditions were recorded in March 2009, corresponding to a typical end of the dry season with yearly minimum river discharge. From September 2009 to March 2010, the 2009–2010 El Niño-related drought period that severely affected Mexico in July 2009 and which was reported as the driest month since the year 1941 (Baringer et al. 2010) resulted in a drastic decrease in the diversity of hydrological conditions. Even though low water flow rates were very similar in March 2009 and March 2010, the sustained deficit in river discharge during the whole 2010 wet season led to a strong decrease in hydrological condition

heterogeneity in March 2010 as demonstrated by the drastically less widespread distribution in PCA (Fig. 4a and b) corresponding to a significant loss in the diversity of hydrological conditions. The general shift in salinity nearing marine values and the decrease in nutrients, chlorophylls, and organic matter loads (DON, DOP, and PON) resulted in a shift from a system globally classified as brackish and mesotrophic (Herrera-Silveira et al. 2011) to a more saline and oligotrophic one. That shift in trophic status was perfectly summarized by the integrative environmental indicator represented by Chlorophyll-a concentrations (Fichez et al. 2010) which, when averaged over the whole lagoon, decreased from 6.3 to 3.7 $\mu\text{g L}^{-1}$ between October 2008 and March 2009, but fell to 0.6 $\mu\text{g L}^{-1}$ in March 2010, thus showing the 2009–2010 drought-related deficit in river inputs to result in a sixfold decrease in phytoplankton stock. This rapid and significant trophic impoverishment proved that the high trophic status of Terminos Lagoon strongly depends on river-borne new nutrient inputs, the input of recycled nutrients from the sediment reservoir being unable to sustain such a high trophic status, even over a relatively short duration. The relative imbalance between the respective influence of river-borne and sediment nutrient sources on the biogeochemical functioning of the Terminos Lagoon converged with previous results showing nitrogen turnover times to range from less than 1 day for inorganic nitrogen in the water column to over 3000 days for sedimentary organic nitrogen (Hopkinson et al. 1988).

Short- to long-term potential consequences

The strong influence of river inputs on the trophic status and hydrological diversity evidenced in the present work was consistent with the Flood Pulse Concept (FPC) which defines flood pulse as the major driving force in wetland systems (Junk and Wantzen 2004). This concept was recently linked in Terminos Lagoon to an adaptive diversification in resource use by consumers (Sepúlveda-Lozada et al. 2017), with periods of high river inputs resulting in higher trophic diversification and lower trophic redundancy, and conversely. Shifts in hydrological diversity and trophic status leading to a strong variability in food supply have been seen to impact entire communities in terms of density, diversity, and physiological state (Wantzen et al. 2002; Junk and Wantzen 2004; Abrantes et al. 2014). The homogenization of hydrological conditions and impoverishment in trophic status caused by the decrease in river inputs that we evidenced in Terminos Lagoon will ineluctably have an impact on the ecological balance of the Terminos Lagoon. Shift in hydrological conditions from hypohaline to euhaline/hyperhaline status in Terminos Lagoon has already been held responsible for having detrimental impacts on the food web (Abascal-Monroy et al. 2015), on juvenile development stages of exploited species, and subsequently on the stock of living resources in the

surrounding coastal system of the Gulf of Mexico (Ramos Miranda et al. 2005; Sosa López et al. 2005; Villéger et al. 2010; Sirot et al. 2015). However, our work demonstrated that the increase in salinity concurred with a loss in hydrological condition diversity and a decrease in trophic status that offer a much more consistent explanation for the loss of functional diversity and biotic homogenization in the fish community of Terminos lagoon reported by those authors. Moreover, Conan et al. (2017) characterized the Terminos pelagic ecosystem as a “nitrogen assimilator” because of its relatively high internal production and weak autochthonous exportation to the Gulf of Mexico. These authors also concluded that “bottom-up” control was dominant for microbial productivity and that the heterogeneity in phytoplankton and free-living prokaryote distribution in the lagoon was largely explained by nitrogen to phosphorus stoichiometry. In such a context, and as already reported for many rivers (Turner et al. 2003; Seitzinger et al. 2010), expected decreases in rainfall and river discharge together with modification in land use will most certainly modify the N versus P balance of nutrient inputs to Terminos Lagoon, hence potentially further impacting its ecosystem structure and functioning.

Even though the inherent variability of transitional systems corresponding to their “buffer capacity” (Carpenter et al. 2001) has been alternatively hypothesized as the most likely driver of present shifts in fish population in Terminos Lagoon (Fichez et al. 2017), predictive climate scenarios strongly suggest that the Terminos Lagoon system might face a future long-term change in its salinity balance and related hydrological conditions and trophic status. While modeling approaches based on various IPCC emission scenarios do not foresee change in rainfall for the next decades in the Mexico-Central America region, a decline by 5% to 30% is expected during the second part of the century (Sáenz-Romero et al. 2010; Met Office 2011; Biasutti et al. 2012; Hidalgo et al. 2013). For example, if no significant precipitation change is expected during the first half of the twenty-first century, precipitation decline is expected in its second half with a decrease of 7% in Guatemala and 10 to 13% in Belize under IPCC emission scenario B2, and of 27 to 32% in Belize and Guatemala under scenario A2 with an averaged reduction of 28% at the regional scale (Barcena et al. 2010). Similarly, based on various emission scenarios, significant reductions in precipitation (as much as 5–10%) and runoff (as much as 10–30%) is anticipated for the 2050–2099 period in northern Central America (Hidalgo et al. 2013) with a projected decrease in precipitation by ~13% in southern Mexico in summer and slight increase in autumn (Colorado-Ruiz et al. 2018). Those numbers come close to the 33% deficit in river discharge we recorded during the 2009 drought when compared to the yearly river discharge averaged over the 1992–2011 time period, and certain authors even claim that an 80% decrease in freshwater discharge from the Usumacinta-Grijalva River catchment may be expected

(Kemp et al. 2016). In Terminos Lagoon as well as in most Central America coastal lagoons, such alleged long-term decrease in rainfall and river discharge will thus result in a long-term shift toward higher salinity, lower diversity in hydrological conditions and lower trophic status of comparable or even greater magnitude than the one we evidenced, with corollary impacts on biodiversity and productivity.

Conclusion

The present study has allowed to mathematically define and represent the spatiotemporal variability of hydrological conditions in Terminos Lagoon yielding a synthetic vision of the global organization of water masses that clearly demonstrated a strong variability which is mainly driven by river inputs. The proposed approach provided evidence of the drastic impact of the 2009–2010 El Niño–related drought period on the salinity and trophic status of the lagoon, showing its sensitivity to climatic events. The occurrence of a 6-month-long severe deficit in river inputs due to that drought was seen to have resulted in a strong decrease in the heterogeneity/diversity in hydrological conditions, with an increase in salinity and a significant trophic status shift from mesotrophic to oligotrophic. As climate change scenarios converge to significant decreases in rainfall in the region, such a relationship between river inputs, hydrological diversity, and trophic status means that the whole trophic network and living resources will be impacted. Such potential impacts on the diversity of environmental conditions must be factored into environmental management plans in order to ensure the sustainability of the current status of Terminos Lagoon as a protected area and as a living resource reservoir for the whole region. Beyond its application to the specific case of Terminos Lagoon, the proposed spatiotemporal intercomparison approach based on the combination using average database PCA coordinates as a reference matrix could be more widely applied in order to efficiently valorise multiparametric datasets.

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