THESE DE DOCTORAT DE L'UNIVERSITE AIX-MARSEILLE

Institut Méditerranéen d'Océanologie
Ecole Doctorale des Sciences de l'Environnement

Variabilité spatiale et temporelle des cycles biogéochimiques à l'interface eau-sédiment dans la lagune de Términos, Mexique.

Présentée par

Montserrat Origel Moreno

Pour obtenir le grade de
Docteur de l'Université Aix-Marseille

Spécialité Océanographie

Soutenue le 9 décembre 2015 devant le jury composé de :

Dr. C. Rabouille, CEA LSCE Gif sur Yvette	Rapporteur
Dr. P-G Sauriau, LIENSs, Université de La Rochelle	Rapporteur
Pr. K. Soetaert, NIOZ, Yerseke, The Netherlands	Examinateur
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Sois reconnaissant envers tous, tous t'enseignent.

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The beginning is the most important part of the work

Platon

Chapitre I.

INTRODUCTION

I. INTRODUCTION

I.1 Généralités

Dans le contexte du changement global, la compréhension du fonctionnement du système océanique et notamment des échanges à ses frontières représente plus que jamais une priorité qui s'intègre pleinement dans les prospectives de recherches nationales et internationales portant sur la protection des ressources naturelles, des écosystèmes et de leurs services (SCOR/IGBP (www.igbp.kva.se), MEDD 2012; Balancing the Future of European Coasts, EEA 2013). Ces zones de transitions incluent les couches mésopélagiques et intermédiaires de l'Océan ainsi que les marges continentales. Ces dernières sont caractérisées par un couplage étroit entre la colonne d'eau et le sédiment, conséquence d'un mélange vertical régulier sinon permanent des masses d'eau atteignant le fond et une influence forte de ces fonds sur le cycle pélagique. De plus, ces régions de l'Océan sont caractérisées par une forte productivité et directement impactées par la société. Les flux d'origine continentale ont augmenté de façon substantielle en réponse au développement des activités agricoles et à la concentration des populations en zones littorales (LOIZC 1996, Newton et al. 2014). En effet, c'est sur la frange littorale que se concentre 10% de la population mondiale et celui-ci est le réceptacle d'apports anthropiques provenant de voies fluviatiles ou atmosphériques. C'est un système à interactions complexes, contrôlé par différents processus à dynamique rapide (crue, tempête..) et lente (sédimentation, minéralisation…), dont l'analyse nécessite le couplage de nombreuses disciplines (biogéochimie, sédimentologie...).

Cette notion de couplage remonte au début du siècle dernier notamment avec Vladimir Vernadsky, minéralogiste et chimiste de renom qui publie en 1926 un ouvrage en russe intitulé "Biosphère". Il est considéré comme le père fondateur de l'écologie globale et le créateur des "Sciences Biogéochimiques". Hutchinson (1948) puis Odum (1971), pionniers de l'étude écologique des systèmes ont largement contribué à faire émerger l'Ecologie comme discipline scientifique et entre autre à avoir introduit les notions de "Cycles Biogéochimiques". Selon Odum (1971) la biogéochimie est l'étude du processus cyclique de transfert des éléments chimiques de l'environnement à partir des milieux abiotiques vers les organismes qui à leur tour retransmettent ses constituants à l'environnement (Odum 1971).

Les principaux éléments qui interviennent dans les cycles biogéochimiques sont le carbone, l'azote, le phosphore, le soufre, le silicium puis une série d'oligoéléments tous impliqués dans les processus biogéochimiques.

Le carbone est un élément clé de la matière vivante, en raison de sa capacité à former de longues chaînes ou des anneaux moléculaires. Il possède un cycle complexe parce qu'il est présent dans toutes les formes vivantes et dans de nombreux composés inorganiques : on le trouve sous forme de carbone élémentaire (diamant, graphite ou forme amorphe), de composés organiques (plus d'un million de molécules différentes), de roches carbonatées dans la lithosphère, de composés inorganiques dissous dans l'océan et les eaux continentales (bicarbonates, carbonates, gaz carbonique) et de gaz présents à l'état de trace dans l'atmosphère (gaz carbonique, méthane, oxyde de carbone, hydrocarbures). La plupart de ces composés sont susceptibles de participer à des réactions chimiques très diverses. Les échelles de temps des processus mis en jeu varient de plusieurs millions d'années, pour ceux qui sont contrôlés par l'activité interne de la Terre, à quelques secondes, pour la photosynthèse ou pour les échanges gazeux air-mer.

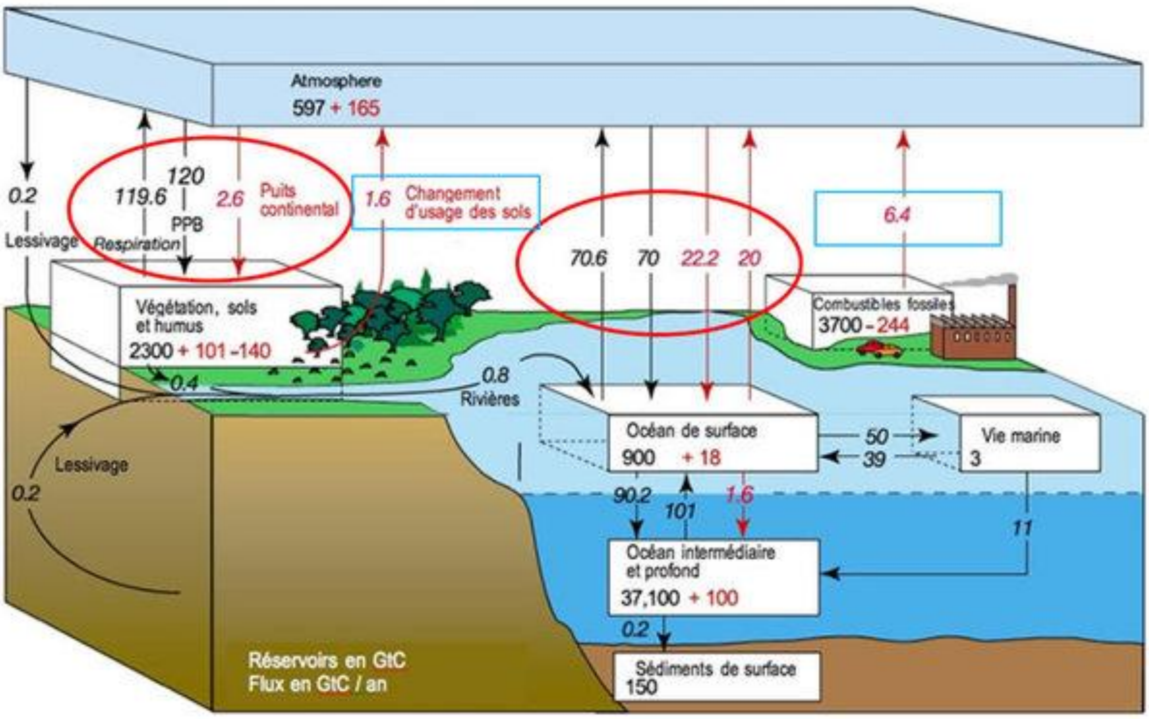

Figure I.1 Cycle global du carbone et les flux en GtC yr^{-1} pour la période pré-industrielle 'naturelle' en noir 'anthropogénique' en rouge (4ème rapport GIEC, «The Physical Science Basis » (2007), issu de Sarmiento & Gruber, 2002 modifié).

Si les stocks de carbones sont principalement formés par les roches carbonatées et la matière organique fossile, les flux d'échanges entre compartiments se font principalement sous forme gazeuse (CO_2) faisant intervenir des processus physico-chimiques ou biologiques (respiration - photosynthèse).

Avant l'ère industrielle, les quantités de carbone échangées entre les différents réservoirs étaient plus ou moins en équilibre. Il n'en est plus de même aujourd'hui, principalement en raison des rejets massifs de dioxyde de carbone dans l'atmosphère résultant de la combustion de combustibles fossiles depuis le début de l'ère industrielle. En effet, si la combustion de matière organique (bois, pétrole, charbon) libère du dioxyde de carbone dans l'atmosphère comme le fait la respiration des êtres vivants, les échelles de temps et de volume mises en jeu dans les rejets anthropiques sont sans commune mesure avec celles impliquées dans le cycle du carbone hors activités humaines (Figure I.1).

L'océan côtier ne représente que 7 % des surfaces marines mais contribue significativement au cycle du carbone global (puits de 1.0 PgC yr^{-1} par rapport aux 1.6 pour l'Océan ouvert (Tsunogai et al. 2003)). Une synthèse récente publiée dans 'Procedia Earth and Planetary Science' souligne que le flux de carbone arrivant dans l'Océan côtier a augmenté significativement depuis la période pré-industrielle mais que seule une petite fraction est exportée vers le large (Regnier et al. 2014). Des études récentes sur les marges continentales avec l'établissement de bilans de carbone, d'azote et de phosphore, ont souligné le rôle de piège de ces systèmes vis-à-vis du CO_2 anthropogène. Si cela reste valable pour les marges dans leur ensemble, les systèmes plus littoraux sont reconnus hétérotrophes, pour la plupart en raison des forts taux de dégradation du carbone organique apporté par les rivières (Hopkinson et al. 2004).

En effet Borges et al. (2005) a montré que dans les zones où le plateau continental était éloigné des côtes et des fleuves, la zone côtière était un puits de CO_2 alors que les zones d'estuaires, de deltas et de baies dominées par les apports continentaux constituaient une source de CO_2. Cette 'source' de CO_2 pour l'atmosphère viendrait équilibrer le puits des zones côtières ouvertes où le métabolisme est dominé par l'autotrophie (Borges et al. 2005).

Une des questions clés pour le carbone océanique est donc de déterminer l'intensité des termes sources/puits de CO_2 dans les estuaires/deltas des fleuves et lagons qui pourraient représenter une source de CO_2 égale à 25-30% du puits océanique net de CO_2 (0.5 Pg/y^{-1}) (Takahashi et al. 2009).

Tel est le cas des écosystèmes sub-tropicaux (Figure I.2) qui sont considérés comme des sources nettes de CO_2 (Takahashi et al. 1993) généralement en été, voire tout au long de l'année pour les zones de la ceinture Caraïbe où les températures restent élevées au cours des cycles saisonniers.

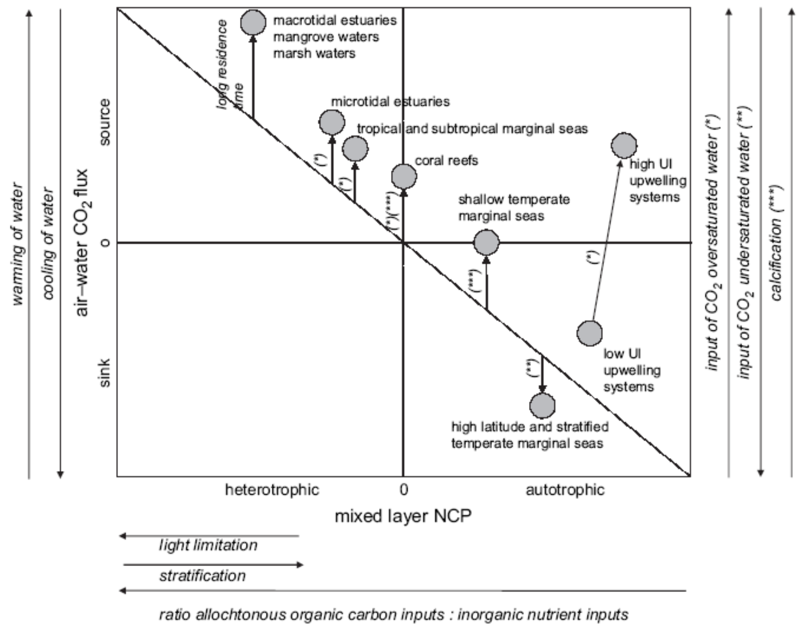

Figure I. 2 Schéma conceptuel du control de la biogéochimie sur les flux air-eau de CO_2 en zone côtière (d'après Borges et al. 2006).

La production de CO_2 dans ces systèmes est liée pour partie aux temps de résidence des masses d'eau et aux processus diagénétiques de dégradation du carbone organique dans les sédiments (Borges et al. 2003).

L'oxygène est en masse, le troisième élément le plus abondant de l'Univers après l'hydrogène et l'hélium, et le plus abondant des éléments de l'écorce terrestre. Il constitue 86 % de la masse des océans, sous forme d'eau. Il existe néanmoins certaines zones présentant des teneurs faibles en oxygène, les OMZ ou "Oxygen Minimum Zones" dont l'une des plus étendues, des plus intenses et des moins profondes est située au sud-est de l'océan Pacifique tropical dans les régions de résurgence côtière (Paulmier et al. 2008). Au niveau global, ces zones couvrent 9%

de l'océan mondial et s'observent dans toutes les régions du monde. Lorsque les concentrations chutent à zéro on parle d'ODZ ou "Oxygen Deficient Zones" (Chang et al. 2010).

En effet, la conjonction d'une stabilisation des masses d'eau (réduction de la turbulence verticale et augmentation des temps de résidence) avec l'augmentation des apports de nutriments conduit à des crises anoxiques néfastes pour le biotope. La question de l'homéostasie des écosystèmes s'est posée dans le contexte des perturbations auxquelles ils sont soumis (Scheffer & Carpenter 2003). Une hypoxie prolongée des eaux de fond de la côte danoise en 2002 s'est traduite par une destruction massive des communautés benthiques et des changements drastiques des caractéristiques de la reminéralisation de la matière organique des sédiments (Conley, 2000). La succession de ce type d´évènements les années suivantes a eu pour conséquence un changement de la structure des communautés benthiques reconstituées et un shift dans le recyclage biogéochimique. Un non retour probable au précédent état de stabilité est à craindre même dans le cas d'un arrêt complet des apports continentaux, ce qui va à l'encontre de la notion de résilience (Conley D., comm pers.) même si actuellement les trajectoires semblent encore réversibles (Worm & Duffy 2003).

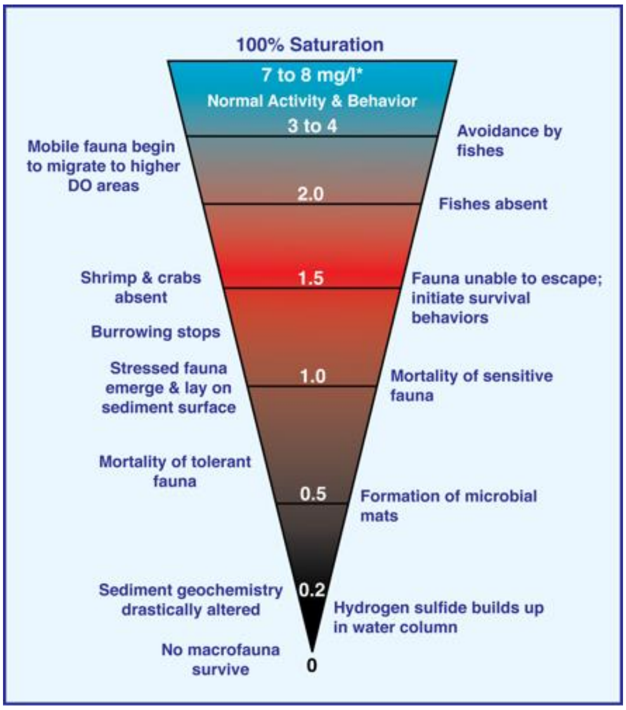

Figure I.3 Différents impacts de la déplétion en oxygène dissous sur l'environnement et les communautés en place.

Les zones côtières impactées par des épisodes d'hypoxies sont en très forte augmentation à l'échelle du globe avec plus de 400 "dead zones" répertoriées dans le domaine côtier représentant une surface de 245 000 km^2 (Diaz & Rosenberg 2008). Les impacts écologiques et socioéconomiques qu'ils induisent sont considérables. Ces phénomènes d'hypoxies résultent d'interactions complexes de processus physiques, chimiques et biologiques qui sont encore mal maitrisées, tout particulièrement en ce qui concerne les rétroactions colonne d'eau-sédiment. L'impact du déficit en oxygène se fait ressentir rapidement sur les communautés pélagiques et benthiques, induisant la fuite lorsqu'elle est possible ou une mortalité de masse dans le cas contraire (Figure I.3).

I.2 Diagenèse précoce

La respiration benthique est un processus important dans les cycles biogéochimiques. La consommation d'oxygène par les sédiments profonds représente la moitié de celle de la colonne d'eau de l'Océan calculée entre 1000 m et le fond (Martin & Sayles 2013). Ceci est d'autant plus vrai pour la zone côtière car les échanges verticaux sont orientés à la fois de la colonne d'eau vers le sédiment (apports de particules vers le fond) et du compartiment sédimentaire vers la colonne d'eau avec des échelles de temps caractéristiques similaires. En effet, les constantes de temps sont généralement supérieures au millénaire dans les sédiments océaniques profonds alors qu'en zone côtière, ces dernières sont inférieures à la décennie. Parallèlement, les sédiments de la zone côtière joue un rôle important dans le contrôle des cycles biogéochimiques pélagiques. Les réactions métaboliques dans les sédiments contribuent de façon prépondérante à la production et à la minéralisation de la matière organique et déterminent les caractéristiques des conditions d'oxydo-réduction des sédiments.

Au cours de la diagenèse précoce, d'intenses transformations ont lieu dans les sédiments qui mènent au recyclage et/ou à l'enfouissement de la matière organique mais également à la transformation de phases particulaires (carbonate, pyrite). Les interactions entre les processus diagénétiques (oxique et anoxique) et les carbonates du sédiment (dissolution et précipitation) peuvent modifier les flux de CO_2 générés par l'activité bactérienne. L'équilibre de ces différents processus détermine donc le sens et l'intensité des flux de CO_2 à l'interface air-mer en milieu côtier.

