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Benthic ecology of tropical coastal lagoons: environmental changes
over the last decades in Terminos Lagoon, Mexico

Christian Grenz^{*1}, Renaud Fichez¹, Carlos Álvarez Silva², Laura Calva Benítez², Pascal Conan³, Adolfo Contreras Ruiz Esparza⁴, Lionel Denis⁵, Silvia Díaz Ruiz² Pascal Douillet¹, Margarita E. Gallegos Martinez², Jean-François Ghiglione³, Francisco José Gutiérrez Mendieta², Montserrat Origel-Moreno¹, Antonio Zoilo Marquez Garcia², Alain Muñoz Caravaca⁶, Mireille Pujo-Pay³, Rocío Torres Alvarado², Jorge Zavala-Hidalgo⁵

¹ Aix-Marseille Université, Université de Toulon, CNRS/INSU, IRD, Mediterranean Institute of Oceanography MIO UM 110, Marseille, France

² Universidad Autónoma Metropolitana, Departamento de Hidrobiología, México D.F., México

³ UPMC Université Pierre et Marie Curie, CNRS, UMR LOMIC 7621, Laboratoire ARAGO, Avenue Fontaulé, BP44, F-66650 Banyuls-sur-Mer, France

⁴ Universidad Nacional Autónoma de México, Centro de Ciencias de la Atmósfera, México D.F., Mexico

⁵ Université Lille 1: Sciences et Technologies, UMR CNRS 8187 LOG, Wimereux, France,

⁶ Centro de Estudios Ambientales de Cienfuegos, Carretera Castillo de Jagua, Km 1 ½, AP. 5, CP. 59350 Cienfuegos, Cuba

*Correspondence: christian.grenz@mio.osupytheas.fr

Abstract

Terminos Lagoon is a 2000 km² wide coastal lagoon linked to the largest river catchment in Mesoamerica. Economic development, together with its ecological importance, led the Mexican government to pronounce Terminos Lagoon and its surrounding wetlands as a Federal protected area for flora and fauna in 1994. It is characterized by small temperature fluctuations but with two distinct seasons (wet and dry) that control the biological, geochemical and physical processes and components. This paper presents a review of available information on Terminos Lagoon. The review shows that diversity of benthic communities is structured by the balance between marine and riverine inputs and that this structuration strongly influences the benthic metabolism and its coupling with the biogeochemistry of the water column. The paper also presents a number of specific drivers and recommendations for a long term environmental survey strategy in the context of expected Global Change in the Centro America region.

Keywords: Multidisciplinary Study; Ecosystem; Estuaries; Coastal lagoon; Terminos Lagoon; Mexico

34 **1 Introduction**

35 In recent years, global concern has arisen concerning the risks of decline in Marine ecosystem health and the associated
36 functions and services they provide. This has brought about a number of innovative studies and much path-breaking
37 research and has led to the development of guidance and policies worldwide. Most of this information underlines the
38 need to observe and manage the state of marine ecosystems as a whole (Tett et al., 2013, Grand Challenge 4 in Borja,
39 2014). Moreover, scientific literature about marine ecosystems has increased exponentially during the last 15 years
40 (Borja, 2014). Coastal ecosystems are likely to have been altered substantially by human activities and probably also by
41 climate drivers of change (climate change related key drivers) (Parry et al., 2007). As stated by Halpern et al. (2008) no
42 marine system is unaffected by human influence and a large fraction (41%) is strongly affected by multiple drivers.

43 Marine ecosystems are highly diverse given their biogeographical characteristics on a global scale. Their morphology
44 controls internal hydrodynamics and exchanges with the adjacent sea, regulating in this way the level of anthropogenic
45 pressures and sensitivity to eutrophication (Kennish, 2002). Semi-enclosed coastal systems (SECS), which usually
46 include open, leaky and choked lagoons and transitional waters (EU, 2000), are sentinel systems and hotspots of coastal
47 vulnerability at a global scale (Newton & Weichselgartner, 2014; Newton et al., 2014 and references therein). Because
48 of the physical connection between the benthic layer and the whole water column, the geochemical and biological
49 dynamics extensively depend on benthic-pelagic interactions.

50 Terminos Lagoon in the southern Gulf of Mexico is one of the largest lagoons situated in the intertropical zone.
51 Considering the extension and shallowness of Terminos Lagoon as well as its potential sensitivity to environmental
52 change, the objective of this paper is to review and combine existing information on what has been identified as a model
53 tropical coastal lagoon in the Gulf of Mexico (García-Ríos et al., 2013) where seasonal signals are distinct from those
54 in temperate regions. The following sections present an overview of the general features of Terminos Lagoon, as well
55 as hydrodynamic characteristics, and benthic habitats with special attention to trophic status and benthic communities
56 as they strongly contribute, together with external loadings, to the biogeochemistry of the water column. In the context
57 of expected Global Change in the Centro America region, the present review also presents a number of specific drivers
58 of change and pressures including land-use, watershed management, river inputs, coastal erosion processes and
59 contaminant levels, to assess what major changes can be expected and what effect they might have on the current
60 environmental status, finally issuing recommendations for a long term environmental survey strategy.

61

62 **2. General features**

63 Terminos Lagoon borders the southern Gulf of Mexico in Campeche and is, by area and volume, Mexico's second
64 largest estuarine system. The lagoon borders two geologic provinces: to the east the Yucatan Peninsula (low rainfall,
65 calcareous soils, and very low surface drainage) and to the west and south the lowlands of Tabasco and the highlands of
66 Chiapas and Guatemala, an area of high rainfall and fluvial soils (Fig. 1). Three main rivers discharge directly into the
67 lagoon: the Candelaria, the Chumpan, and the Palizada (a tributary of the Grijalva-Usumacinta) with a catchment area
68 totaling 49 700 km².

69 The average freshwater flow rate is approximately $12.5 \cdot 10^9 \text{ m}^3 \text{ yr}^{-1}$, with the Palizada River catchment area on the
70 western coast of the lagoon accounting for most of the fresh water inputs. Tidal regime is mixed, mostly diurnal with a
71 mean range of 0.3 m (Contreras Ruiz Esparza et al, 2014).

72 The continental shelf (Campeche Sound) is one of the most important fishery areas in the western central Atlantic region.
73 Campeche Sound (Tabasco/Campeche) contributes 34% of the total Mexican fishery yield in the Gulf and Caribbean
74 coasts, including penaeid shrimps, mollusks, demersal and pelagic fishes (CONAPESCA, 2008).

75 Parallel to fisheries, crude oil extraction in the Gulf of Mexico represents a large economic activity with, Petroleros
76 Mexicanos (PEMEX), a major non-OPEC oil producer (top 10) operating here since 1938. PEMEX is a state-owned
77 company extracting around 2 million barrels per day in Bahia de Campeche (Cantarell oil field). More significantly,
78 revenues from the oil industry (including taxes and direct payments from PEMEX) accounted for about 32% of total
79 Mexican government revenues in 2013. This activity has generated the urban development of Ciudad del Carmen, the
80 largest town (located on the western tip of the island) and in 1994, it contributed to a great extent to the declaration of
81 Terminos Lagoon as a Protected Area of Flora and Fauna (APFFLT). Ten years later the lagoon was designated as a
82 wetland of international importance (RAMSAR) and today represents the largest such zone in Mexico, at 705,016
83 hectares (www.ramsar.org). Unfortunately, PEMEX's activity continues to grow within the protected area, potentially
84 threatening the whole ecosystem through accidental oil spills and pipeline leaks (e.g. Ixtoc-1 in 1979-1980).

85 The vast wetlands surrounding Terminos Lagoon provide ideal conditions for the migration and breeding of numerous
86 species such as sea bass, shellfish, shrimp, and manatees, amongst others. This area also harbors the highest
87 concentration of dolphins in the Gulf. This protected area is also one of the most important bird wintering areas in the
88 Gulf of Mexico and its level of marine and terrestrial flora and fauna diversity is considered as very high (Yáñez-
89 Arancibia et. al., 1988). The coastal fringe is occupied by vast areas of mangroves and the lagoon comprises various
90 habitats including important oyster and sea grass beds (Moore & Wetzel, 1988).

91 The area presents two climatic seasons (Yáñez-Arancibia et al., 1983): the rainy season (Jun-Sep) and the dry period
92 which splits into a period with dominant north winds and winter storms (Nov-Mar) and a second with lower wind forcing
93 (Feb-May). The average evaporation is 1512 mm a^{-1} and the average rainfall is 1805 mm a^{-1} (Yáñez-Arancibia & Day,
94 1988). Nevertheless, a strong variability in rainfall and subsequent freshwater discharge to the lagoon has recently been
95 linked to climate variability and to the ENSO regime (Fichez et al., 2017).

96 Terminos Lagoon stretches over more than 2000 km^2 (Fig. 1). The lagoon is connected to the sea through two inlets:
97 'Carmen Inlet' on the western side (4 km width) and 'Puerto Real Inlet' on the eastern side (3.3 km width). These are
98 separated by a carbonate-rich barrier (Carmen Island, 30 km long and 2.5 km wide). Terminos Lagoon is shallow with
99 an average depth of 2.4 m, with the exception of the tidal flats and the deep channel on the eastern part of each inlet.
100 The eastern entrance is influenced by transparent marine waters which form an interior delta. In the western inlet, the
101 suspended terrigenous materials of the Palizada River estuary, generate high turbidity and contribute to the formation of
102 an exterior delta oriented towards the west in the Gulf of Mexico.

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104

105

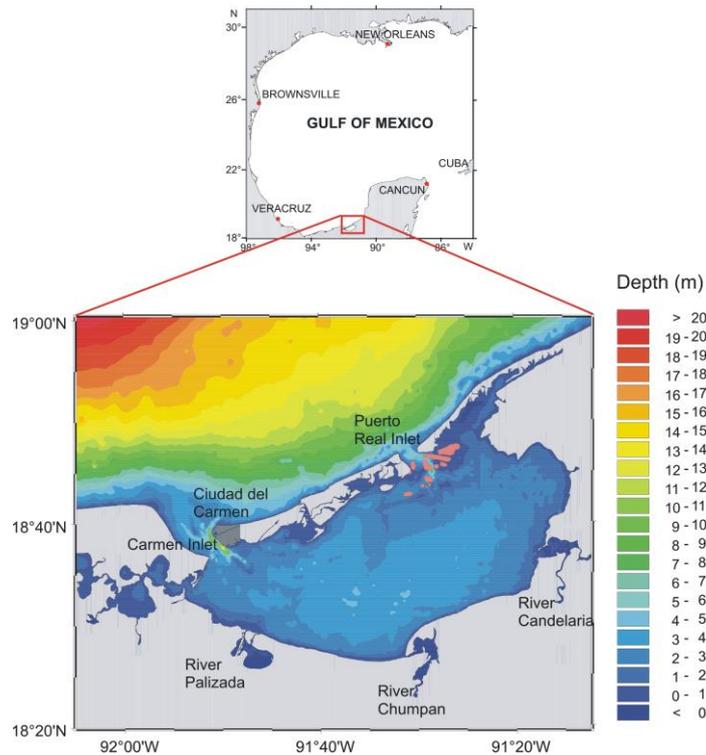


Fig. 1. Bathymetric map of the study area with major rivers and connections to the Gulf of Mexico.