Les processus contrôlant la diagenèse précoce comprennent une activité biologique, principalement sous la forme d'une décomposition bactérienne de la matière organique, la bioturbation liée à l'activité de la méio- et macrofaune qui va gérer la répartition verticale de la matière organique dans la colonne sédimentaire ainsi que les phénomènes de néoformation (authigenèse)/dissolution de phase(s) minérale(s).

L'activité bactérienne correspond à une succession de réactions d’oxydoréduction qui font intervenir un donneur d’électron (le réducteur étant toujours le carbone contenu dans la matière organique) qui sera oxydé et un accepteur d’électron (l’oxydant) qui sera réduit (Figure I.4). Les oxydants sont des réactifs limitants qui se succèdent depuis l’interface eau-sédiment vers la profondeur du sédiment en fonction de la décroissance de leur potentiel d’oxydoréduction.

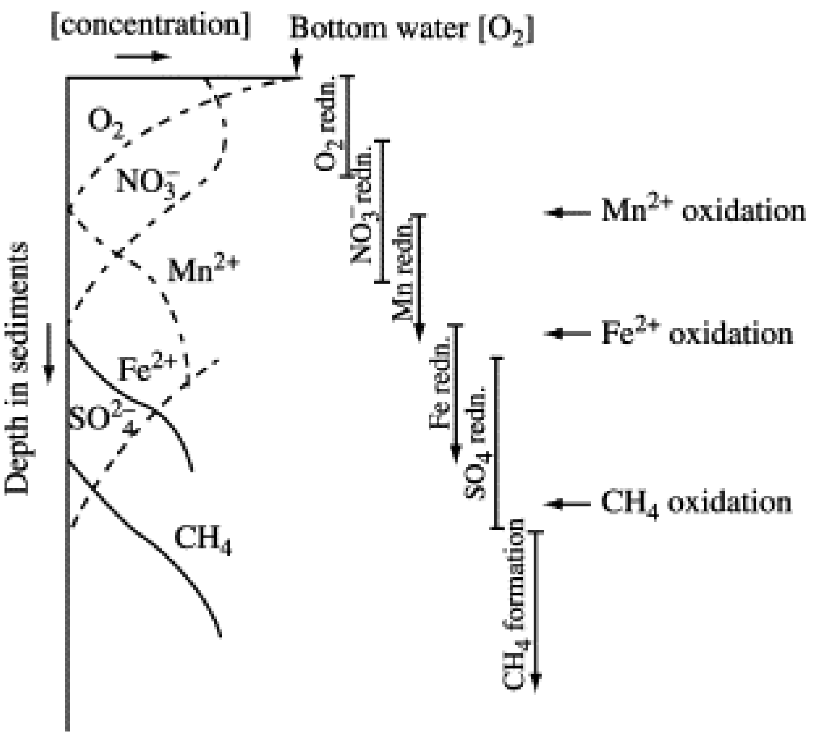

Figure I.4 Représentation schématique de la succession des accepteurs d'électrons dans la colonne sédimentaire et zonation théorique des réactions de minéralisation de la matière organique (réactions liées à l’activité bactérienne).

Tableau I.1 : Réactions primaires d'oxydation de la matière organique établies selon Froelich et al. (1979) dans les sédiments marins et valeurs de l'énergie libre standard par mole de carbone organique. Les équations sont établies suivant la stoechiométrie pour une mole de matière organique proposée par Redfield : C106/N16/P (Redfield et al. 1963).

	$\Delta G°$ (KJ/mol)
Oxydation de la Matière Organique (M.O.) par l'oxygène (1)	
$138O_2 + M.O. + 18HCO_3^- \rightarrow 124CO_2 + 16NO_3^- + 122H_2O + H_3PO_4$	-479
Dénitrification (2)	
$94.4NO_3 + M.O. \rightarrow 52.2N_2 + 13.6CO_2 + 84.8H_2O + HPO_4^{2-} + 92.4HCO_3^-$	-453
Oxydation par les oxydes de manganèse (3)	
$236MnO_2 + M.O. + 104H_2O + 364CO_2 \rightarrow 236Mn^{2+} + 470HCO_3^- + HPO_4^{2-} + 8N_2$	-349
Oxydation par les oxydes de fer (4)	
$424FeO_3 + M.O. + 104H_2O + 740CO_2 \rightarrow 424Fe^{2+} + 846HCO_3^- + HPO_4^{2-} + 16NH_3$	-114
Oxydation par les sulfates (5)	
$53SO_4^{2-} + M.O. \rightarrow 53HS^{2-} + 39CO_2 + 39H_2O + HPO_4^{2-} + 67HCO_3^- + 16NH_4^+$	-77
Production de méthane (6)	
$M.O. \rightarrow 53CH_4 + 53CO_2 + HPO_4^{2-} + 16NH_4^+$	-30

L'énergie libérée (Tableau I.1) lors de la minéralisation varie selon la nature des oxydants. Ainsi l'oxygène est d'abord utilisé, puis le nitrate et le nitrite, l'oxyde de manganèse, les oxydes de fer, le sulfate et enfin l'oxygène lié à la matière organique (Froelich et al. 1979).

La dégradation de la matière organique particulaire à l'interface eau-sédiment provoque, en raison des gradients d'oxydoréduction, des réactions de transformation (diagenèse précoce) qui modifient la distribution et la mobilité non seulement du C, de N et du P particulaire mais aussi de nombreux éléments nutritifs et contaminants dissous (Fe, Zn, Cu, Mn, Hg, etc., Figure I.5).

De toute la biomasse nouvellement formée dans la zone photique, seule une petite partie atteint les fonds océaniques et est finalement enfouie dans les sédiments. On estime que 1 à 0,01% de cette production est enfouie profondément dans les sédiments (Schulz et al. 1994). Ce pourcentage dépend fortement de l'intensité de la productivité primaire, de la profondeur de la colonne d'eau et de la teneur en oxygène des masses d'eau et des sédiments de surface, de la taille et de la densité des particules, de l'adsorption des surfaces minérales et de la porosité du sédiment.

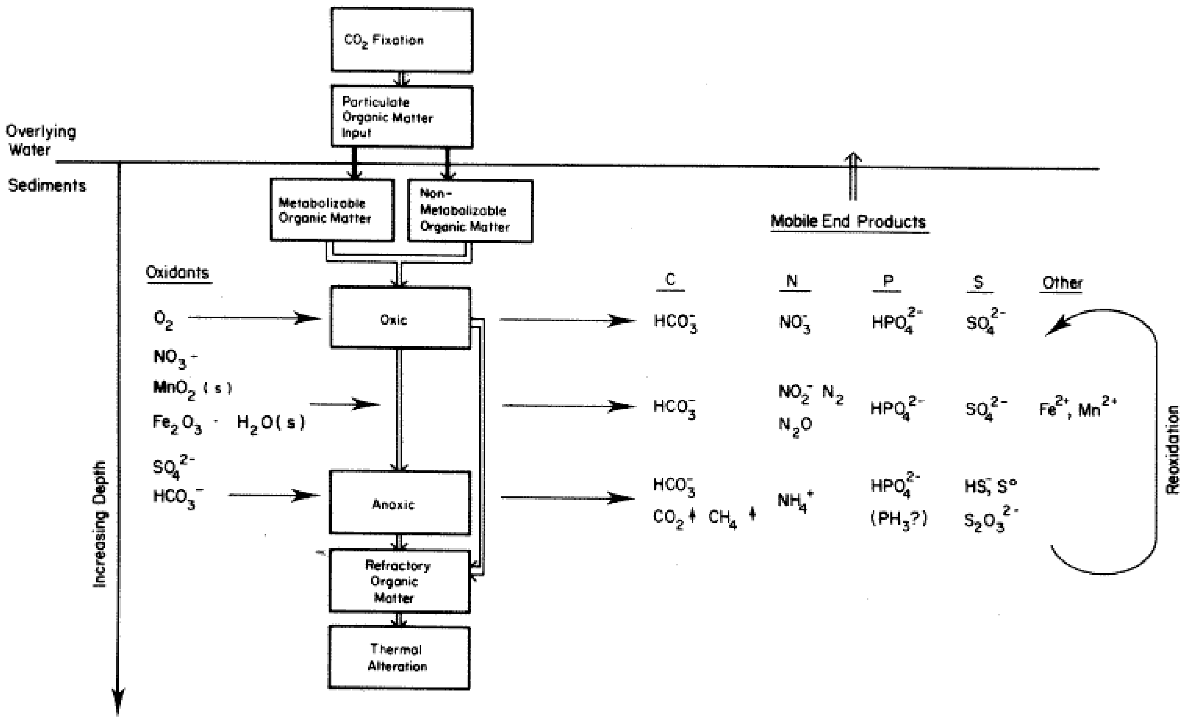

Figure I.5 Les cycles biogéochimiques majeurs et leurs interactions (d'après Jorgensen 1983)

En zone côtière, où les temps de résidence des particules lors de leur chute sont plus faibles, les apports de matière organique sont bien plus importants en quantité et plus labile en termes de réactivité (Hammond et al. 1996, Sachs et al. 2009).

En conséquence, les profondeurs de pénétration de l'oxygène dans le sédiment varient de quelques mm (1 à 5.5 mm en zone côtière, Revsbech et al. 1981) à quelques dizaines de mm en zone profonde (Figure I. 6, Grundmanis & Murray 1982).

L'importance des processus anaérobiques dans la minéralisation benthique se trouve donc augmentée d'autant plus que la hauteur de la couche oxydée est réduite (Thamdrup et al. 1998).

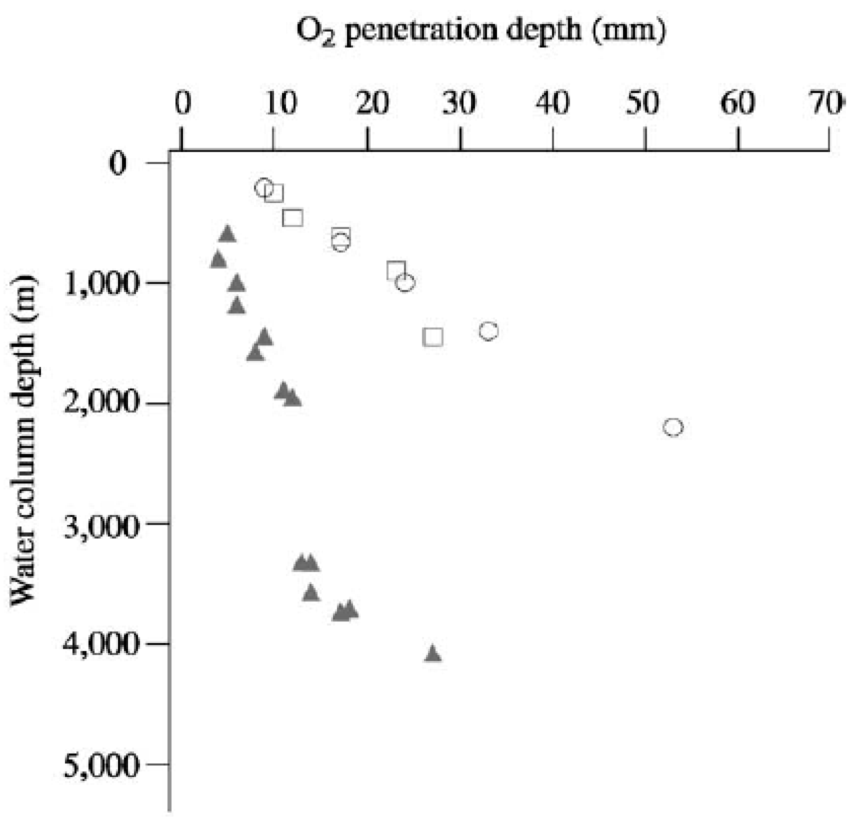

Figure I.6 Hauteur de la couche oxydée des sédiments de marges continentales en Atlantique et Pacifique (Lohse et al. 1996, Reimers et al. 1992), d'après Martin & Sayles (2013).

Concernant l'azote, contrairement au phosphore et à la silice, il existe plusieurs formes de nutriments azotés en fonction de leur état d'oxydation interconnectées dans un cycle complexe largement dominé par l'activité des micro-organismes (Figure I.7). En aérobie, ce cycle comprend des processus chemo-autotrophiques de nitrification comme l'oxydation de l'ammonium (Nitrosomonas) et des nitrites (Nitrobacter). En milieu anaérobique, les processus bactériens de dénitrification et d'anammox conduisent à la libération d'azote gazeux. Enfin l'ammonification intervient à tous les niveaux durant la minéralisation. Les cyanobactéries (Trichodesmium) sont capables de fixer l'azote gazeux pour leur besoin azoté.

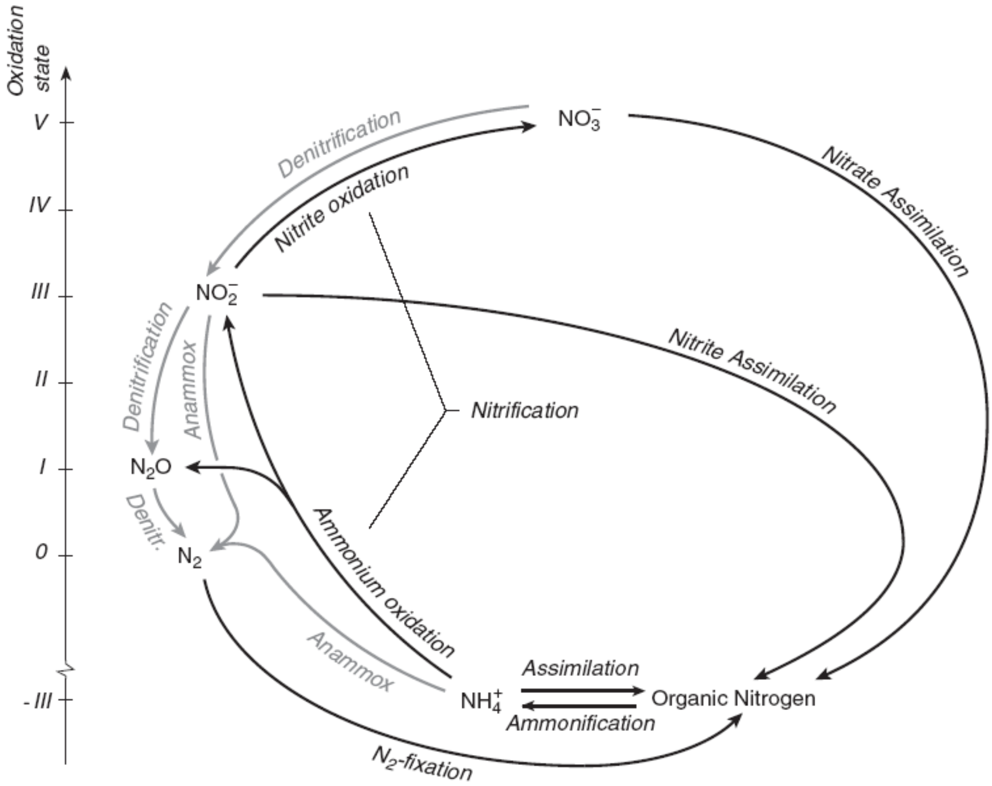

Figure I.7 Formes chimiques principales et transformations de l'azote dans le domaine marin en fonction de leur état d'oxydation, sous condition aérobie (en noir) et anaérobie (en gris), d'après Gruber 2008.

Dans les écosystèmes marins où les sulfates abondent, la sulfato-réduction assure une part importante de la minéralisation de la matière organique (Canfield 1989, Pallud & Van Cappellen 2006). Les bactéries sulfato-réductrices réduisent en anaérobiose les composés oxydés (sulfates) en sulfures. Ces derniers sont à leur tour oxydés en sulfates soit par les bactéries phototrophes anoxygéniques dans les milieux anoxiques éclairés, soit par les thiobacilles ou les thiobactéries aérobies dont le métabolisme nécessite la présence d'oxygène moléculaire (revue de Canfield et al. 1993, Thamdrup & Canfield 1996). Dans certains environnements tels que les marais salants, la sulfato-réduction est le processus de respiration dominant (Howes et al. 1984, Kostka et al. 2002). La métanogenèse arrive en dernière position, la réduction des sulfates étant énergétiquement plus favorable que celle du méthane.

La zonation évoquée précédemment (Figure I.4) est une représentation idéalisée de la répartition des accepteurs d'électron et des processus de minéralisation. La réalité est bien plus complexe en raison de l'influence de :

1. L'hydrodynamisme local qui pour les sites peu profonds peut transformer rapidement la structuration verticale de la colonne sédimentaire (remise en suspension et/ou re-déposition de particules), ou générer un flux d'advection conduisant à la ventilation des couches superficielles des sédiments,
2. des apports extérieurs de matière organique à l'échelle d'une crue notamment dans les deltas et les estuaires,
3. des phénomènes de bioturbation qui vont redistribuer la matière organique une fois déposée et les accepteurs d'électrons.

La résultante est une instabilité liée aux processus physique et biologique (remaniement sédimentaire) qui engendre une répartition tridimensionnelle des éléments et dynamique dans le temps (Aller 1994). Lorsque la profondeur est plus grande ou dans le cas des sédiments cohésifs où le renouvellement des éléments nutritifs et de l'oxygène se fait par diffusion, un état d'équilibre peut s'instaurer dans les couches superficielles des sédiments.

Les éléments réduits produits lors des processus de minéralisation y compris ceux issus de la réduction des oxydes de Fe^{2+} et de Mn^{2+} sont ré-oxydés dans ou aux abords de la couche oxique des sédiments. De ce fait la consommation de l'oxygène par les couches superficielles des sédiments, telle que mesurée par incubation, reflète à la fois la minéralisation oxique de la matière organique et la ré-oxydation des éléments réduits produits par les métabolismes anaérobiques (Canfield et al. 1993).