Waters are mostly oligo- to mesohaline, with a tendency to euhaline in some parts of the system; the east inlet is characterized by marine waters whereas the west inlet is mesohaline to oligohaline near the river mouths (Bach et al., 2005). Predominant sediments are silt and clay, with calcareous sands (shells and shell fragments) present in the eastern part and close to the barrier island only. The sediments of the western part are silty-clay (Yañez-Arancibia et al., 1983). A study by Yañez-Correa (1963) compared the sediment structures of both inlets, and showed that sediment accumulation outside Carmen Inlet in the west contributed to the formation of a small alluvial delta outside the lagoon, due to the predominant seaward direction of the currents. Conversely, in the east at Puerto Real Inlet, the existence inside the lagoon of a submarine alluvial delta composed of coarse sediment fraction of marine origin reveals an inward component of the currents; one of the main sources of sediments is thus offshore derived waters entering the lagoon. The few published studies dealing with hydrodynamic modeling in Terminos Lagoon (Kjerfve et al., 1988; Jensen et al., 1989; Contreras Ruiz Esparza et al, 2014) converge to describe a general circulation pattern from east to west, with a net westward transport of the water masses entering the lagoon through Puerto Real Inlet and exiting through Carmen Inlet during the dry season, and a dominant net export of water through both inlets during the wet period. Tidal effects combined with freshwater inputs tend to bend the southwestward current into a cyclonic circulation inside the lagoon - with a vortex core located in the northeast part - while predominant winds from the east (67 % from 45° to 135°) tend to drive the river plumes toward Carmen Inlet (Contreras Ruiz Esparza et al, 2014). Based on tidal current measurements in and around the inlets, David and Kjerfve (1998) estimated that fifty percent of the lagoon water volume was renewed in 9 days. However, long term trends of residence times of the water masses for the whole lagoon remain difficult to estimate, considering that water replacement in Terminos Lagoon does not behave linearly but decays exponentially

(Yanez-Arancibia & Day, J. 2005). The recent development of a 3-D hydrodynamic modeling approach of Terminos Lagoon accounted for tidal forcing only (Contreras Ruiz Esparza et al, 2014) and thus prevented the computing of water mixing and renewal indicators (Umgiesser 2014). However, a relatively simple water budget could be established using the net freshwater inputs (river + groundwater + net precipitation) previously estimated at $12.5 \cdot 10^9 \text{ m}^3 \text{ yr}^{-1}$ (Fichez et al. 2017) and the water volume of $4.65 \cdot 10^9 \text{ m}^3$ (Contreras Ruiz Esparza et al, 2014), yielding an average flushing time (T_f , Monsen et al., 2002) of 135 days, a value within the 1 to 5 months range previously reported by Robadue et al. (2004) for different seasonal conditions.

3. Water column biogeochemistry

Terminos Lagoon is a “choked” lagoon subject to significant fresh water inputs, so salinity is strongly variable at the spatial as well as temporal scale. Recent results from a survey (currently October 2008 to September 2010, 10 samplings over a network of 34 stations) yielded an average salinity of 25.7 at 1 m depth (standard deviation = 8.1) with values ranging from 3 to 37 (Fichez et al. 2017). Such high variability may be related to the high variability in precipitation and subsequent river discharge, sea level and wind patterns, as documented in Fuentes-Yaco et al. (2001).

Nevertheless, the distribution of salinity in Terminos Lagoon for January 2010 (Fig. 2) may be considered as a good example of the general pattern of spatial variability.

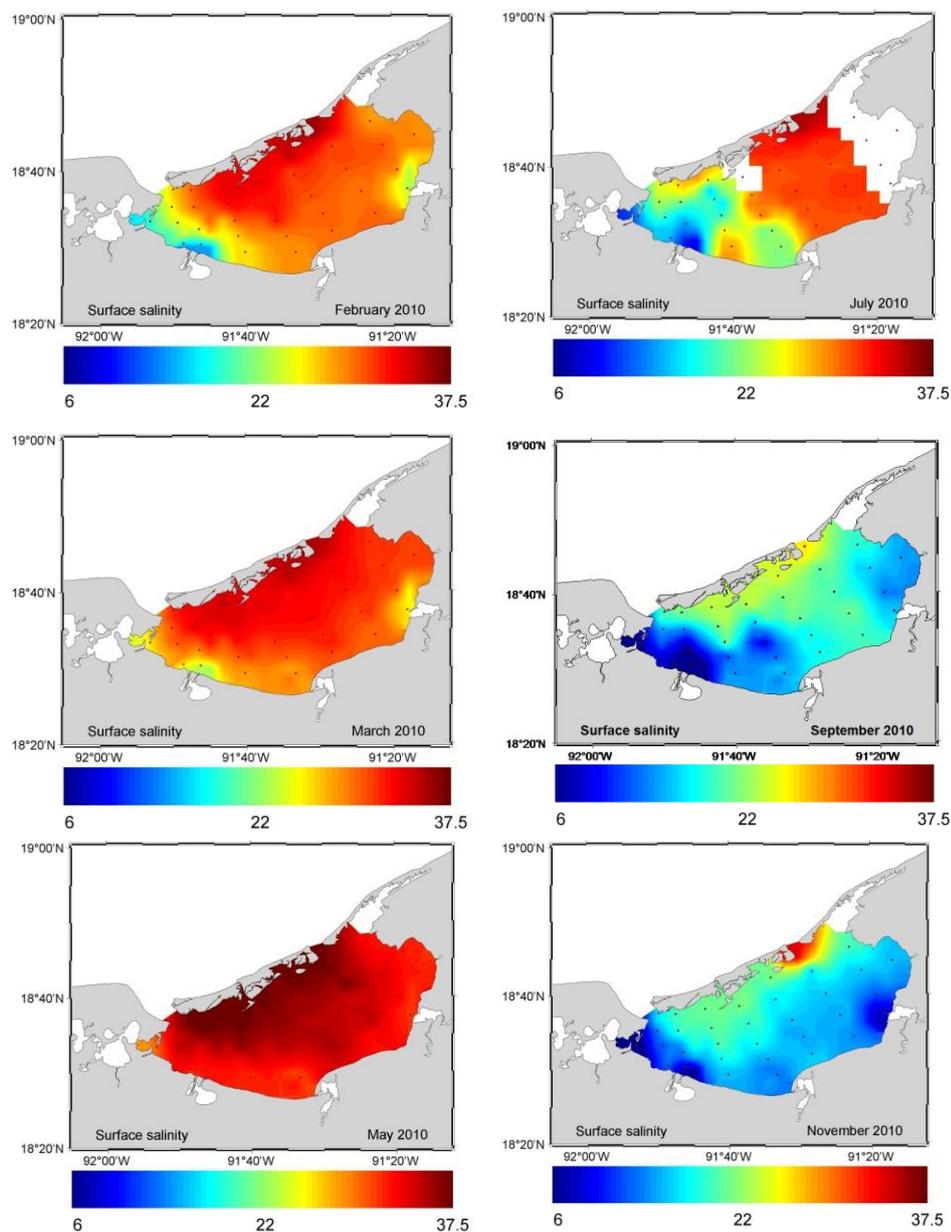
Lower salinities are generally measured in the vicinity of Palizada River, with Candelaria and Chumpan Rivers contributing to a lesser extent to freshwater inputs to the lagoon. Highest salinities in the range of 33 to 36, similar to those of adjacent marine waters, are measured close to Puerto Real Inlet and, according to the general hydrodynamic pattern, the more marine water bodies tend to travel to the southwest along the coast of Carmen Island. Salinity varies considerably within the lagoon as a function of the imbalance between those two sources of input.

Quite surprisingly, the trophic status (dissolved inorganic and organic material and particulate organic material) of Terminos Lagoon has been poorly documented. Silicate concentrations generally correlate to salinity as freshwater transports huge quantities of silica originating from soil leaching. In the Gulf of Mexico, marine offshore waters have silicate concentration of roughly $2 \mu\text{M}$ whereas coastal waters are generally in the range of 20–40 μM . Concentrations in the lagoon are around 70 μM on average with strong temporal and spatial variability, as for salinity.

Inorganic nitrogen concentrations generally come within the 0 to 4 μM range with some very occasional peaks close to or above 10 μM in the vicinity of the Palizada River. Concentrations in the middle of Terminos Lagoon are - in most cases - significantly below 1 μM . Nitrates + nitrites concentrations are higher during the wet season than during the dry season.

Phosphate (orthophosphate) concentrations come within the 0 to 1.00 μM range with an average value of roughly 0.13 μM . It is clear from the recent study by Conan et al. (2017) that phosphate distribution in the lagoon is for the most part (spatially and temporally) disconnected from nitrogen. During their study, the authors identified the Palizada River and Puerto Real Inlet as the two main sources of NO_3 and NH_4 , whereas PO_4 originated from Candelaria and Chumpan R.

178 inputs, and primarily from the mineralization of organic phosphorus (PP and DOP) by bacterial activity. This impacted
179 the stoichiometry of particulate organic matter (N:P ratio) throughout the lagoon.



207 Fig. 2. Spatial variability in salinity measured in Terminos Lagoon in 2010 during the dry (left) and rainy (right) seasons
208 (modified from Fichez et al., 2017).

209
210 When averaged over the whole lagoon, dissolved inorganic N:P ratio ranges from 3:1 to 18:1 with an average value of
211 9:1, thus suggesting that nitrogen is the most probable element to limit pelagic primary production. However, ratios well
212 over the 16:1 Redfield Ratio and as high as 353:1 were occasionally measured (mostly close to the Palizada River
213 mouth), demonstrating that such an assumption must not be applied uniformly to the whole lagoon system.

214 On average, concentrations in dissolved organic nitrogen and phosphorus are around 15 and 0.6 μM , respectively. Some
215 strong spatial variation can be observed with occasional high concentrations in the north-east part of the lagoon, possibly
216 due to export of organic compounds from the mangrove. On average, concentrations in particulate organic carbon,
217 nitrogen and phosphorus are around 70, 10 and 0.5 μM , respectively.

218
219 Chlorophyll a as an indicator of phytoplankton biomass and potential eutrophication process has been more extensively
220 documented. Average concentration in the lagoon, as reported by various authors, ranged broadly between 1 and 10 mg
221 m^{-3} , with the lower values being measured as a whole in Puerto Real and the highest close to the Palizada estuary.
222 Chlorophyll a versus total chloropigment ratio was recorded as being recurrently close to 0.75, demonstrating a relatively
223 healthy population of pelagic primary producers. There is virtually no assessment of primary production barring two
224 publications, which report a gross primary production rate of 478 $\text{g C m}^{-2} \text{a}^{-1}$ at one station of the lagoon (Rivera-Monroy
225 et al., 1998) and variations from 20 to 300 $\text{gC m}^{-2} \text{a}^{-1}$ (Day et al., 1982), suggesting a potential shift from oligotrophic to
226 eutrophic conditions.