La progression des apports de nutriments depuis les continents se traduit par une augmentation de la productivité primaire engendrant une amplification du métabolisme (respiration) et notamment dans les estuaires ou zones côtières. (Frankignoulle et al. 1996). Les zones côtières tropicales sont soumises comme ailleurs à une accélération des pressions liées aux activités humaines et à l’accroissement des populations riveraines le tout s’ajoutant aux problèmes liés au changement climatique. De ce fait la connaissance des processus naturels fondamentaux tels que le cycle du carbone et des éléments associés est nécessaire afin de déterminer l’état actuel des conditions environnementales et les éventuels dérives ou risques encourus que ce soit en terme de bilan de matière ou d'hypoxie («Dead Zones» (Diaz & Rosenberg 2008).

I.3 Objectifs et organisation du mémoire :

L'objectif principal de cette thèse concerne la quantification des flux d'oxygène et de sels nutritifs dans une lagune tropicale et la détermination de leurs rôles dans les cycles biogéochimiques.

Ce travail s'inscrit dans le cadre d'un programme bilatéral franco-mexicain JEST (Joint Environmental Study of Laguna de Términos) qui a bénéficié de supports techniques et financiers de l'IRD, de la UNAM, de la UAM, et de l'ancien programme PNEC devenu EC2CO-DRILL. Ce programme multidisciplinaire comprenait plusieurs approches au niveau hydrodynamique, production pélagique, polluants (Hydrocarbures, HAP, Métaux), macrobenthos ainsi qu'une étude du compartiment sédimentaire sous l'aspect du métabolisme benthique. C'est dans cette dernière partie qu'interviennent les travaux de cette thèse et qui visent à apporter des éléments de réponse aux questions suivantes :

- Quel est le niveau de variabilité spatiale et temporelle des taux de minéralisation benthique dans la Lagune de Términos ?
- Quelles sont les principaux forçages qui contrôlent cette variabilité et les processus qui gouvernent le sens et l'intensité des flux ?
- Sont-ils différents de ceux des systèmes tempérés compte tenu de l'alternance de saisons sèches et humides et du faible gradient thermique ?
- Quelle est la contribution de ces flux benthiques dans les bilans biogéochimiques de la lagune et varie t-elle saisonnièrement ?

Pour répondre à ces questions, une stratégie de mesure a été mise au point sous la forme de mesures de flux par incubation de sédiments prélevés dans la lagune de Términos, en tenant compte des évènements majeurs qui conditionnent la dynamique de ce système. Compte tenu de sa faible profondeur, de son immense étendue, nous avons privilégié des campagnes courtes mais fréquentes de trois jours avec 4 stations aux caractéristiques différentes et des campagnes longues d'une semaine avec 13 stations couvrant l'ensemble de la lagune. A signaler ici que ce type de mesures, avec ce degré d'intensité que cela soit au niveau spatial ou temporel, n'a jamais été effectué dans cette lagune.

Le manuscrit est construit autour de 6 chapitres dont ce premier chapitre introductif. Les suivants concernent :

Le **chapitre 2 : Présentation du site d'étude**. Ce chapitre décrit très précisément les caractéristiques majeures de la lagune de Términos sous la forme d'une synthèse de l'article co-signé soumis à Marine and Freshwater Research. Cet article, présenté dans l'annexe 1, compare les caractéristiques de la lagune par rapport à d'autres systèmes bordant l'ensemble du Golfe du Mexique.

Le **chapitre 3 : Matériel et Méthodes.** La première partie de ce chapitre présente les sites spécifiquement étudiés qui ont fait l'objet de mesures de flux ainsi que le calendrier. La partie suivante décrit la méthodologie des mesures et les protocoles d'échantillonnage et de traitement des échantillons puis les analyses effectuées.

Le **chapitre 4 : Variabilité spatiale.** Ce chapitre présente les résultats des campagnes spatiales effectuées pendant les saisons sèches en mars 2009 et 2010 et humides en octobre 2009 et novembre 2010. Ce chapitre est rédigé sous la forme d'un article en voie de soumission à Estuarine Coastal Shelf Science. Il aborde respectivement les caractéristiques des sédiments en place, la variabilité des flux selon la saison et le site avec une tentative d'explication des facteurs de contrôle de ces flux en fonction de la qualité et quantité de la matière organique des sédiments.

Le **chapitre 5 : Flux dans sites contrastés** expose l'étude du suivi des 4 stations de références selon la même démarche que précédemment. Un article également en cours de soumission est présenté et vient confirmer les hypothèses énoncées dans le chapitre précédent quant aux taux de minéralisation benthique et leur variabilité selon les saisons.

Le **chapitre 6 : Le cycle de l'azote.** Ce chapitre montre un essai de modélisation portant notamment sur les termes non mesurés mais simulés de minéralisation anoxique et de leur contribution dans la minéralisation totale. Cette partie également rédigée sous la forme d'un article en cours de préparation permet d'approcher le bilan du carbone dans les sédiments.

Le **chapitre 7 : Synthèse et conclusion.** Ce dernier chapitre reprend les résultats majeurs acquis lors de ce travail, puis définit quelques pistes pour les prospectives.

En annexe C, une seconde publication intitulée « Global climate change and local watershed management as potential drivers of salinity variation in a tropical coastal lagoon (Laguna de Terminos, Mexico) » en correction après présentation auprès de la revue Aquatic Sciences, décrit le phénomène El Nino qui a eu lieu en 2009 et ses conséquences notamment sur la réduction drastique des apports pendant la saison des pluies et leur impact sur la distribution des salinités, pouvant expliquer certaines différences observées dans les flux et décrites dans les articles précédents.

There is a river in the ocean. In the severest droughts it never fails, and in the mightiest floods it never overflows. Its banks and its bottom are of cold water, while its current is of warm. The Gulf of Mexico is its fountain, and its mouth is in the Arctic Sea. It is the Gulf Stream.

Matthew Fontaine Maury, Oceanographer

Chapitre II.

Présentation de la lagune de Terminos

II. Présentation de la lagune de Terminos

Les lagunes côtières du golfe du Mexique sont caractérisées par un régime microtidal (marnage < 40 cm) mais pouvant générer de forts mouvements d'eau qui affectent les barrières sédimentaires. Les lagunes estuariennes présentent des zones de mélange entre les eaux marines et côtières, et les eaux douces et à priori de gradients de salinité en fonction des apports des rivières. Si ces apports sont faibles, les lagunes côtières peuvent devenir hypersalines par évaporation (Kjerfve & Magill, 1989). Tel est le cas de nombreuses lagunes de la Péninsule du Yucatán comme les lagons de Celestun, Chuburna, Xtampu et Las Coloradas situés dans la partie nord de la Péninsule et soumis à des apports fluviaux réduits (salinités de 50 à 400, Torrentera & Dodson, 2004). Plus au sud, le régime hydrique et pluviométrique entraine des apports terrestres plus intenses et donc des dessalures de la plupart des lagunes côtières.

La lagune de Términos localisée au Sud-Est du golfe du Mexique, de latitude 18°38'36''N et longitude 91°49'51''O, est caractérisée par un climat tropical humide avec une précipitation annuelle de 1100 à 2000 mm. Le régime climatique est caractérisé par trois saisons marquées au cours de l'année avec :

a) une période sèche de février à mai,

b) une période des pluies de juin à octobre et,

c) une période de fronts également humide d'octobre à février.

Au cours de cette dernière période, l'ensemble de la zone est principalement influencé par des masses d'air provenant du continent nord-américain (Canada, USA et Mexique nord-est) qui génèrent des fronts froids accompagnés de vents soufflant du Nord au Sud, à des vitesses pouvant atteindre 30 m s^{-1}. La rencontre de ces masses d'air froides avec des masses d'air chaudes d'origine maritime et tropicale entraine la formation de nuages pouvant causer des précipitations torrentielles même en hiver (Monreal-Gomez. et al, 2004).

Le golfe du Mexique est situé dans la ceinture des ouragans qui frappent chaque année les côtes du Mexique, avec des vents violents qui peuvent dépasser les 200 km/h et provoquer des dégâts matériels et humains aux conséquences désastreuses. La plupart du temps ces cyclones provenant des caraïbes perdent de leur intensité aux abords du Quitana Roo et se transforment en dépressions tropicales lorsqu'elles traversent la Péninsule du Yucatán.

En dehors de ces situations particulières, l’évaporation est modérée à élevée; les vents proviennent du Sud-Est la plupart de l’année sauf en hiver où ils sont orientés Nord à Nord-Est. En effet, en se basant sur des données météorologiques de l’aéroport de Ciudad del Carmen, les vents les plus fréquents sont orientés entre 45 et 135 (67 % du temps, Figure II.1).

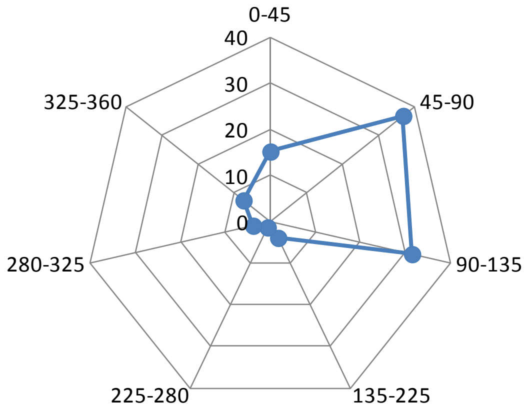

Figure II.1 Rose des vents calculée sur une série de données mesurées de la station météorologique de l'aéroport de Ciudad del Carmen (données journalières de 1990 à 2011).

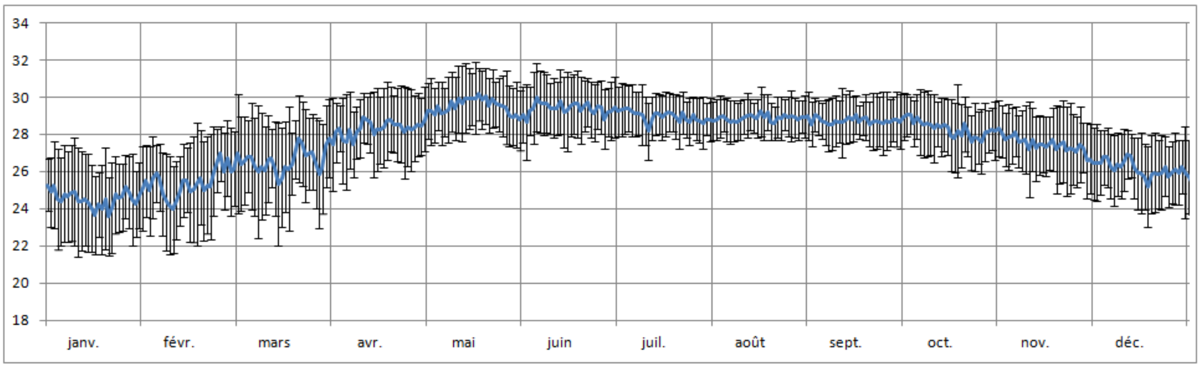

Figure II.2 Evolution de la température moyenne de l'air (°C) mesurée à la station météorologique de l'aéroport de Ciudad del Carmen (données journalières de 1990 à 2011 – moyennes et écart-types).

Les températures moyennes de l'air sont minimales en hiver entre 24 et 26 °C et maximales en été aux alentours de 30 °C (Figure II.2). L'écart interannuel de température est de 4 °C en hiver et plus réduit en été (2°C).

La lagune est à la limite de deux provinces géologiques. La Péninsule du Yucatan au Nord Est, est caractérisée par un faible taux de précipitation, un sol calcaire et aucun drainage superficiel significatif. A l’ouest et au sud la lagune est caractérisée par les plaines de Tabasco et les régions montagneuses de Chiapas et Guatemala, des zones de plus fortes précipitations et des sols fluviaux. Le système fluvial Usumacinta-Grijalva (le plus grand fleuve du Mexique et le deuxième dans le Golfe du Mexique après le Mississippi) se déverse dans le Golfe du Mexique à l’ouest de la lagune de Términos. La Palizada issue du système Grijalva-Usumacinta se jette directement dans la lagune et représente la plus importante des 3 rivières avec la Candelaria, et la Chumpan (Yáñez-Arancibia & Day 1988). Caractérisée par sa faible profondeur (entre 2 et 4 m), la lagune de Téminos a une surface approximative de 2000 km^2 et de 2500 km^2 environ si l'on inclut les marais maritimes et les systèmes fluviaux-lagunaires associés (Yáñez-Arancibia & Day, 1988) (Fig II.3).

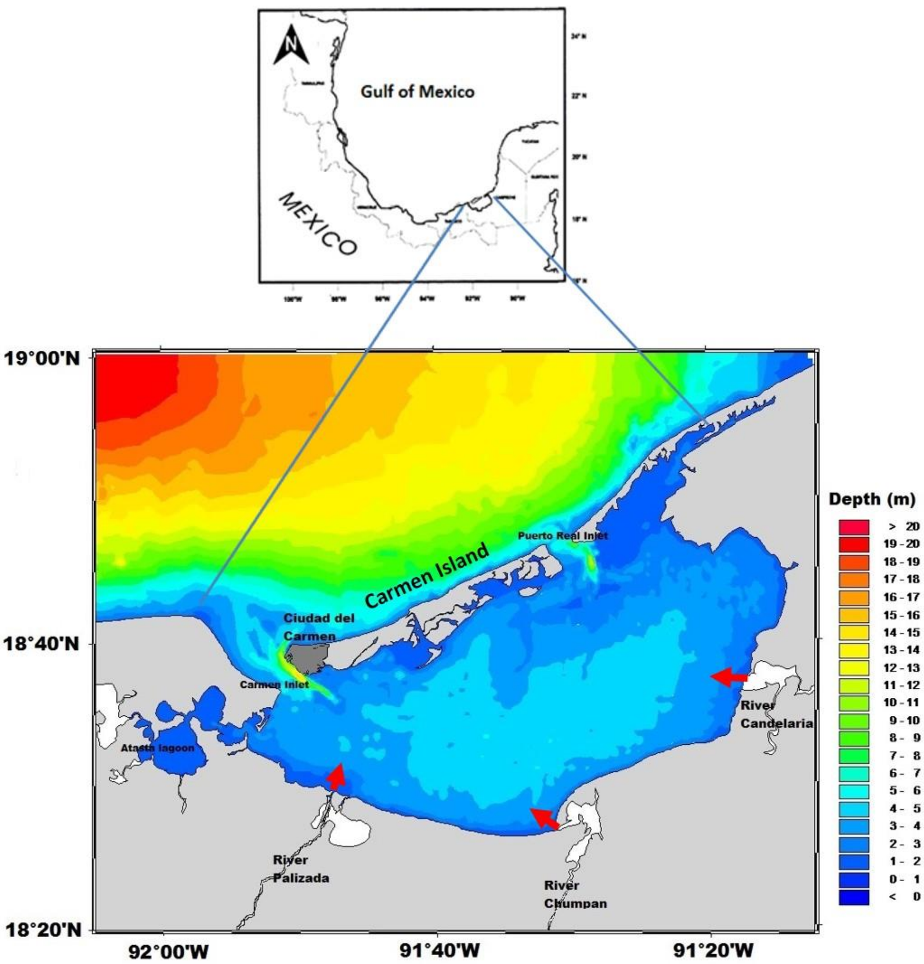

Figure II.3 Position géographique de la Lagune de Terminos et distribution des profondeurs

La lagune s'étend sur environ 80 km de long pour 25 km de large. Deux passes de part et d'autre de l'île de Carmen permettent les échanges avec les eaux du Golfe du Mexique : la passe de Puerto Real à l'Est et celle de Carmen à l'Ouest. Les passes sont caractérisées par des "canyons" de 12 m de profondeur et présentent des courants extrêmement forts largement générés par la marée. La marée est de type semi-diurne, avec un marnage moyen annuel de 0,45 m. Les courants dans les passes sont orientés dans l'axe des canyons et atteignent 2 m s^{-1}.

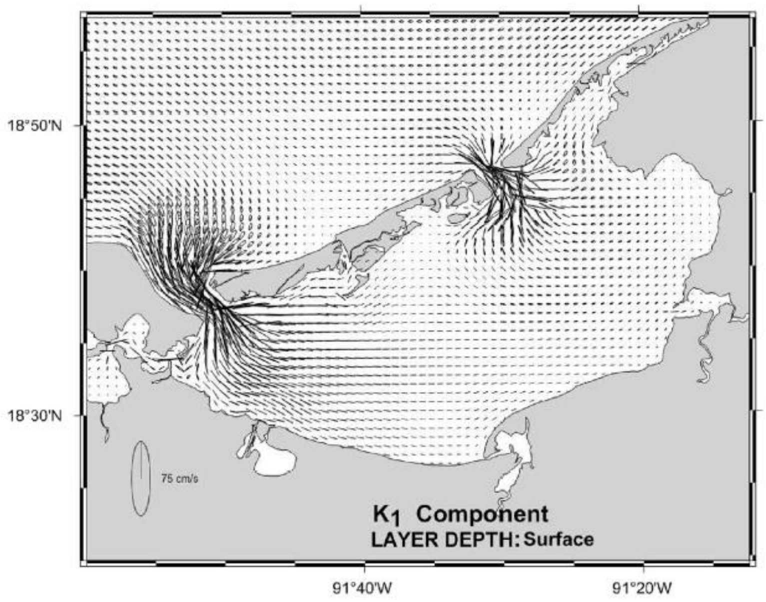

Figure II.4 Ellipses de variance des courants de surface modélisées dans la lagune de Terminos en relation avec la composante harmonique K1 (issu de Contreras et al. 2014)

Plus au centre de la lagune, les courants de marée s'estompent rapidement pour n'atteindre plus que quelques cm s^{-1}. La circulation générale montre une gyre cyclonique longeant le sud de la lagune en direction de l'Est et un retour par le Nord vers Isla del Carmen. Ces situations hydrodynamiques sont probablement différentes en cas de vent, non pris en compte dans le modèle Mars-3D utilisé par Contreras et al. (2014). En effet, plusieurs auteurs ont décrit une circulation transitoire avec entrée d'eau du large à l'Est et sortie à l'Ouest soit par des mesures soit par des modèles (Mancilla-Peraza & Vargas-Flores 1980 ; Jensen et al. 1989 ; David & Kjerfve 1998). Cette circulation semble être confirmée par la présence d'un delta de flot ou de remplissage du côté interne de la passe de Puerto Real à l'Est et d'un autre de jusant ou de vidange préférentielle à l'extérieur de la passe de Carmen à l'Ouest (Figure II.4). Concernant les temps de résidence des masses d'eau (David & Kjerfve, 1998), un temps de résidence moyen de 9 jours a été calculé (50% flushing time) en se basant sur les courants de marée mesurés dans les passes. Cette valeur est possiblement surestimée et ne prend probablement en compte que les zones proches des passes alors qu'au centre de la lagune des vitesses très faibles ont été mesurées (Figure II. 4, Contreras et al. 2014).