227 A recent study on biogeochemical cycling in Terminos Lagoon has shown that the water column behaves globally as a
228 sink, and in particular as a "nitrogen assimilator" due to the elevated production of particulate and dissolved organic
229 matter and the weak exportation of autochthonous matter to the Gulf of Mexico (Conan et al., 2017). The same study
230 has revealed that "bottom-up" control largely accounts for the observed variability in phytoplankton productivity.
231 Phosphates delivered by Palizada River inputs and strong on site bacterial mineralization of organic matter result in
232 maximal phytoplankton production in the western part of the lagoon.

233 A nutrient and carbon budget calculated by Reyes et al. (1997) and David (1999) showed that Terminos Lagoon is
234 slightly autotrophic (carbon sink) on a yearly basis with a net production rate of +0.2 $\text{mol C m}^{-2} \text{yr}^{-1}$, even though the
235 authors themselves underlined the fact that such results should be taken with great caution due to the evident gaps in
236 available datasets.

237 238 **4. Seagrass**

239 Seagrass meadows are known to play a number of important ecological roles in estuarine and shallow-water coastal
240 ecosystems: they enhance primary production and nutrient cycling, stabilize sediments, elevate biodiversity, and provide
241 nursery and feeding grounds for a range of invertebrates and fish. (Orth et al., 2010; Cullen-Unsworth & Unsworth,
242 2013). The highest productivity of seagrasses is during the dry season as a result of higher water clarity, according to
243 Moore & Wetzel (1988). In Terminos Lagoon, the distribution of the seagrass communities clearly reflects the conditions
244 of water movement, clarity and water salinity. Seagrasses develop denser meadows along the lagoon shoreline of Carmen
245 Island and in particular in the delta of Puerto Real where high water transparency and salinities, and high percentage of
246 calcium carbonate in the sediments, have been measured (Calva & Torres, 2011).

247 The communities are dominated by the turtle grass *Thalassia testudinum* and in lower density by *Halodule wrightii* (Raz-
248 Guzmán & Barba, 2000). *H. wrightii* grows in the shallowest areas while *T. testudinum* extends down to depths of 3 m
249 (Ortega 1995). Total primary production of *T. testudinum* in the Lagoon is estimated at 260 T a^{-1} (Moore & Wetzel,

1988). Epifauna associated to the seagrass meadows is abundant and includes epibenthic amphipods and their predators, i.e. crustacean species of Hippolyte and Pink shrimp (Negreiros-Fransozo et al., 1996; Corona et al., 2000).

5. Mangroves

Mangrove forests play an important role in the functioning of tropical coastal systems. A classification of mangrove forest based on the importance of hydrodynamic exchange describes different categories that are present in Terminos Lagoon: (1) riverine tidal forests that receive high inputs of freshwater, (2) fringe forests which are flushed regularly by tide, (3) basin forests which are less regularly flushed, and (4) scrub forests which have very slow flushing and low nutrient levels (Lugo & Snedaker, 1974). Terminos Lagoon is bordered almost completely by extensive mangrove swamps composed by three dominant species: *Rhizophora mangle* L. (red mangrove), *Avicenia germinans* L. (black mangrove) and *Laguncularia racemosa* Gaertn.f. (white mangrove) (Day et al., 1987). These authors measured higher productivity near the river mouths, probably caused by a number of factors which include lower salinity, higher nutrient inputs and a lower hydrogen sulfide level due to lower sulfate concentrations in freshwater. Since stresses are lower, productivity is higher, resulting in more available energy for building biomass. The productivity and the extent of mangrove forests in the area are directly related to high fisheries productivity (Yañez-Arancibia & Day, 1982).

6. Benthic fauna

Besides the importance of benthic diversity that has been underlined in numerous studies (Yañez-Arancibia & Day, 1988) benthos in Terminos Lagoon represents a major trophic resource, and plays an important role in the biogeochemical budget of such a shallow system.

Ayala-Castañares (1963) and Phleger and Ayala-Castañares (1971) described the taxonomy and the distribution of foraminifers in Terminos Lagoon. They reported densities in the range of 250-900 ind.10 cm⁻², which suggests relatively high rates of organic matter production, probably consecutive to high river runoffs. Their distribution reflects the circulation in the lagoon, with open-gulf foraminifers close to Puerto Real Inlet and along the southeast side of Carmen Island, while lagoon foraminifers occur close to Carmen Inlet. A mixed fluvial assemblage was also observed in and near the river mouths.

Marrón-Aguilar (1975) described the systematic and abundances of polychaetes throughout Terminos Lagoon, while Reveles (1984), focused on polychaete species associated with seagrass beds of *Thalassia testudinum*, and Hernández and Solís-Weiss (1991) examined those found in the mangrove *Rhizophora mangle*. In the seagrass beds and mangroves, polychaetes dominated in both abundance and species diversity. Their distribution is closely linked to the salinity gradient, turbidity and sediment types, and three assemblages may be identified: a first group, localized in the eastern part of the lagoon, is mainly characterized by families Spionidae and Cirratulidae. The second group is located in the central part and the south of the lagoon, with families Cirratulidae and Lumbrinereidae, while the third group located close to Carmen Island is characterized by families Capitellidae and Nereidae.