Le caractère semi-fermé de cette lagune soumise à des apports significatifs d'eau douce entraine des fluctuations importantes de salinité à la fois au niveau spatial et temporel. Le basculement des régimes climatiques entre une saison sèche puis une saison humide, la position des trois rivières sur le flanc Sud avec prédominance des apports de la Palizada à l'Ouest, la variabilité du niveau marin (marées astronomiques et barométriques) et l'influence des vents entrainent une structuration haline des masses d'eau particulièrement marquée avec de forts gradients (Fuentes-Yaco et al. 2001 ; Bach et al. 2005).

Un suivi spatio-temporel d'octobre 2008 à septembre 2010 sur un réseau de 34 stations dans le cadre du programme JEST (http://cbs.izt.uam.mx/hidrobiologia/jest/) a permis de déterminer une salinité moyenne à 1 m de profondeur sous la surface de 25,7 (SD = 8,1) et des minima et maxima de 3 à 37 respectivement. En fonction des précipitations et des débits des rivières associés, les plus faibles salinités sont observées pendant la saison humide et à l'inverse, les plus hautes salinités pendant la saison sèche (Figure II.5).

Les dessalures s'observent en général près de l'embouchure de la Palizada puis un peu plus au Nord-Ouest vers les lagons Atasta et Pom. Les rivières Chumpan et Candelaria plus à l'Est ne contribuent qu'à hauteur de 10 % à l'ensemble des apports d'eau douce vers la lagune. Les plus fortes salinités entre 33 et 37, proches de celles du domaine marin extérieur, se rencontrent vers la passe de Puerto Real et, en accord avec la circulation moyenne de la lagune, ces eaux marines ont tendance à se diriger vers l'Ouest en longeant Isla del Carmen.

La variabilité temporelle est largement dominée par la succession des saisons sèches et humides, une des caractéristiques du régime climatique tropical. Les gammes de température et d'irradiance sont plus réduites que dans les zones tempérées avec de faibles gradients saisonniers. En conséquence la lagune de Términos est caractérisée par des eaux "marines" (>25) pendant la saison sèche et des eaux "saumâtres" pendant la saison des pluies (< 25) en fonction des apports des rivières (Figure II.6).

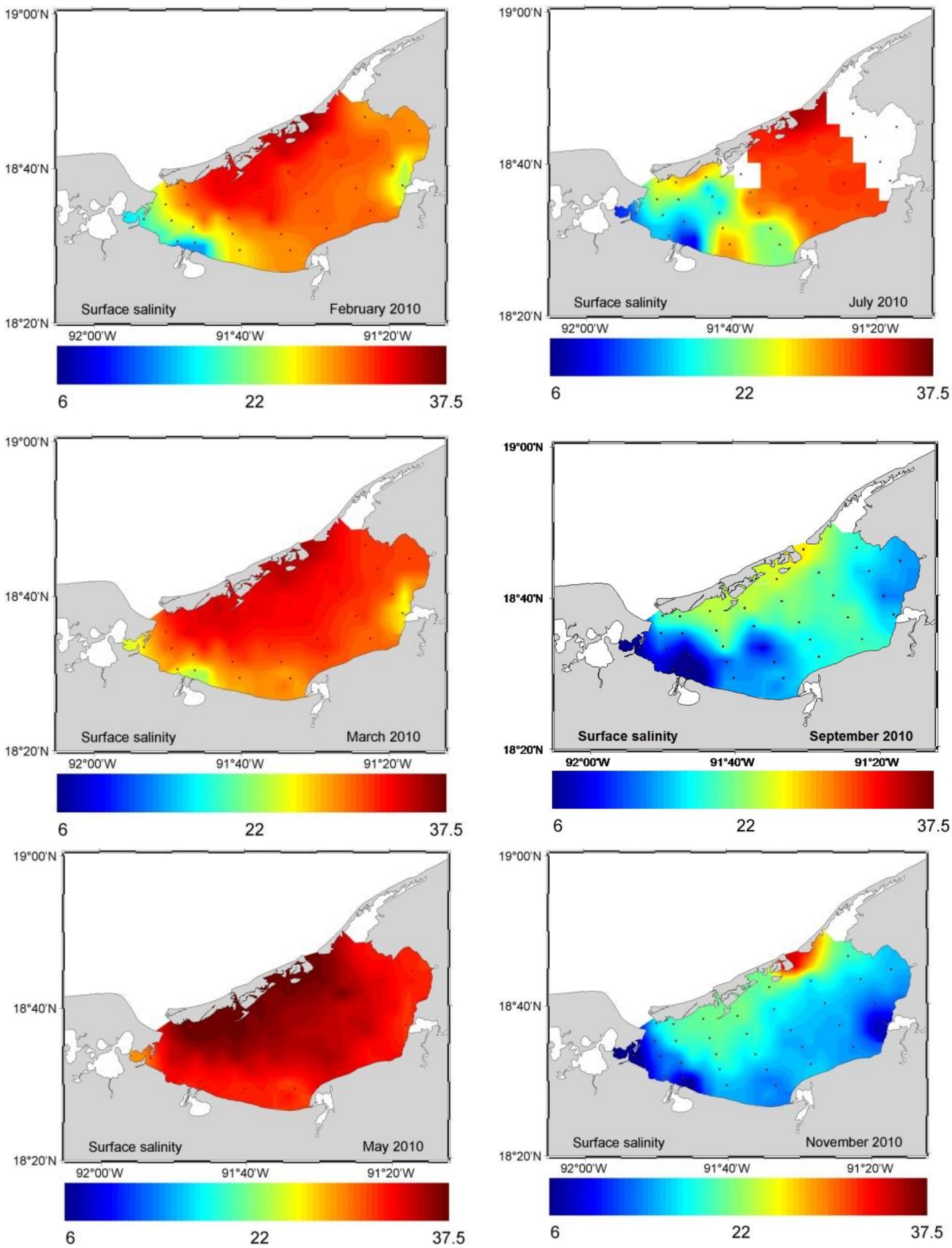

Figure II.5 Variabilité spatiale de la salinité mesurée dans la lagune de Términos sur le réseau de 34 stations (point noirs) en 2010. Saison sèche (gauche) et humide (droite) (données du programme JEST)

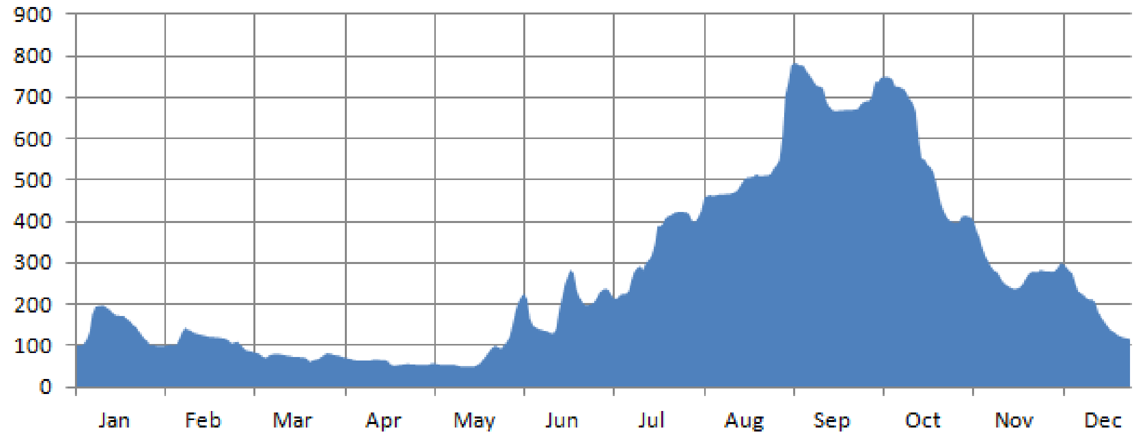

Figure II. 6 Débits journaliers de la Palizada mesurés en 2010 ($m^3 s^{-1}$, données de CONAGUA).

Cette caractéristique n'est pas d'ordre général car des régimes d'oscillations climatiques comme les phénomènes tels que El Niño peuvent impacter significativement la salinité à l'échelle de la lagune. Les mesures faites au cours du programme JEST montrent très clairement qu'en 2009, les salinités moyennes de la lagune étaient significativement plus fortes en septembre (34,4 ± 2,0) et octobre (32,6 ± 4,3) qu'en octobre 2008 (13,7 ± 5,7) ou septembre 2010 (17,0 ± 5,4), l'année 2009 étant sous l'influence d'un évènement El Niño Modoki (Fichez et al. en correction, Annexe C).

Dans ce contexte la nécessité de tenir compte des fluctuations climatiques comme El Niño dans l'exploitation des séries temporelles devient indispensable. Les changements des caractéristiques halines de la lagune sont reliés à celles du régime hydrologique avec un effet certain sur l'état trophique du milieu lagunaire dont il faut tenir compte sur le long terme. Un exemple typique correspond aux articles de Ramos-Miranda et al. (2005) et de Sosa-Lopez et al. (2007) qui ont reliés l'augmentation de salinité entre la période 1980-1981 (moyenne = 24,67; SD = 7,74) et celle de 1998-1999 (moyenne = 26,8; SD = 8,09) comme facteur explicatif d'un changement drastique des populations ichtyologiques. Compte tenu de la forte variabilité spatio-temporelle des conditions hydrologiques de la lagune de Términos, il faut être prudent quant aux conclusions issues de comparaisons de données historiques dans le contexte du changement climatique.

La lagune de Términos tout comme le plateau continental (Campeche Sound) contribue à hauteur de 34% de la pêche total du Mexique dans l'ensemble Golfe du Mexique – Caraïbes, dominée par les crevettes, mollusques, poissons demersaux et pélagiques. (CONAPESCA 2008, Grenz *et al*. en révision). De plus, l'exploitation des gisements pétrolifères dans le Golfe du Mexique au large de la lagune de Términos représente une source de revenus majeure pour le pays (32 % du budget 2013). Depuis 1938, l'entreprise nationalisé Petroleros Mexicanos ou PEMEX figure dans le top 10 des producteurs de pétrole hors OPEC avec une production d'environ 2 millions de barils par jour (Cantarell oil field). Au niveau local, cette exploitation a généré le développement exponentiel de la ville de Ciudad del Carmen, la plus grande agglomération localisée à l'Est de l'Isla del Carmen. La progression de la population urbaine est de l'ordre de 2 à 3 % par an avec un doublement du nombre d'habitants au cours des 12 dernières années (INEGI 2008).

Compte tenu des enjeux environnementaux et des conflits entre exploitation pétrolière, pêcherie et loisirs, en 1994 le gouvernement mexicain a déclaré la lagune comme zone de protection renforcée pour le faune et la flore (APFFLT). Dix ans après, la lagune a intégré la liste des sites RAMSAR et représente aujourd'hui le plus grand des sites au Mexique avec une superficie de 705 016 hectares (www.ramsar.org). Malheureusement, PEMEX, qui opère dans la zone de protection, représente un risque potentiel non négligeable de pollution chronique (fuites de pipelines) ou accidentelle (e.g. Ixtoc-1 en 1979-1980).

Les vastes étendues de zones humides localisées aux abords de la lagune de Términos représentent un site de prédilection pour la migration et le développement de nombreuses espèces telles que les perciformes, les bivalves et les crevettes, ainsi que des populations plus spécifiques de lamantins et de dauphins. Ce site représente d'ailleurs l'endroit du Golfe du Mexique où les plus fortes concentrations de dauphins peuvent être rencontrées. La zone de protection abrite la plus grande communauté d'oiseaux migrateurs en hiver et comme toutes les zones à fort gradients environnementaux, est caractérisée par un très haut niveau de biodiversité animale et végétale que ce soit dans le domaine marin ou terrestre (Yañez-Arancibia et. al. 1988). La frange côtière est colonisée par de vastes étendues de mangroves et dans la partie nord par de denses herbiers de zostères (Moore & Wetzel, 1988). Selon une analyse portant sur un inventaire des forêts dans les zones humides bordant la lagune de Términos, la déforestation au profit d'usages agricoles s'est développée à partir des années 70. Les zones humides ont perdu environ 13 000 hectares en superficie et les forêts sont passées de 1970 à 2000, respectivement de 49 à 33% de la surface étudiée (Challenger, 1998). Un rapport du SEMARNAT (2002) précise qu'entre 1976 et 2000, l'extension spatiale de la jungle est passée de 7,1 à 2,4 millions d'hectares et a occasionné des dégâts pour un tiers de la superficie (Velázquez et al., 2001) en raison notamment du développement des zones urbaines.

Les herbiers à zostères jouent un rôle écologique fondamental dans les estuaires et systèmes côtiers peu profonds comme par exemple les fonctions de :

- contributeur à la production primaire et aux cycles des nutriments,
- stabilisateur des sédiments,
- maintien de la biodiversité,
- de protection et de sources trophiques pour une large gamme d'organismes invertébrés et de poissons (Fonseca 1989, Orth et al. 2010, Unsworth & Cullen 2010, Cullen-Unsworth & Unsworth 2013).

Ces écosystèmes représentent 15 % du stockage de carbone au niveau global (Duarte et al 2010 ; Kennedy et al. 2010). Leur fort besoin en énergie lumineuse, qui se traduit par une importante productivité, entraine une sensibilité aux conditions environnementales notamment pour ce qui concerne la qualité des eaux y compris les nutriments et la turbidité (Koch 2001).

Dans la lagune de Términos, la distribution des herbiers de zostères est largement dominée par les conditions d'hydrodynamisme, de clarté de l'eau et de salinité. De ce fait les formes les plus denses de ces herbiers se trouvent localisées le long de l'Isla de Carmen et surtout autour du delta interne de la passe de Puerto Real où l'on trouve des conditions favorables de transparence et de salinité de l'eau et un fort taux de carbonates dans les sédiments (Figure II.7, Moore & Wetzel 1988 ; Cruz-Ábrego et al 1994).

Les communautés d'herbiers sont dominées par la « turtle grass » *Thalassia testudinum* et dans une moindre mesure les espèces *Halodule wrigtii* et *Syringodium filiform* (Yáñez-Arancibia & Day 1982 ; Raz-Guzmán & Barba 2000). *Halodule* est limitée aux plus faibles profondeurs alors que *Thalassia* s'étend jusqu'à des fonds de 3 m (Ortega 1995). Dans les herbiers de phanérogames et les mangroves, le benthos est dominé en abondance et en diversité spécifique par les Polychètes avec plus de 73 espèces décrites par Cruz-Ábrego et al. (1994).

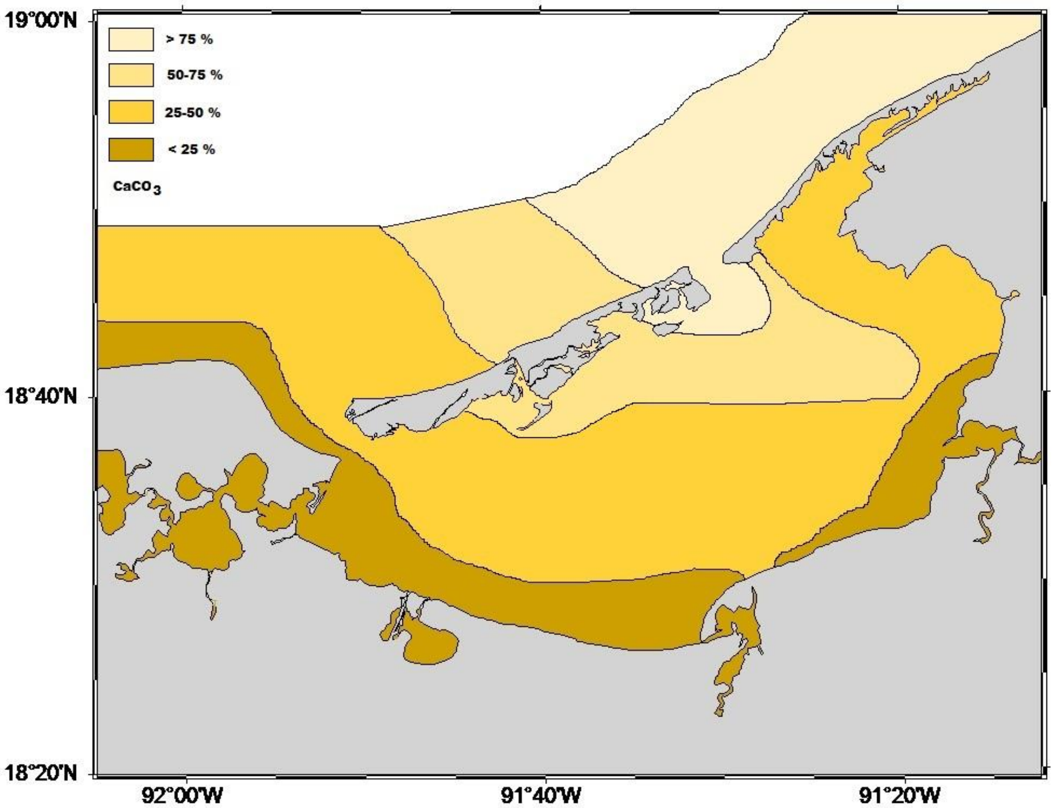

Figure II.7 Carbonate de calcium dans les sédiments en pourcentage de poids sec (redessiné à partir de Yañez-Correa 1963)

La distribution de ces espèces est le reflet des gradients de salinité, la turbidité et les caractéristiques sédimentaires. Trois assemblages majeurs se démarquent :

- dans la partie Est du lagon, une dominance des familles de Spionidés et de Cirratulidés
- dans la partie centrale et la frange Sud, une dominance des familles de Cirratulidés et de Lumbrinéreides
- dans la zone proximale de l'île de Carmen où l'on trouve les familles de Capitellidés et de Néreides (Cruz-Ábrego et al. 1994).

Selon les conclusions de Marquez-Garcia (2010) environ 30% de la lagune serait en processus de déposition sédimentaire. La formation du delta interne à Puerto Real est expliquée par la décélération des courants entrants dans la lagune par l'Est, de masse d'eau charriant de grandes quantités de sédiments issus de processus d'érosion des côtes extérieures à la lagune.

Anyone who has never made a mistake has never tried anything new

Albert Einstein

Chapitre III.

MATÉRIEL ET MÉTHODES

III MATÉRIEL ET MÉTHODES

III.1 Sélection des sites d'étude et présentation du calendrier

La UNAM dispose d'une station de recherches localisée sur l'Isla del Carmen qui permet un accès direct à la lagune par Estero Pago, sorte de bras de rivière traversant la mangrove (Figure III.1).

Figure III.1 Localisation de Base Marine de la UNAM, à l'extrémité ouest de l'Isla del Carmen, et étendu de la zone urbaine de Ciudad del Carmen de part et d'autre de l'aéroport.

Ce centre équipé de laboratoires a servi de base pour effectuer les expérimentations ex situ et le conditionnement des échantillons (prétraitements et congélations). A part pour l'oxygène et l'ammonium, l'ensemble des autres analyses ont été effectuées de retour à Mexico dans les locaux de la UAM, dans le mois suivant les campagnes (voir après).

Le choix des stations d'échantillonnage a été guidé, en premier lieu, par l'exigence d'une couverture spatiale homogène sur l'ensemble de la lagune au cours de périodes critiques qui gouvernent le régime climatique (variabilité spatio-temporelle) et en second lieu, par celle d'un suivi temporel plus resserré de 4 stations afin de quantifier les impacts majeurs liés aux activités urbaines, aux apports fluviaux et aux herbiers de zostères. La présentation des résultats se fera donc sous la forme de deux chapitres distincts (Chapitre IV Variabilité spatiale et Chapitre V Variabilité temporelle).

Sur la base du suivi JEST qui s'est effectué d'octobre 2008 à novembre 2010, un réseau de 35 stations a été visité tous les deux mois environ pour étudier la distribution des caractéristiques biogéochimiques de la colonne d'eau et des sédiments. Nous avons sélectionné au sein de ce réseau, une série de 13 stations pour les incubations de carottes sédimentaires. Ceci correspond au nombre maximal de stations pouvant être traitées compte tenu de la durée de chaque campagne (une semaine) à raison de 2 stations par jour. Les stations sont représentées dans la Figure III.2 , Tableau III.2 et la chronologie dans le Tableau III.1.

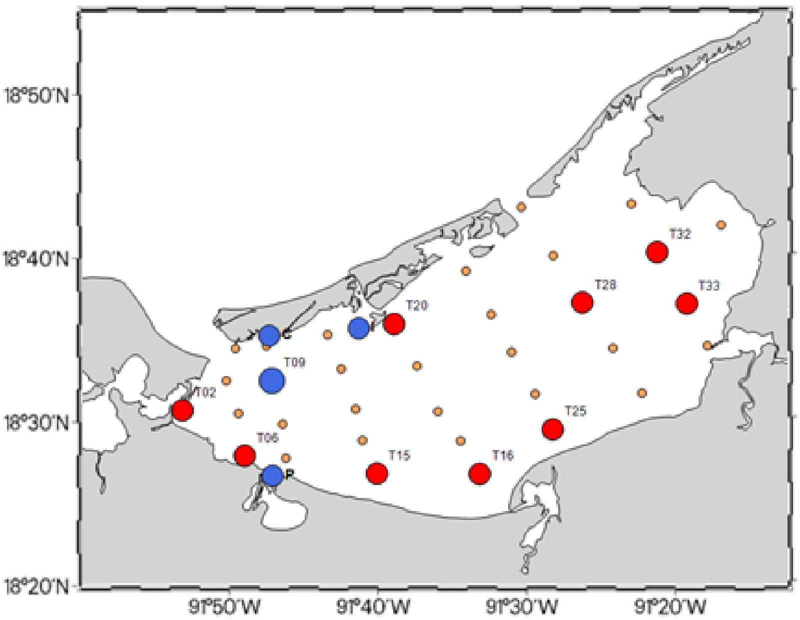

Figure III.2. Localisation des stations de prélèvement (en bleu et rouge) dans le réseau JEST (tous les points).

La localisation des stations a pris en compte les recommandations et les rapports préliminaires de Bach et al. (2005) (Figure III.3)

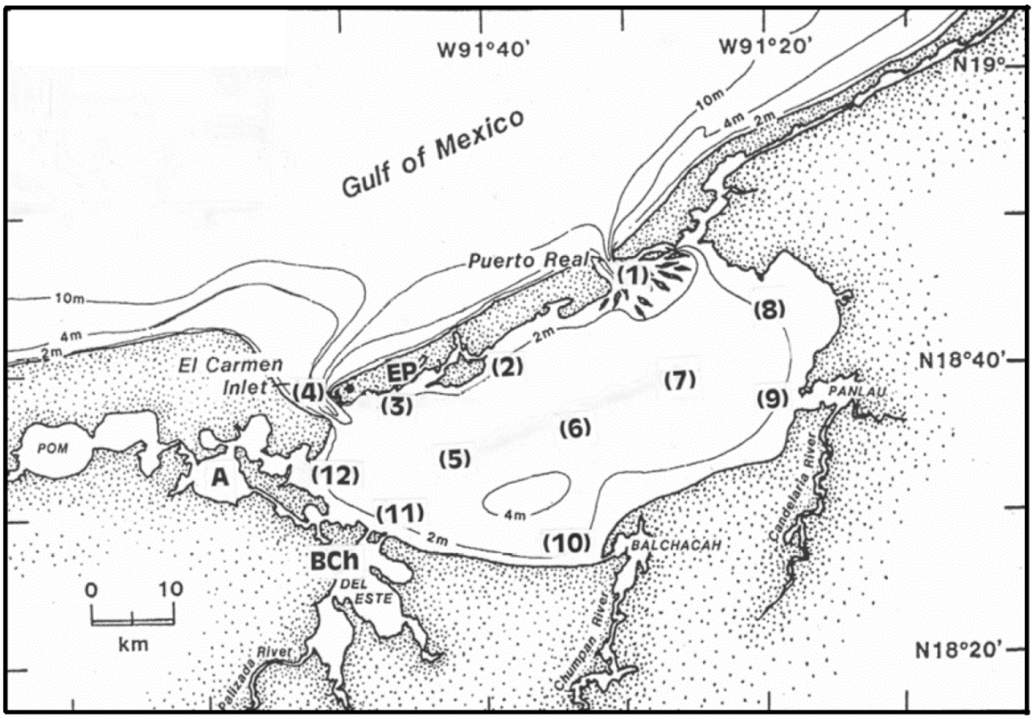

Figure III.3 Localisation des stations d'observation préconisées dans la cadre d'un plan de 'monitoring' de la lagune de Términos (Bach et al. 2005)

Tableau III.1 : Chronologie des sorties

Date	Campagne	Stations
20-21 Octobre 2008	JEST-01	C, I, P
18-19 Novembre 2008	JEST-02	C, I, P
13-21 Mars 2009	JEST-03	C, I, 9, P, 2, 6, 15, 16, 20, 25, 28, 32,33
08-09 Juin 2009	JEST-04	C, I, 9, P
08-09 Septembre 2009	JEST-05	C, I, 9, P
21-27 Octobre 2009	JEST-06	C, I, 9, P, 2, 6, 15, 16, 20, 25, 28, 32,33
30-01 Decembre 2009	JEST-07	C, I, 9, P
09-10 Fevrier 2010	JEST-09	C, I, 9, P
13-20 Mars 2010	JEST-10	C, I, P, 2, 6, 15, 16, 20, 25, 28, 32,33
04-06 Juillet 2010	JEST-13	C, I, 9, P
23-28 Novembre 2010	JEST-14	C, I, P, 2, 6, 15, 16, 25, 28, 32,33

Tableau III.2 : Coordonnées géographiques des stations étudiées dans la Lagune de Terminos

Station	N GWS84	W	Campagne
T02	18°33'42.00	91°53'15.00	Spatiale
T06	18°33'20.00	91°49'40.00	Spatiale
T09	18°35'28.00	91°47'15.00	Spatiale et Temporelle
T15	18°29'30.00	91°40'17.00	Spatiale
T16	18°29'23.00	91°33'30.00	Spatiale
T20	18°38'52.00	91°38'56.00	Spatiale
T25	18°32'03.00	91°28'39.00	Spatiale
T28	18°40'13.00	91°26'34.00	Spatiale
T32	18°43'30.00	91°21'30.00	Spatiale
T33	18°40'00.00	91°19'34.00	Spatiale
C	18°38'26.90	91°47'51.76	Spatiale et Temporelle
P	18°29'34.99	91°47'24.37	Spatiale et Temporelle
I	18°38'09.88	91°41'52.03	Spatiale et Temporelle

En parallèle du suivi spatial et pour évaluer la variabilité temporelle, trois stations ont été sélectionnées afin de cibler les impacts des apports terrigènes (P), l'influence de la zone urbaine (C) et celle des herbiers (I) et une 4ème de référence (station T09). Ces stations ont été suivies tous les deux mois environ sur la même période d'octobre 2008 à novembre 2010.

- La station P, au Sud-Ouest de la lagune, sous influence des apports du bassin versant, localisée au débouché de la rivière Palizada,

- La station C, à l'Ouest, proche de la ville de Carmen, la station la plus impactée a priori par les activités anthropiques,

- La station I, sur le flanc Sud de l'Isla del Carmen, caractérisée par la présence des zostères marines (*Thalassia testudinum)*

- La station 09, station de référence au milieu du triangle formé par les 3 stations P, C, et I et éloignée des influences précédentes.

III.2 Prélèvement de sédiment

En raison de la profondeur moyenne relativement faible de l'ensemble de la lagune (< 4m), l'utilisation d'embarcations lourdes telles que les navires océanographiques devenait impossible. Nous avons donc privilégié des embarcations plus légères de type « lanchas », sorte de bateau à fond plat utilisé par les pêcheurs locaux pour toutes les profondeurs de la lagune y compris à l'extérieur. De ce fait le carottier multitube devenait inopérant en raison de son poids. Nous avons donc développé un carottier monotube à usage manuel pour des profondeurs allant jusqu'à 5 m. La tête du carottier est gréée d'un tube de 15 cm de diamètre et de 50 cm de long. L'enfoncement du tube à partir de la lanchas est assuré par une barre métallique de 4 m de haut fixée en haut de la tête du carottier. Le sédiment est prélevé par succion grâce à une valve anti-retour logée également dans la tête du carottier. (Figure III.4, III.5 et III.6)

Figure III.4 Echantillonnage de sédiment avec le carottier monotube

Figure III.5 Carotte avec le sédiment après fermeture de l'extrémité inférieure

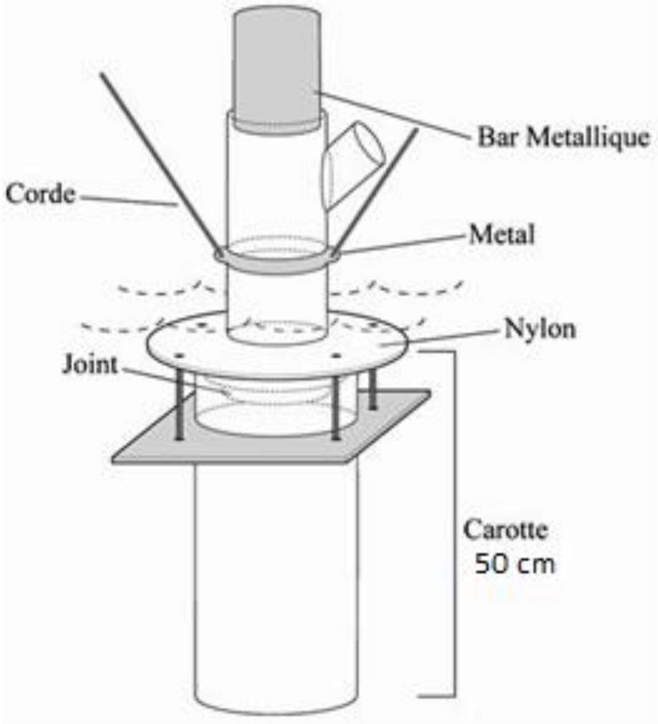

Figure III.6 Dispositif de prélèvement incluant une valve anti-retour pour assurer la succion.

Ce dispositif permet de prélever des carottes de sédiments avec une eau surnageante limpide. Des prélèvements d'eau de fond sont effectués à l'aide d'une bouteille Niskin. Cette eau est transférée dans un cubitainer placé au noir dans une glacière. Après prélèvement, les carottes de sédiment sont transportées au laboratoire et mise en incubation au noir à la température du milieu dans un délai de 2 à 4 h selon la distance entre les stations et le laboratoire de terrain.

Au laboratoire, la hauteur de l'eau surnageante dans les carottes est mesurée. Généralement cette hauteur est comprise entre 15 et 25 cm correspondant à un volume d'eau surnageante de 2.5 à 4.5 l. Considérant une surface plane, la surface de contact entre l'eau surnageante et le sédiment est de 176,7 cm^2.

III-3 Dispositif d'incubation

Les tubes carottiers sont en polypropylène et possèdent chacun un chapeau adapté à son diamètre. Dans la partie supérieure il y a deux orifices dont l'un sert à insérer une mini-sonde d'oxygène (UNISENSE) et l'autre est utilisé pour le prélèvement des échantillons par un système de tuyauterie entrée - sortie avec embouts LUER-Lock. Un agitateur magnétique fixé au centre du chapeau coté intérieur de la carotte et entrainé par un aimant U en rotation à l'extérieur assure l'homogénéisation de l'eau surnageante pendant l'incubation (Figure III.7). La vitesse de rotation est réglée de manière à brasser l'eau surnageante délicatement par une agitation n'entrainant pas de processus de remise en suspension (Viollier et al. 2003).

Le logiciel *Sensor Trace Basic* pilote les mini-sondes UNISENSE et les prélèvements sont effectués environ toutes les 2 heures pendant un cycle de 12 à 18 heures (Denis et Grenz, 2003). La durée d'incubation varie en fonction de l'intensité des échanges à l'interface eau-sédiment, ainsi qu'en fonction du volume d'eau dans la carotte. Les calculs des flux sont basés sur l'augmentation ou la diminution en fonction du temps des solutés dans l'eau surnageante.

Figure III. 7 Dispositif d'incubation comprenant un moteur Lab-Egg 8W (0-2000 tour/min, en bleu), un aimant U (en rouge), les mini-sondes UNISENSE et un système de prélèvement (entrée – sortie) connecté à la nourrice). On distingue le barreau aimanté blanc sous le chapeau du haut.

Lors de l'incubation, des prélèvements d'eau surnageante sont effectués à raison de 120 ml par prélèvement qui sont automatiquement remplacés par la même quantité d'eau de fond provenant de la nourrice. Cet apport provoque une dilution (si la concentration [C]nourrice<[C]carotte) ou une augmentation de la concentration dans l'eau surnageante (si [C]nourrice>[C]carotte). Une correction est intégrée dans le calcul du flux.