285 Mollusks have received extensive attention due to the exploitation of two bivalve species. [García-Cubas \(1988\)](#)
286 published a review of all the mollusks encountered in this lagoon, and several studies have been carried out on the
287 exploited bivalves *Rangia cuneata* and *Crassostrea virginica*, mainly concerning their distribution ([Ruiz, 1975](#)), the
288 physiology of their reproduction ([Rogers-Nieto and García-Cubas, 1981](#)) as well as the behaviour of larval stages
289 ([Chávez, 1979](#)).

290 Based on previous works, [García-Cubas \(1988\)](#) identified four typical subsystems in Terminos Lagoon: a- Interior
291 lagoon (western part of the area, but with limited connections to Terminos Lagoon - salinity lower than 10 in summer
292 periods) associated with rivers and characterized by 3 bivalve species of commercial interest (*Rangia flexuosa*, *R.*
293 *cuneata* and *Polymesoda caroliniana*); b- lagoons joined to the southwest part of Terminos Lagoon where naturally
294 occurring reefs of *Crassostrea virginica* and their typically associated community are found (salinity in the range 0-15);
295 c- The main lagoon central basin, where eight gastropod species and nine bivalve species constitute the mollusk
296 community and are submitted to a wide range of salinity throughout the year (10-36);d- An area of strong marine
297 influence located close to Carmen Island (salinity ranging from 28 to 38), where a broad community of eight gastropods
298 and nine bivalves dominates, mainly in association with *Thalassia testudinum* beds.

300 Additional extensive studies have been conducted on fish distributions in the lagoon. Most fish have a direct trophic link
301 with benthic macrofauna ([Yáñez-Arancibia and Day, 1988](#)), even if only 10% of the species are permanent residents in
302 the lagoon (45% use the lagoon as a nursery, and 45% are occasional visitors). While half of the fishes are primarily
303 carnivorous, a quarter are higher carnivorous and the last quarter is constituted of herbivorous, detritivorous or
304 omnivorous fishes. A maximal juvenile flow into the lagoon was recorded in September-November, mainly via Puerto
305 Real inlet.

306 As described above, the diversity of benthic communities is strongly structured by the balance between marine and
307 riverine inputs and this structuration strongly influences the benthic metabolism and its coupling with the
308 biogeochemistry of the water column.

310 **7. Benthic metabolism**

311 Dissolved and particulate exchanges between sediments and the water column remain poorly documented, and most
312 budgets are based on the assumption that the benthic boundary layer is in balance ([Gomez-Reyes et al., 1997](#); [David,](#)
313 [1999](#)). Studies of sediment-water exchanges of nutrients remain poorly documented, except in the mangrove forest
314 ([Rivera-Monroy et al., 1995](#); [Day et al., 1996](#)) or seagrass beds of *Thalassia testudinum*.

316 In a fringe mangrove, sediment and nitrogen exchanges at the sediment-water interface have been estimated using a 12
317 m-long flume extended through a fringe forest from a tidal creek to a basin forest. [Rivera-Monroy et al. \(1995\)](#)
318 demonstrated that the tidal creek was the main source of ammonium ($0.53 \text{ g m}^{-2} \text{ a}^{-1}$) and nitrate and nitrite ($0.08 \text{ g m}^{-2} \text{ a}^{-1}$),
319 while the basin forest was the principal source of total suspended sediments ($210 \text{ g m}^{-2} \text{ a}^{-1}$). On the contrary, net
320 export of particulate nitrogen occurred from the fringe forest to the tidal creek ($0.52 \text{ g m}^{-2} \text{ a}^{-1}$), while less particulate

321 nitrogen was exported to the basin forest ($0.06 \text{ g m}^{-2} \text{ a}^{-1}$). They also demonstrated that the exchanges were highly variable
322 with seasonal weather forcing, as salinity (hence nutrient concentrations) in the creek was influenced by inputs from
323 rainfall and river discharge to the lagoon. Moreover, as the Carbon to Nitrogen ratio of particulate matter exported during
324 ebb tides was generally higher than particulate matter imported into the forest during flooding, they suggested that there
325 is a greater nitrogen loss during ebb tide caused by the export of nitrogen deficient detritus from fringe and basin
326 mangroves.

327 Several works describing nutrient dynamics have been published on *Thalassia testudinum* seagrass beds located off the
328 inner littoral of Carmen Island (Stevenson et al., 1988; Hopkinson et al., 1988; Kemp et al., 1988). Rates of NH_4
329 regeneration in sediments of *T. testudinum* beds were ten times higher in surficial sediments (0 to 2 cm) than at depth
330 (18 to 20 cm). Turnover-time for ammonium pools in surface sediments were about 1 day. Both anaerobic decomposition
331 and denitrification are important biogeochemical processes in Terminos Lagoon seagrass beds and rates of ammonium
332 regeneration were sufficient to supply >70% of the nitrogen required for seagrass growth in this system (Kemp et al.,
333 1988). Nitrogen uptake measured in intact cores showed low rates ranging from $0.8 \mu\text{molN m}^{-2} \text{ d}^{-1}$ in February ('Nortes')
334 to $50 \mu\text{molN m}^{-2} \text{ d}^{-1}$ in August (rainy season). Separate nitrogen uptake by leaf, root, rhizome, and sediment components
335 measured in small serum bottles suggest that N fixation provides 10 to 40% of nitrogen demand of the seagrasses
336 (Stevenson et al., 1988). The highest uptake rates occurred just prior to the *Thalassia testudinum* production peak in
337 February (Rojas-Galaviz et al., 1992). Measurements of stocks of organic and inorganic nitrogen in sediment, water and
338 the biota indicates that biotic stocks of $13220 \mu\text{mol m}^{-2}$ dominated abiotic stocks of $19 \mu\text{mol m}^{-2}$ of nitrogen in the
339 *Thalassia* system, with less than 0.2% of the nitrogen being in the inorganic form (Hopkinson et al., 1988). A large
340 percentage of the total organic nitrogen pool (94%) is contained in dead material (746 versus $12610 \mu\text{mol m}^{-2}$, living
341 and dead material, respectively) and 97% of the organic nitrogen is located in the sediments, as opposed to the water
342 column. Approximately 75% of the inorganic nitrogen is in the sediments, as opposed to the water column (Hopkinson
343 et al., 1988), while inorganic nitrogen uptake requirements are 7.5, 2.5, and $4.0 \text{ mmol N m}^{-2} \text{ d}^{-1}$ for phytoplankton,
344 epiphytes and *T. testudinum*, respectively. The nitrogen turnover times ranged from less than 1 day for inorganic nitrogen
345 in the water column to over 3000 days for sedimentary organic nitrogen (Hopkinson et al., 1988).