Lorsqu'aucune variation significative de la concentration n'est mise en évidence dans l'eau de fond lors de la période d'incubation, la valeur moyenne est utilisée pour la correction décrite précédemment. Par contre, lorsqu'une évolution significative de l'eau de fond est mise en évidence dans la nourrice, la correction est effectuée pour chaque échantillonnage à partir de la concentration dans l'eau de fond mesurée au temps du prélèvement (Denis et Grenz, 2003)

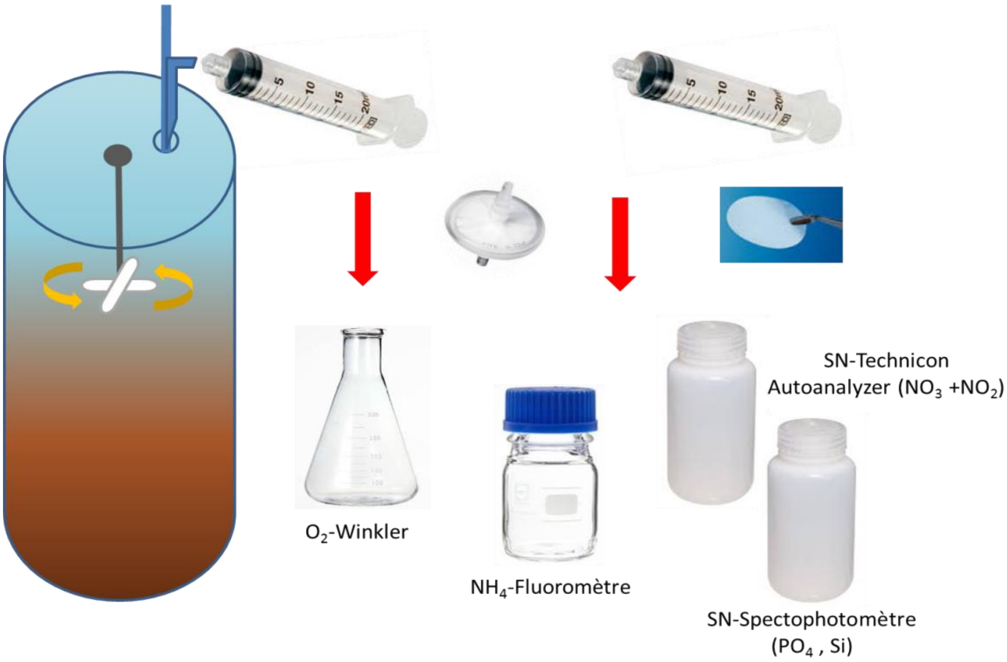

Figure III.8 Prélèvements à la seringue des échantillons pendant une incubation et pré-traitement pour les analyses chimiques.

Tel que présenté dans le schéma de la figure III.8, les échantillons pour les analyses des sels nutritifs sont prélevés par deux seringues de 60 ml chacune. Le premier tiers de la première seringue est utilisé pour l'oxygène (contenance 16 ml rempli jusqu'à débordement), les deux seconds tiers pour le rinçage et le prélèvement pour l'ammonium (contenance flacons Schott en pyrex de 50 ml). La seconde seringue est filtrée sur membranes GFF et répartie en deux flacons à scintillation de 20 ml chacun (polyéthylène) préalablement rincés à l'acide chlorhydrique 10% puis avec le surplus d'eau, pour les analyses de sels nutritifs (DIN, PO_4 et Si).

Les réactifs (Winkler et NH_4) sont ajoutés juste avant la fermeture des flacons. Le dosage de l'oxygène effectué entre deux temps de prélèvements pendant l'incubation et celui de l'ammonium après un temps de réaction préconisé pour les réactifs (entre 9 et 24 h). Les échantillons de sels nutritifs sont congelés pour analyse ultérieure de retour au laboratoire à Mexico.

III-4 Dosage de l'Oxygène dissous

III-4.1 Méthode mini-sondes

Les sondes polarographiques de Clark fonctionnent avec deux électrodes, une anode en argent et une cathode en platine immergées dans un électrolyte de KCl mi-saturé. La chambre de l'électrolyte est séparée de la solution échantillonnée par une membrane de Téflon (hydrophobe) qui est tenue par un anneau plastique. Les molécules d'oxygène de la solution échantillonnée diffusent à travers cette membrane. On impose entre les deux électrodes une différence de potentiel de l'ordre de -600 à -800 mV. L'oxygène diffusant à travers la membrane est réduit en eau par les électrons libérés à la cathode et le courant qui s'établit entre les deux électrodes est proportionnel à la concentration en oxygène dans l'électrolyte et donc dans le milieu. Le très faible courant produit est amplifié et converti en une tension proportionnelle à la concentration en oxygène dans le milieu moyennant une calibration.

Les mini-sondes d'oxygène UNISENSE (Figure III.9) sont des capteurs de type Clark avec une cathode de garde en or. A l'extrémité de mesure, la taille en pointe de très petite dimension entraine un temps de réponse minimal et une sensibilité insignifiante aux mouvements. Elles permettent de faire des mesures fiables et rapides avec une haute résolution spatiale. Le capteur doit être connecté à un pico-ampèremètre hautement sensible (Unisense Manual, 2007).

Figure III.9 Mini-sondes avec son boitier Unisense

Les capteurs d'oxygène sont sensibles à la température, à la salinité et à la solubilité de l'oxygène. Il est nécessaire d'exécuter le calibrage et les mesures dans des solutions ayant des températures et salinités identiques (Unisense Manual, 2007). Les mini-sondes ne consomment pas ou peu d'oxygène pendant la mesure (Briand et al. 2004).

Nous avons utilisé les deux procédures suivantes pour une calibration à 2 points des sondes. On place la pointe du capteur dans une solution de calibration (« eau extérieure ») maintenue à 100 % de saturation par bullage. Pour la valeur à zéro, on utilise du sédiment anoxique correspondant à un échantillon de carotte sédimentaire stocké au noir dans un flacon scellé. Les capteurs d'oxygène répondent de manière linéaire dans la gamme de 0 à 100% d'oxygène, un calibrage à deux points étant suffisant pour faire la courbe de calibration (Unisense Manual, 2007). La perméabilité des membranes des mini-sondes change avec le temps, une calibration est donc nécessaires avant chaque expérience d'incubation.

L'utilisation de mini-sondes pour l'oxygène permet de suivre la concentration d'oxygène en continu dans l'eau surnageante des carottes en fonction du temps. L'avantage de visionner les concentrations en temps réel étant de pouvoir fixer la fin d'une incubation avant l'anoxie (Figure III.10).

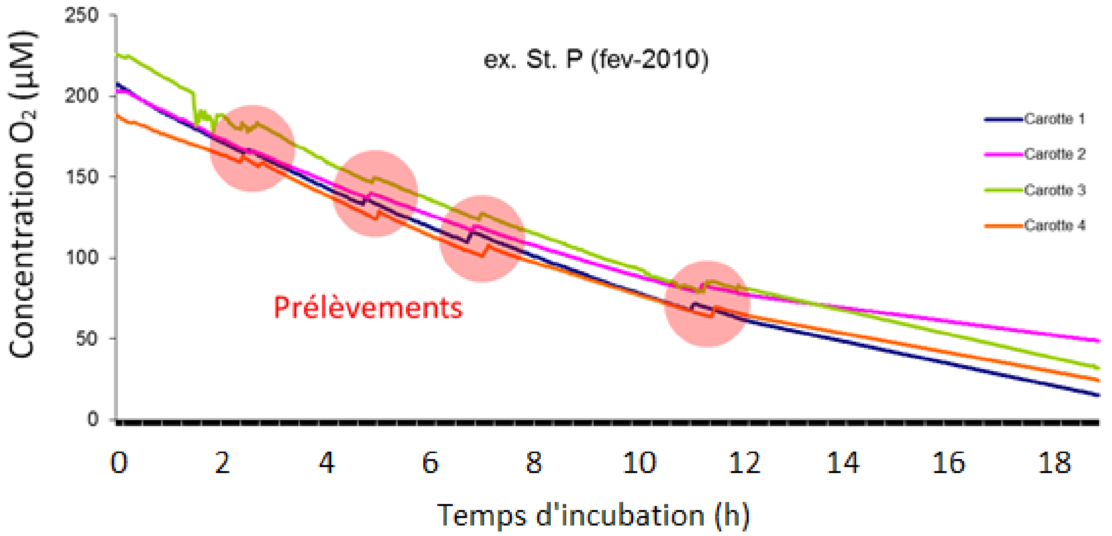

Figure III.10 Exemple de cinétique d'incubation pour 4 carottes d'une même station. Les points rouges correspondent aux prélèvements successifs à la seringue avec une ré-oxygénation d'environ 10 µM dans chaque carotte.

III-4-2 Méthode Winkler

L'oxygène dissous est, après la température et la salinité, le paramètre océanographique le mieux documenté et fait encore appel à la méthode chimique classique proposée en 1888 par Lajos Winkler et modifie par Strickland & Parsons (1972).

La base de la méthodologie est la fixation de l'oxygène par le sulfate de manganèse sous forme de $Mn(OH)_3$ et libération, par le réactif de Winkler (KI+KOH), d'iode en quantité proportionnelle à celle d'O_2 dissous. L'iode libéré est dosé par le thiosulfate de sodium grâce à un titrateur par point d'équivalence.

Afin d'utiliser un volume restreint de prélèvement lors de l'incubation nous avons utilisé des flacons de 16 ml environ au lieu des volumes recommandés de 100 à 150 ml par Aminot et Chaussepied (1983). Le volume de chaque flacon, c'est à dire le volume analysé, doit être connu avec précision. L'entretien des flacons et bouchons consiste en un lavage correct à l'eau du robinet, puis à l'eau distillée. La perte d'un éclat de verre de bouchons peut modifier sensiblement le volume du flacon : ce dernier sera donc à nouveau déterminé. Les volumes de flacon sont obtenus par différence des pesées des flacons remplis et vide. L'analyse de l'oxygène doit être faite dans un délai aussi réduit que possible après échantillonnage en évitant tout contact avec l'air. Compte tenu de la réduction du volume du flacon, les volumes de réactif ont été adapté soit 200 µl de réactif 1 (solution de MnII 3 $mol.l^{-1}$) et 2 (solution basique d'iodure OH^- : 8 $mol.l^{-1}$; I : 4 $mol.l^{-1}$).

Une fois le précipité rassemblé dans la moitié inférieure du flacon, les échantillons sont analysés après ajout de 300 µl de réactif 3 (acide sulfurique ; H^+ : 10 $mol.l^{-1}$). La titration se fait sur un titrateur Metrohm Titrino muni d'un agitateur magnétique.

La précision de la méthode Winkler est de 0.1 µM, très grande en comparaison d'autres techniques qui sont aux environs de 5 % (Briand et al. 2004) (Figure III.11)

Figure III.11 Dosage du l'Iode par le thiosulfate sur tritrateur Metrohm

III-5 Analyse des sels nutritifs

Les sels nutritifs azotés sont dosés selon la méthode colorimétrique automatique décrite par Tréguer et Le Corre (1975) repris dans Aminot et Kérouel (2004) à l'aide d'une chaine d'Auto-Analyseur Technicon.

Le principe du dosage correspond en une réduction des nitrates en nitrites par passage sur une colonne Cd-Cu. Les ions nitrites ainsi formés ainsi que ceux contenus initialement dans l'échantillon sont ensuite déterminés par dosage spectrophotométrique après la formation d'un diazoïque avec la sulfanilamide qui sera couplé avec le chlorhydrate de N-naphtyl-éthylènediamine. Parallèlement, les nitrites seront déterminés de façon identique sans l'utilisation de la colonne de réduction. La différence entre des deux analyses sur un même échantillon permet de déduire la concentration en nitrates. La ligne de base est réglée en analysant de l'eau déionisée MilliQ-plus. Une correction de l'effet de turbidité dû à la teneur en sel de l'eau de mer est appliquée aux hauteurs de pic pour le calcul des concentrations. La calibration de chaque voie d'analyse est réalisée à chaque séquence de dosage à l'aide de solutions standard couvrant la gamme des concentrations rencontrées pour chaque élément. Ces solutions sont préparées à partir de produits ultra-purs (Merck).

Le dosage des phosphates est réalisé selon la méthode de Murphy et Riley (1962). Les ions phosphate forment en milieu acide ($pH<1$), avec les ions molybdate, un complexe phosphomolybdique de coloration jaune qui est réduit en présence d'acide ascorbique (vitamine C) pour former un complexe de couleur bleue (Absorbance à 800 nm).

Le dosage des silicates est effectué selon la méthode de Mullin et Riley (1955) adaptée par Strickland et Parsons (1972). Le silicium dissous forme avec le molybdate d'ammonium, un complexe silicomolybdique qui prend une fois réduit une coloration bleue (Absorbance à 810 nm).

Le dosage des phosphates et silicates se font par lecture au spectrophotomètre aux absorbances respectives et moyennant des courbes de calibrations réalisés pour chaque campagne.

Le dosage de l'ammonium est réalisé par une méthode fluorométrique à l'ortho-phtaldialdéhyde (OPA) de sulfide de sodium et de borate de sodium (Holmes et al. 1999, adaptée par Chifflet et al. 2003). Cette technique est plus sensible que la méthode au bleu d'indophénol classiquement utilisée.

Les précisions analytiques (écart-type entre réplicats) sont les suivantes:

Nitrate : ± 0.040 $\mu mol.l^{-1}$ limite de détection 0.050 $\mu mol.l^{-1}$,

Nitrite : ± 0.025 $\mu mol.l^{-1}$ limite de détection 0.010 $\mu mol.l^{-1}$.

Silicates : ± 0.01 $\mu mol.l^{-1}$ limite de détection 0.03 $\mu mol.l^{-1}$.

Phosphates : ± 0.01 $\mu mol.l^{-1}$ limite de détection 0.01 $\mu mol.l^{-1}$.

Ammonium : ± 1 $nmol.l^{-1}$ limite de détection 1.5 $nmol.l^{-1}$.

Pour plus de commodité et compte tenu des faibles concentrations en nitrites, nous avons combiné les données de Nitrates + Nitrites. En conséquence les données de NO_3 présentées dans l'ensemble du manuscrit correspondent en fait à NO_{2+3}.

III-6 Caractérisation des sédiments

III-6-1 Sous-échantillonnage

Les sédiments ont été sous-échantillonnés en 6 carottes de diamètre interne de 2,6 cm, chacune étant sectionnée en 10 niveaux de 4 mm de hauteur (Figure III.12).

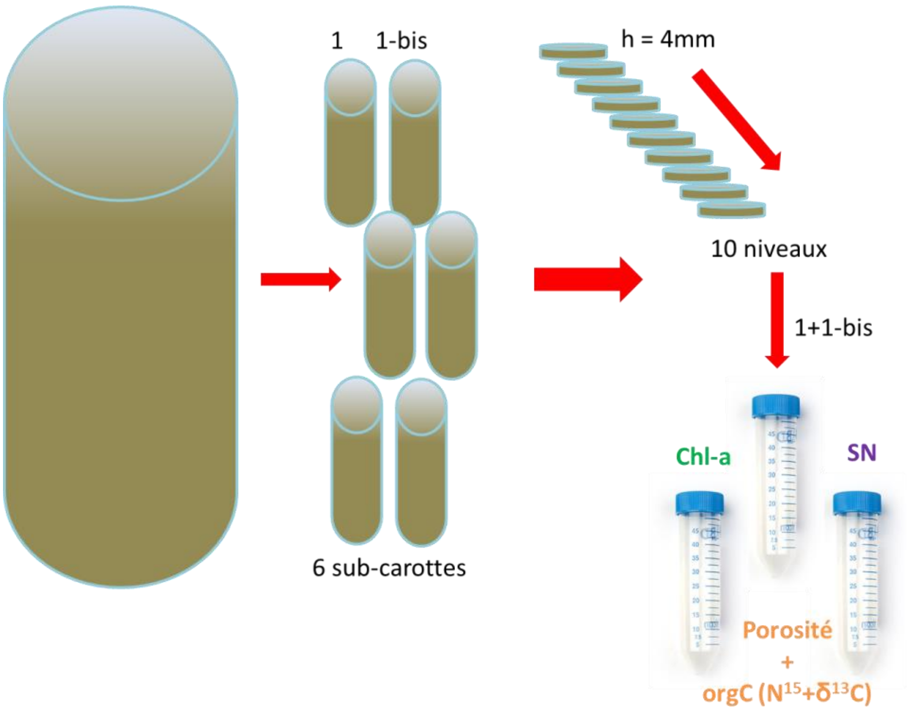

Figure III.12 Schéma de découpe des carottes de sédiment ayant servi pour l'incubation

Deux échantillons de 2 sous-carottes distinctes sont regroupés puis placés dans un flacon en polycarbonate conique préalablement étiqueté.

III-6-2 Analyses

La teneur en eau correspond au rapport de la masse d'eau sur la masse du sédiment humide exprimée sous forme d'un pourcentage. L'échantillon de sédiment humide est séché à l'étuve à 60 °C jusqu'à obtention d'un poids constant. La teneur en eau est calculée par différence entre les poids vide, humide puis sec selon la formulation suivante (Denis et Grenz, 2003) :

$$\text{Teneur d'eau} = \left(\frac{\text{Pds humide} - \text{Pds sec}}{\text{Pds humide} - \text{Pds vide}}\right) \times 100$$

La porosité est un rapport de volumes et ne possède donc pas d'unité. Elle varie entre 0 et 1. Globalement, des sédiments de type sableux seront caractérisés par de faibles porosités, allant de 0,3 à 0,5, alors que des sédiments de type vaseux peuvent avoir des porosités supérieures à 0,95 dans les centimètres superficiels du sédiment. En profondeur dans le sédiment, la compaction conduit à une diminution générale de la porosité qui dépend ainsi du taux de sédimentation (Denis et Grenz, 2003)

La formule de calcul de la porosité est :

$$\text{Porosité} = \frac{\frac{\text{Pds humide} - \text{Pds sec}}{1.035}}{\left(\frac{\text{Pds humide} - \text{Pds sec}}{1.035}\right) + \left(\frac{\text{Pds sec} - \text{Pds vide}}{2.56}\right)}$$

pour une densité d'eau de 1,035 (salinité de 35) et une masse volumique de 2560 kg m^{-3}.

Les pigments sédimentaires sont composés de chlorophylle a et de produits de dégradation ou pheopigments (chlorophyllides, pheophorbides et pheophytins) (Tietjen, 1968). Ces pigments proviennent soit des communautés du phytobenthos en place, de détritus locaux ou de matériel sédimenté produits dans la colonne d'eau. L'extraction des pigments s'opère sur des échantillons broyés dans un mortier dont environ 1 g de matériel humide est placé dans 13 ml d'acétone à 90 %. Après centrifugation à 2500 tours min^{-1} pendant 30 min, le surnageant est récupéré et une première lecture au spectrophotomètre à 750 nm et 665 nm est effectuée. Une seconde lecture après ajout de 0,2 ml d'acide chlorhydrique au 33 % est effectuée à 750 nm et 665 nm. (Strickland & Parsons, 1972). L'équation pour le calcul est donnée par l'équation suivante (unité en µg g^{-1}) :

$$Chlorophylle\ a = \frac{\left(26{,}7\ \times (665nm - 750nm) - (665ac. - 750ac.)\right) \times 10)}{(poids\ \text{sec}\ du\ sédiment)}$$

$$Pheopigments = \frac{\left(26{,}7\ (1{,}7\ \times (665nm - 750nm)) - (665ac. - 750ac.)\right) \times 10)}{(poids\ \text{sec}\ du\ sédiment)}$$

L'extraction des eaux interstitielles pour l'analyse des sels nutritifs s'effectue directement par centrifugation des tubes coniques contenant les échantillons de sédiment (SN figure 26). Après une centrifugation à 4500 tours min^{-1} pendant 20 minutes, l'eau surnageante est récupérée puis analysée moyennant une dilution selon la salinité et la profondeur considérées. Les méthodes de dosages sont identiques à celles décrites dans le chapitre III-5.

Les échantillons pour les analyses élémentaires du carbone et de l'azote des sédiments et leurs isotopes sont issus des flacons pour la porosité. Une décarbonatation est effectuée par ajout de 50 µl d'HCL 0.1 N dans 10 mg de sédiment, renouvelé deux à trois fois jusqu'à disparition des bulles (Harris et al, 2001). Après un séchage de 2 h à 60 °C, l'échantillon est analysé par la méthode à haute combustion de Dumas, sur la ligne CHN d'un spectromètre de masse

INTEGRA CN de SERCON qui fournit en parallèle la valeur de l'abondance naturelle $\delta^{15}N$ (Raimbault et al. 2008). Plusieurs tests ont permis d'affiner le protocole, notamment pour l'azote, dosage pour lequel un second échantillon non-acidifié de 50 mg est utilisé (Hedges and Stern, 1984).

III-7 Calcul des flux totaux

Le calcul des flux à l'interface eau-sédiment est effectué par ajustement d'une droite de régression sur les concentrations en fonction du temps. Si la régression est significative, alors le flux peut être calculé, sinon il est estimé nul. Un flux d'oxygène est calculé pour chaque carotte placée en incubation. (Denis et Grenz, 2003)

Les pentes des droites de régressions étant calculées sur des concentrations en µM, soit µmol dm^{-3}, on doit multiplier le résultat obtenu par un facteur 1000 pour obtenir les flux en µmol m^{2} h^{-1}. Ainsi le flux peut être estimé à partir de la formule

$$\text{Flux} = \frac{\left(\left(\frac{\Delta C}{\Delta t}\right)_{\text{Carotte}} - \left(\frac{\Delta C}{\Delta t}\right)_{\text{Nourrice}}\right) x \left((\text{Hauteur d'eau})(\pi)(\text{Rayon}^2)\right) x\ 1000}{(\pi)(\text{Rayon}^2)}$$

Soit en simplifiant :

$$\text{Flux} = \left(\left(\frac{\Delta C}{\Delta t}\right)_{\text{Carotte}} - \left(\frac{\Delta C}{\Delta t}\right)_{\text{Nourrice}}\right)(\text{Hauteur d'eau})(1000)$$

avec

Flux : µmol m^{-2} h^{-1}
C : Concentration : µM
t : temps : h
H : Hauteur d'eau surnageant : m
R : Rayon interne du tube de prélèvement : m

L'évolution de la concentration dans l'eau de fond est généralement faible au cours de l'incubation et n'intervient que très peu sur les flux calculés (Denis et Grenz, 2003).

Malgré le faible volume échantillonné la correction associée au remplacement d'eau (avec l'eau de fond de la nourrice) est appliquée de manière systématique. Tous les tests statistiques ont été réalisés avec Statistica. En cas d'échec du test de normalité ou d'équivalence des variances des distributions, des tests non paramétriques ont été effectués. Les autres traitements statistiques sont explicités dans les parties Matériel et Méthodes des articles.

Because there’s nothing more beautiful than the way the ocean refuses to stop kissing the shoreline, no matter how many times it’s sent away.

Sarah Kay

Chapitre IV.

Spatio-temporal variability in benthic exchanges at the sediment water interface of a shallow tropical coastal lagoon (south coast of Gulf of Mexico)

Montserrat Origel Moreno [1], Christian Grenz [1], Karline Soetaert[2], Lionel Denis[3], Pascal Douillet[1], Renaud Fichez[1].

Spatio-temporal variability in benthic exchanges at the sediment water interface of a shallow tropical coastal lagoon (south coast of Gulf of Mexico)

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Abstract

The sediment in Laguna de Términos, the largest and shallowest system in the Southwest portion of the Gulf of Mexico was intensively studied between 2009 and 2010. This system features a broad range of ecological and hydrobiological characteristics driven by annual weather cycles (dry and wet seasons). Due to large river discharges during the wet season, the salinity gradients ranged from 3 to 36 throughout the lagoon and different pelagic processes were inferred as consequence. A selection of 13 stations was investigated for oxygen and nutrient fluxes at the sediment-water interface, using a lab incubation technique with 15 cm diameter sediment cores. Sediment Oxygen Demand (SOD) fluctuated between 1327 ± 161 and 2248 ± 359 µmol m^{-2} h^{-1} for dry and wet seasons respectively. Silicate fluxes were also significantly higher during the wet seasons (89.4 ± 15.9 µmol m^{-2} h^{-1}) than during the dry season (46.5 ± 11.4 µmol m^{-2} h^{-1}). PO_4 fluxes were low all over the study period without seasonal trend. No significant difference was measured for DIN fluxes but we highlighted a tendency to reversed directions which showed a DIN uptake during the wet season (2.9 ± 18.8 µmol m^{-2} h^{-1}) and conversely an efflux during the dry season (24.3 ± 7.3 µmol m^{-2} h^{-1}). SOD correlated to organic matter and chloropigment content of the sediments probably as a result of increased

organic matter sedimentation. Silicate fluxes responded to enhanced chloropigments in the sediments. Stations located in the northern portion of the lagoon are characterized by dense sea grass beds and microbenthic algae which potentially intercept nutrients regenerated at the sediment-water interface through benthic primary production. During both seasons, benthic nutrient fluxes overwhelmed largely riverine inputs and benthic carbon mineralization rates approximated a significant proportion of the pelagic carbon production. The results indicate that benthic processes as in Laguna de Términos are largely driven by weather variability and that they contribute substantially to carbon and nutrient budgets in shallow sub-tropical systems.

1. Introduction

Due to human activities, large concentrations of contaminants and nutrients have accumulated in sediments of natural water bodies, changing the environmental conditions. The processes that govern the fate of these substances in the sediment result from, the complex interactions with the biogeochemical cycles of major redox and biogenic elements as C, N, O, P and Si (Middelburg & Soetaert 2004). In shallow systems the pelagic biogeochemical cycles are strongly linked to the sediment compartments where organic matter mineralization preferentially occurs, resulting in enhanced nutrient fluxes and oxygen uptake rates at the water-sediment interface (Archer and Devol 1992, Cowan & Boynton 1994, Grenz et al. 2003). Denitrification, the dissimilatory reduction of NO_3^- to produce N_2O, depends on anoxic conditions (Rivera-Monroy et al. 1995) and occurs nearly exclusively in sediments. Therefore, together with different external sources such as river inputs, surface runoff, atmospheric precipitation, the biogeochemical dynamics in the sediment ultimately controls the variation of pelagic nutrient concentrations over inter-annual time scales (Soetaert & Middelburg 2009). On shorter time scales, the soluble nitrogenous compounds released from the sediments during the decomposition of organic matter can supply 30-100% of dissolved N utilized by phytoplankton in overlying water (Lerat et al. 1990, Grenz et al. 2010).

The sediment oxygen demand (SOD) is a component of the dissolved oxygen balance of natural water bodies such as rivers, lakes or coastal zones. SOD is the oxygen transfer from the water column into the sediment and results from microbial and chemical consumption inside the sediment, including oxidation of organic matter and of inorganic and metal species produced via suboxic and anoxic organic carbon degradation (Rasmussen & Jorgensen 1992, Cai and

Sayles, 1996, Bolałek & Graca 1996). As oxygen in sediments is utilised both directly for organic matter respiration (aerobic mineralisation) and for reoxidation of reduced substances formed by anoxic mineralisation, SOD is a good measure for total system mineralisation.

Laguna de Términos is a shallow estuarine system on the South coast of Gulf of Mexico, influenced by different physical environments including wind, tides and river inputs, as well as heavy nutrient discharges, high turbidity and turbulence levels. This lagoon has been selected as a pilot site of the Global Environment Facility (GEF) Gulf of Mexico Large Marine Ecosystem Program (GoM-LME). Dissolved and particulate exchanges between sediments and the water column have been poorly documented in this system. Studies of sediment-water exchanges in Laguna de Términos have exclusively been conducted in mangrove forests (Rivera-Monroy et al., 1995; Day et al., 1996) or *Thalassia testudinum* seagrass beds (Yáñez-Arancibia and Day, 2005). It is expected that driving forces in both temperate and tropical systems strongly differs, as seasonal changes due to temperature and light are less pronounced in the tropical zone, yet these areas often are constrained by large fluctuations in precipitation which gives rise to pronounced wet and dry seasons.

Furthermore, in contrast to high latitudes, seasonal changes due to temperature and light are less defined in the tropical zone and as those oligotrophic systems are under increased anthropogenic influence (Grenz et al. 2003) information about their metabolic state is strongly needed. In this paper, we describe exchange rates measured at the sediment water interface in a tropical lagoon, to assess the importance of sediments in total system metabolism and to investigate how much of the variability can be ascribed to the alternations of rainy and dry seasons.

2. Materials and methods

2.1 Study site

Laguna de Términos is located at 18°38’36’’N and 91°49’51’’W, in the state of Campeche, Gulf of Mexico (Figure IV.1). It is a large shallow lagoon stretching over a surface of 1,936 km^2 with an average depth of only 2.4 m, corresponding to a total water volume of 4.65 km^3 (Contreras Ruiz Esparza et al. 2014). When including adjacent marshes and fluvial-lagoon systems the surface extends to approximately 2,500 km^2 and together with the surrounding wetlands it forms the largest RAMSAR site in Mexico stretching over a total area of 7,050 km^2 (Mitsch & Hernandez, 2013)

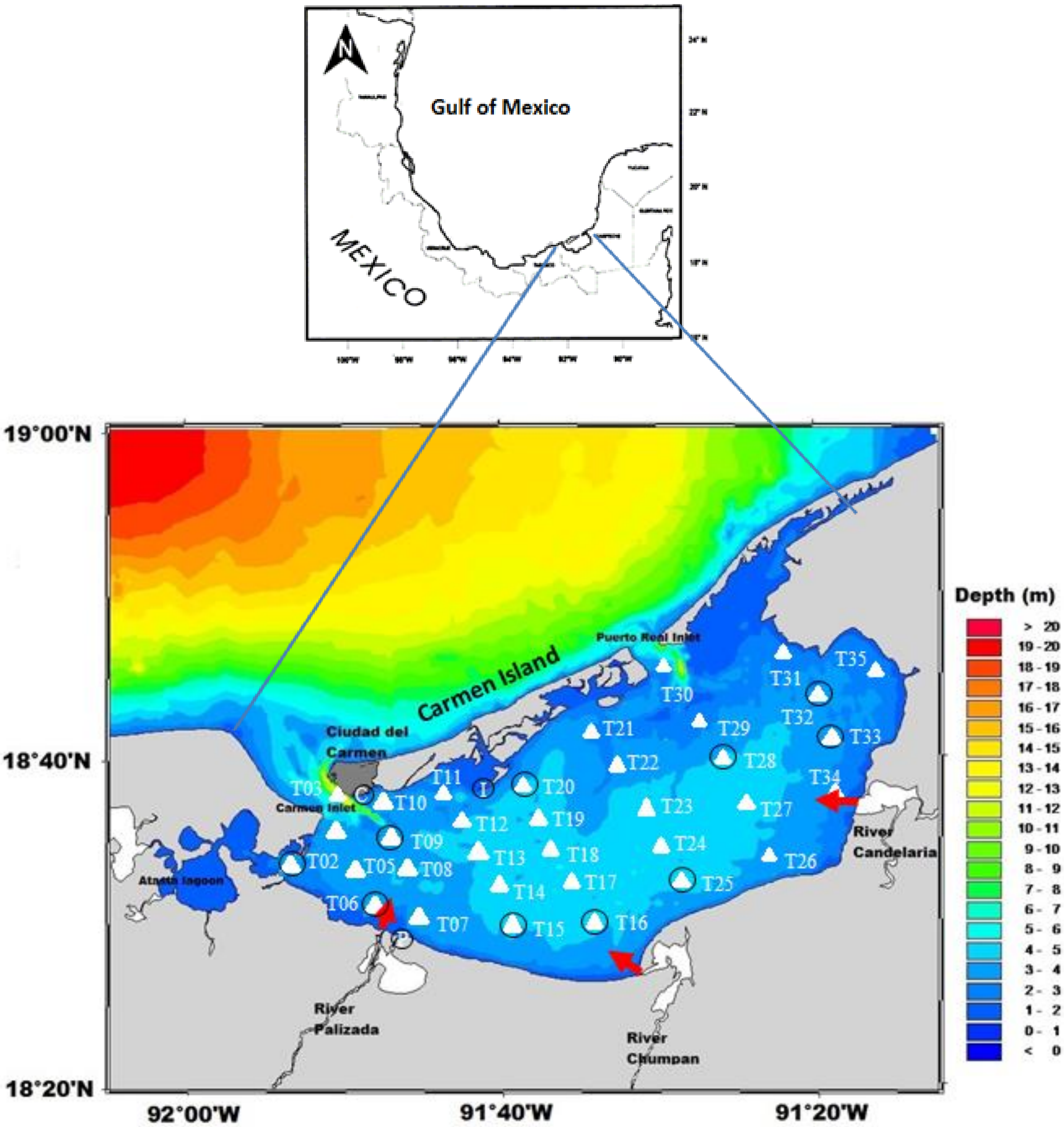

Figure IV.1 Depth distribution in Laguna de Términos and location of the sampling stations visited during four field trips in 2009 and 2010. Triangles correspond to water column samplings, circles to sediment corings and red arrows to main river outflows. The main town (Cuidad del Carmen) is located at the western tip of Carmen Island (dark grey).

The regional weather is humid tropical with an annual precipitation from 1650 to 1850 mm yr[1]. There are three different seasons, the first dry season from March through May, the rainy season from June through September, the second dry season extending from October through February ('nortes'), a period marked by intermittent storms (Yañez-Arancibia & Day, 2004 Bach et al., 2005). Laguna de Terminos receives large volumes of seasonally-varying flows of freshwater from a 49,700 km^2 watershed that drains portions of the Yucatan Peninsula, the lowlands of Tabasco, and the highlands of Chiapas and Guatemala. Laguna de Términos is part of the larger Usumacinta/Grijalva delta system, second in size to the Mississippi delta in the Gulf of Mexico region, and yielding similar suites of anthropogenic impacts and resource management challenges (Bach et al., 2005). The Usumacinta River flooding from Guatemala to Mexico is the largest river in Mesoamerica and one of the most significant shared water resources in the Western Hemisphere (Yañez-Arancibia & Day. 2005).

A selection of 13 stations (Table IV.1) was sampled for the determination of oxygen and nutrient fluxes at the sediment-water interface during the dry (March 2009 and 2010) and rainy seasons (October 2009, November 2010). That action was conducted in the frame of the multidisciplinary JEST (Joint Environmental Study of Laguna de Términos) project, jointly to a 2 years hydrological survey over a network of 35 stations (Fig. IV-1, Fichez et al., in review) and to the study and modelling of hydrodynamic processes (Contreras Ruiz Esparza et al. 2014).

Table IV.1 Location of the sampling sites in latitude and longitude and their sediment characteristics according to Yáñez-Arancibia (in Bach et al. 2005).

Station	° North	° West	Sediment type
C	18°38'26.90	91°47'51.76	Transitional sand
I	18°38'09.88	91°41'52.03	Transitional sand
P	18°29'34.99	91°47'24.37	Muddy clay
2	18°33'42.00	91°53'15.00	Muddy clay
6	18°33'20.00	91°49'40.00	Muddy clay
9	18°35'28.00	91°47'15.00	Muddy clay
15	18°29'30.00	91°40'17.00	Muddy clay
16	18°29'23.00	91°33'30.00	Transitional sand
20	18°38'52.00	91°38'56.00	Muddy clay
25	18°32'03.00	91°28'39.00	Transitional sand
28	18°40'13.00	91°26'34.00	Muddy clay
32	18°43'30.00	91°21'30.00	Clay
33	18°40'00.00	91°19'34.00	Clay

2.2 *Core sampling procedure and benthic incubations*

Due to shallowness, sediment samples were taken with a custom-built sediment core sampler equipped with 15 cm i.d, x 45 cm long acrylic core liners. An anti-return valve located at the head of the corer allowed to pull the core out of the sediment bed with very limited perturbation.

A 5 m long metal pipe used to sink the corer in the sediment and pull it out from the boat side, permitted to sample even the deepest stations in the middle of the lagoon. At each station, four cores were retrieved and bottom water sampled (ca 20 l) from a Niskin bottle. Water samples were transferred in an inflatable reserve tank excluding bubbles, and were used both as bottom water control and as replacement water during the core incubation. While water samples were preconditioned on board, a CTD profile was recorded by means of a SEABIRD 19+ equipped with a fluorimeter.