347 8. Drivers of environmental change

348 Terminos Lagoon and its surrounding wetlands are oppositely impacted by their conservation status and by human
349 development pressure. Urbanization, wastewater discharge, industrialization, alteration of the hydrologic regime,
350 agricultural and cattle production, petroleum extraction and fishing have been exhaustively addressed as the most
351 important deleterious issues (Robadue 2004). Land cover is one of the most systemic indicators of environmental change
352 in the protected area surrounding Terminos Lagoon. Between 1974 and 2001, 31 % of the area was detrimentally
353 affected, resulting mainly from the replacement of tropical forest and mangroves by grassland and urban areas (Soto-
354 Galera et al., 2010).

355 Between 1986 and 2001 however, the protected status of Terminos Lagoon prompted some positive action in terms of
356 environmental restoration and protection, allowing to reduce losses in natural habitats by half and demonstrating the

357 potential of efficient remediation strategies. A mangrove restoration experiment headed by the Gulf of Mexico Large
358 Marine Ecosystem Based Assessment and Management Project (GEF LME-GoM) identified increasing salinity in the
359 porewater of mangrove soils as responsible for the most long term deleterious effects and defined remediation based on
360 hydrological restoration and local community involvement which yielded an inversion in the receding mangrove
361 dynamics (Zaldivar-Jiménez et al., 2017).

362 Currently, the fluvial-lagoon systems of Terminos Lagoon are disturbed. According to Herrera et al. (2002) and
363 EPOMEX (2002), the zones having registered the most change are the river-mouths of the three main rivers (the
364 Candelaria, the Chumpan, and the Palizada), due to excessive inputs of terrigenous materials and growth of oyster reefs.
365 According to Márquez-García (2010), about 30% of the lagoon is in the process of sediment deposition meaning that
366 the lagoon is facing a major sediment accumulation problem. The formation of an internal delta at the mouth of Puerto
367 Real involves the retention of sandy sediments in Terminos Lagoon due to the decrease in current velocity within the
368 system. Conversely, the processes of erosion-deposition in the lagoon generate changes in the depth of the system and
369 erosive morphology of some parts of the coastal area. This can lead to various problems ranging from the siltation or
370 death of seagrasses to constraints in small boat navigation. Approximately 42 m of beach have been lost in the eastern
371 side of Puerto Real Inlet, a process aggravated by poorly engineered breakwaters that partially disrupt littoral transport
372 (Márquez-García et al., 2013). These changes primarily in the east part of the lagoon have likely transformed the
373 biogeochemical characteristics of the sediments, thus impacting the distribution of benthic species and lagoon
374 biodiversity.

375 Significant changes in fish population have been reported since 1980, including alteration in fish taxonomic and
376 functional diversity combined, with decreases of 41 % and 58 % in fish abundance and biomass, respectively (Ramos
377 Miranda et al., 2005; Villéger et al., 2010; Sirot et al., 2015, Abascal-Monroy et al., 2016; Sirot et al., 2017). Such
378 changes in biota have been tentatively linked to a loss of favorable habitats and a sustained increase in salinity due to
379 decreasing river inputs to the lagoon (Sosa-Lopez et al., 2007). However, such a sustained trend in salinity increase is
380 supported neither by long term surveys of rainfall and river discharge, nor by modeling outputs that foresee stability in
381 rainfall during the first half of the 21st century. The observed differences have been related to strong inter-annual
382 variability in runoff, potentially related to ENSO conditions (Fichez et al., 2017). It is true, however, that the very same
383 climate change modeling approaches foresee reductions of rainfall by 5 to 30 % in the region during the second half of
384 the 21st century (Biasutti et al., 2012; Hidalgo et al., 2013), corresponding to an overall reduction in runoff of up to 80
385 percent in the central Yucatan Peninsula and Guatemalan highlands, and of 20 percent in the Veracruz, Tabascan and
386 Campeche lowlands (Imbach et al., 2012; Kemp et al., 2016). Such alteration in hydrologic regime will dovetail with
387 sea level rise, leading to flooding of the most coastal lowlands including Terminos Lagoon, whose surrounding wetlands
388 have been identified as some of the most critical areas in the region in terms of submersion risk and flooding (Ramos
389 Reyes et al., 2016).

390 Considering pollutants, the highest dissolved Total Polycyclic Aliphatic Hydrocarbons (PAH) concentrations were
391 reported from the Carmen Inlet, whereas water masses close to the Palizada River estuary supported an abundant
392 bacterial community of PAH degraders (Conan et al., 2017). PAH concentrations in oyster tissues were reported to range

393 from 2.5 to 42.5 $\mu\text{g g}^{-1}$ (Norena-Barroso et al., 1999). The predominance of low and medium molecular weight alkylated
394 compounds over their parent compounds indicated the petrogenic source of these PAHs, hence pointing to offshore oil
395 activities as a major source of PAHs inputs. A study in the western part of Terminos Lagoon showed that PAH
396 concentrations in fish flesh exceeded the maximum values recommended by international regulations (greater than 40.0
397 $\mu\text{g g}^{-1}$ for the epibenthic *Petenia splendida*) (Orozco-Barajas et al., 2014).

398 Chlorpyrifos was detected in the water at concentrations up to 72 pg l^{-1} , and amongst organochlorine compounds,
399 PolyChloroBiphenyl (PCB) averaged 1177 pg l^{-1} and DDT 279 pg l^{-1} , respectively (Carvalho et al., 2009a). Residues of
400 chlorinated compounds were present in both the sediments and the biota, with DDT averaging 190 pg g^{-1} and 5876 pg
401 g^{-1} in sediments and oysters, respectively. Concentrations of residues did not reach alarming levels and were in fact
402 lower than those reported for other coastal lagoons of the region (Carvalho et al., 2009b). The Palizada River is by far
403 the major contributor (85 % to 99 % depending on the considered metal) of riverborne metal inputs to the lagoon (Páez-
404 Osuna et al., 1987). Reported concentrations of total metals in lagoon water were higher than in pristine environments
405 (Vazquez et al., 1999) but not very different than in other coastal waters. The authors related the highest metal
406 concentrations in the lagoon to anthropogenic inputs from rivers as well as to more diffuse atmospheric input from the
407 nearby petroleum industry, but no direct evidence was provided.

408 Comparisons between metal concentrations in the oyster *Crassostrea virginica* with previous data (Vazquez et al., 1993)
409 showed that whereas zinc concentrations remained virtually unchanged since the mid-1970s, the levels of cadmium
410 decreased and concentrations of copper and lead increased significantly. In a recent paper dealing with the study of the
411 effect of various contaminants on the oyster *C. virginica* (Gold-Bouchot et al., 1995) the authors concluded that the
412 pollution level in Terminos Lagoon could be considered as moderate.

413 Long-term effects of pesticides and heavy metals were studied in aquatic mammals inhabiting Terminos Lagoon. Heavy
414 metals and pesticides in bottlenose dolphins (*Tursiops truncatus*) were present in skin and blubber biopsy samples, albeit
415 in lower concentrations than those recorded in other studies (Delgado-Estrella et al., 2014).

417 9. Conclusions and recommendations

418 The great variability and heterogeneity in the numerous variables that control and characterize transitional water systems
419 greatly hinders the potential for inter-comparison between very diverse sites, because tropical coastal lagoon systems
420 are driven, for example, by very specific factors when compared to temperate ones (Ortiz-Lozano et al., 2005; Camacho-
421 Ibar & Rivera-Monroy, 2014). While most of the coastal lagoons in the world are more or less exposed to the same set
422 of detrimental factors arising from human development and sea level rise, global climate change impacts can on the
423 other hand be strongly geographically dependent, even at the regional scale. This variability is particularly strong in the
424 Gulf of Mexico and Central America region, and joint simulations foresee an increase in the mean annual discharge of
425 the Mississippi-Atchafalaya River by 11 to 63 percent, compared to a severe decrease by up to 80 percent for the
426 Usumacinta-Grijalva River (Kemp et al., 2016). Such a contrasting forecast regarding the two major watersheds of the
427 Gulf of Mexico is of major consequence to their respective downstream coastal systems and prefigures a drastic
428 environmental shift in Terminos Lagoon.

429 Considering the sensitivity of the biota to the balance between riverine and marine influences, salinity is obviously an
430 essential indicator of the main alteration process that will impact the Terminos Lagoon system on a long term and global
431 scale. In the absence of a structured environmental monitoring plan focusing on the hydrology of Terminos Lagoon in
432 particular, urgent action should be taken to gather information on the ongoing trends in environmental change. Indeed,
433 the previously exposed arguments demonstrate that salinity is the most obvious basic indicator of environmental change
434 to be continuously measured in various representative parts of the lagoon.

435 Larger scale studies are required to more precisely capture the dimensions and nature of the changes produced and their
436 effects on the structure and function of the landscape. Additionally, deeper examination of the history of land use should
437 be conducted to better interpret elements concerning the causes of changes and modifications occurring in the area.
438 Regional trends over the past 30 years have replaced forests with pastures, and there is a call today for more efficient
439 and proactive conservation policies through paid environmental services.

440 Regarding pollutants, environmental threats seem to be primarily localized around urban areas and river mouths, or
441 restricted to specific ecosystem components, especially in the highest trophic levels. Furthermore, studies on emerging
442 pollutants are entirely absent in Terminos Lagoon and are urgently needed.

443 Finally, even if several compartments of the benthic ecosystem have been studied, some topics remain to be assessed,
444 such as sediment-water exchanges of nutrients and benthic carbon mineralization in the lagoon, as well as the processes
445 related to microphytobenthic productivity. Such information may be of prime importance in understanding the
446 functioning of Terminos Lagoon and for calculating accurate budgets in order to preserve this protected but threatened
447 ecosystem.

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