Upon return to the laboratory, within a couple of hours after core collection, the sediment cores were placed in a temperature controlled bath which was maintained near *in situ* temperature, and incubated in the dark. The cores were sealed with tops equipped with magnetic stirrers and gas-tight sampling ports. As detailed in Grenz et al. (2003), oxygen and nutrient flux rates were measured by monitoring the changes in concentration of overlying water at 2 h time intervals over a period of 8 h. Water samples (120 ml) were withdrawn with a syringe through sampling port at each time, and then filtered through GFF filters for nutrient analysis. The oxygen fluxes were analysed by microelectrodes Clark-type sensor, (Unisense Microsensor Multimeter) within each core. The sensors were calibrated by Winkler titration. Fluxes were calculated as slopes of linear regressions of oxygen and nutrient concentrations against time. Aerial fluxes were calculated by multiplying the rates of concentration change with the water height in each core tube. In spite of the low sampling volume with respect to overlying water volume, the correction for water replacement (with bottom water from the reserve tank) was systematically applied (Denis & Grenz 2003). Nutrients were analysed by Auto-Analyzer according to Tréguer & Le Corre (1975).

2.3 Sediment analysis

At the end of the benthic flux rate experiments, the cores were subsampled in 10 successive 0.4 cm thick slices (2.6 cm diameter) down to 4 cm depth. A first set was wet and dry weighted to determine porosity calculated from water content and assuming a bulk density of 2.65 g cm^{-3} (Berner, 1980). The remainder was used for determination of particulate organic carbon and nitrogen using a Carlo Erba elemental analyser coupled to a mass spectrometer for stable isotope ratio measurements (according to Kristensen and Andersen, 1987). A second set of sub-samples was used for chloropigments, extracted with 10 ml of acetone, centrifuged at 3000 rpm for 10 min and analysed on a spectrophotometer before and after addition of two drops of 1.2 M HCl (Strickland & Parson, 1972, Plante-Cuny et al. 1993).

2.4 Data analyses

The environmental factors and sediment water fluxes were analysed using two-way factorial analyses of variance (ANOVA) to test differences as a function of sampling site and seasons (SigmaPlot 12.0, Systat Software Inc.). Person product moment correlation matrix was performed to determine relationships between variables. A significance level of $p < 0.05$ was used unless otherwise indicated. Kruskal-Wallis and Mann-Whitney Rank Sum tests for unpaired t-Tests, were carried out each time normality assumption of the variables with homogeneous variance was not satisfied (Shapiro-Wilk test).

3. Results

3.1 Water and sediment characteristics

Due to freshwater inputs mainly originating from the Palizada River located in the south west part of Laguna de Términos, a salinity gradient ranging from 6 to 37 in surface waters was measured during the dry (March) and wet (October and November) seasons (Figure IV.2). Lowest mean salinities calculated over the whole lagoon were measured during the wet season (less than 22). Inversely during the dry season, mean salinities were higher (around 30) and the lowest salinities were found only near the River mouths (March). A salinity distribution close to the one observed during the dry season was observed in October 2009, a period of strong positive salinity anomaly related to an El Niño Modoki driven drought episode (Fichez et al., in review). Surface water temperatures were less variable ranging from 25.5 to 30 °C (mean 27.7 °C). Sediment porosity varied from 0.5 to 0.8 according to stations.

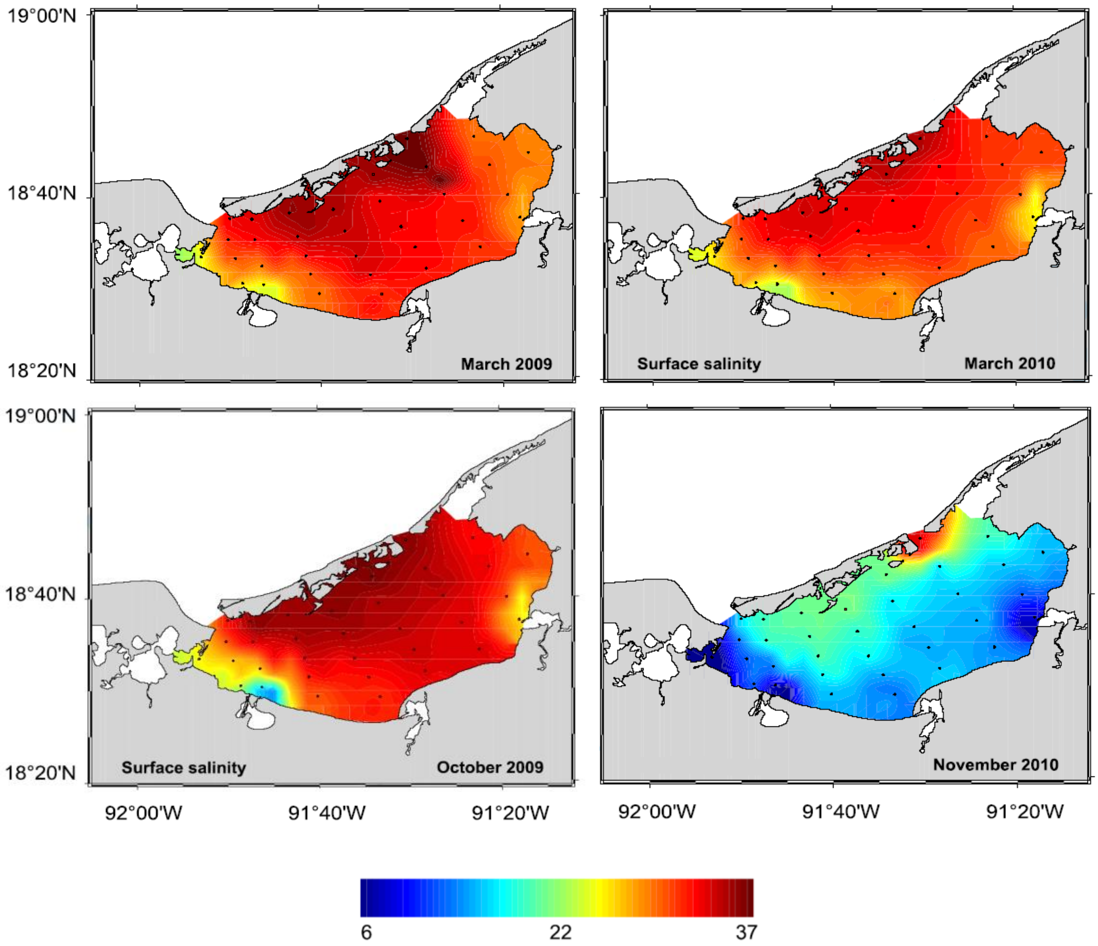

Figure IV.2 Spatial distribution of salinity during dry (March) and wet (October-November) seasons of years 2009 and 2010.

Deepest stations and sites close to river mouths were characterized by muddy sediments whereas shallow stations along Isla del Carmen were characterized by coarse sands with high calcium carbonate contents (> 50 % Yañez-Correa, 1969). Sediment organic matter content fluctuated around a mean value of 21.0 and 1.5 mg g^{-1} for Organic carbon and Nitrogen respectively but with a high spatial and temporal variability (Figure IV.3a & b). Molar ratio of C versus N varied between 5 and 35, even as high as 55 at station I in March 2010. The mean value of 25.7 denotes nitrogen depleted detritus for most of the sediments but with a high degree of variability (sd > 50 % for n=49).

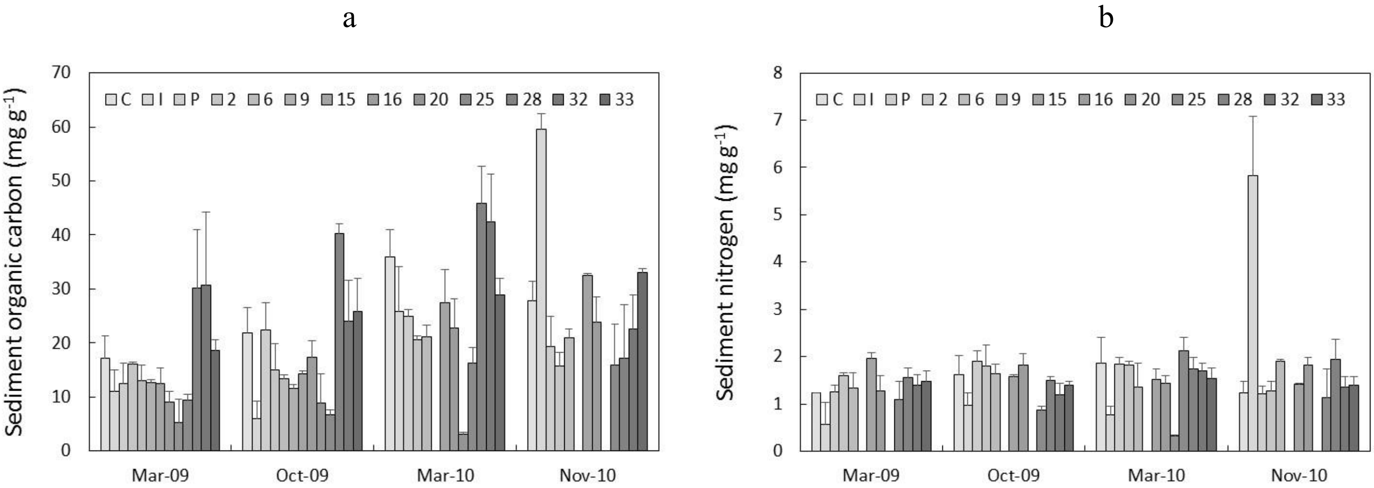

Figure IV.3 Sediment organic matter content for the 13 stations sampled during the dry (March) and wet (October-November) seasons of years 2009 and 2010 (a: Organic carbon, b: Nitrogen, bars indicate sd for triplicates)

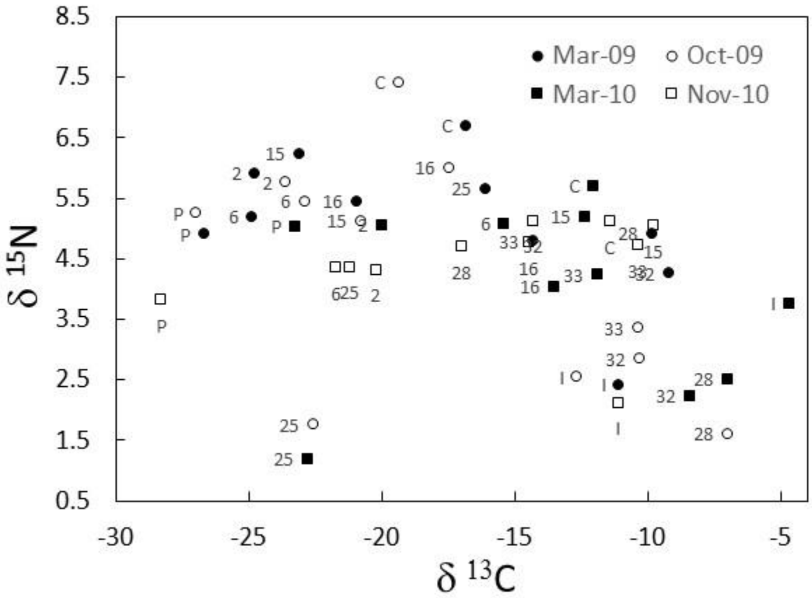

Figure IV.4 Plot of stable isotopes in surface sediments of the 13 stations sampled during the dry (March) and wet (October-November) seasons of years 2009 and 2010 (Wet season in hollow symbols, dry season in plain symbols).

The distribution of carbon and nitrogen stable isotopes opposed station I (-5 to -13 ‰ $\delta^{13}C$ and 2.2 and 3.7 ‰ $\delta^{15}N$) on one side to station P (-23 to -29 ‰ $\delta^{13}C$ and 3.8 to 5.3 ‰ $\delta^{15}N$) respectively corresponding to seagrass and terrestrial end members (Figure IV.4). Values between -20 and -30 ‰ $\delta^{13}C$ and 3.5 to 6.5 ‰ $\delta^{15}N$ mostly gathered a group of western stations, namely stations P and 2 at all times, station 6 at all times except for March 2010, station 15 in March and October 2009 and station 16 in March 2009. Most other samplings were distributed within the -5 to -20 ‰ range for $\delta^{13}C$ and within a larger range of 1.5 to 7.5 ‰ for $\delta^{15}N$, station C generally showing $\delta^{15}N$ values in the highest range. Station 25 strongly departed from all other groups in October 2009 and March 2010 with values close to -23 ‰ $\delta^{13}C$ and 1.5 ‰ $\delta^{15}N$. No clear seasonal trend could be established as most differences between sampling times were too close to analytical errors.

Vertical distribution of chlorophyll (Figure IV.5) and phaeopigment (Figure IV.6) in the sediments exponentially decreased with depth. Unfortunately, samples from March 2010 were defrosted inadvertently and the whole series had to be discarded. The samples from March 2009 showed the lowest values (0.7 and 20 µg g^{-1} for Chla and Phaeopigments).

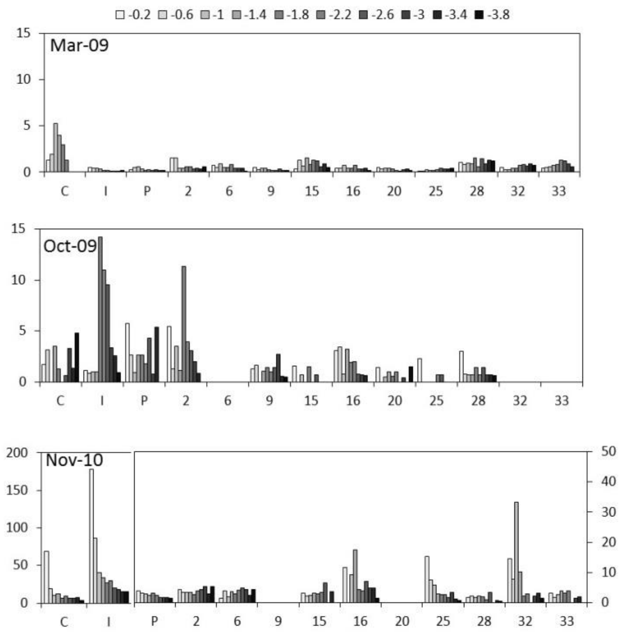

Figure IV.5 Spatial distribution of sediment chlorophyll profiles during dry (March 2009) and wet (October 2009 - November 2010) seasons (each layer is 0.4 cm thick, data in mg g^{-1}).

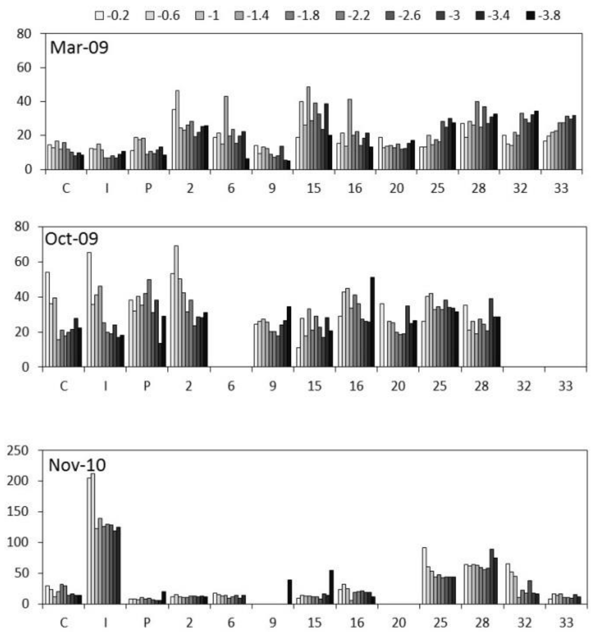

Figure IV.6 Spatial distribution of sediment phaeopigment profiles during dry (March 2009) and wet (October 2009 - November 2010) seasons (each layer is 0.4 cm thick, data in mg g^{-1})

During the wet seasons in October 2009 and November 2010, a significant increase was observed (1.8 and 8.9 µgChla g^{-1} and 30.4 and 34.9 µgPheo g^{-1} respectively). Highest values were encountered in the upper layers at station I (178.3 and 211.8 µg g^{-1} for Chla and Phaeopigments). The ratio of Chla contents over the sum of pigments (Chla + Phaeo) fluctuated similarly with highest values during the wet season.

The results of the ANOVA tests showed that salinity and sediment organic carbon were the environmental factors that differed significantly among sampling sites and seasons (Table IV.2). In contrast, porosity, bottom water NH_4 and NO_3 significantly differed among sampling sites only, whereas temperature, sediment Chla and bottom water $Si(OH)_4$ significantly differed among seasons. Finally, sediment nitrogen and related C/N, bottom water O_2 and PO_4 did not significantly differed in space or in time ($p > 0.05$).

Table 2. Two-way ANOVAs (F) and Kruskal-Wallis (H) tests to examine the differences in environmental conditions and benthic fluxes as a function and sampling site and season (* p < 0.05).

	Season	p	Site	p
Environmental conditions				
Salinity	$H_{3,48}$ = 16.73*	<0.001	$H_{12,48}$ = 25.25*	0.014
Temperature (°C)	$F_{3,48}$ = 5.12*	0.005	$F_{12,48}$ =1.08	0.405
Porosity	$F_{3,48}$ = 0.21	0.886	$F_{12,48}$ =4.26*	<0.001
Sediment				
organic Carbon (µg g^{-1})	$H_{3,48}$ = 12.23*	0.007	$H_{12,48}$ =25.44*	0.013
Nitrogen (µg g^{-1})	$H_{3,48}$ = 7.32	0.062	$H_{12,48}$ =16.01	0.191
C/N (molar)	$H_{3,48}$ = 5.10	0.165	$H_{12,48}$ =19.71	0.073
Chlorophyll (µg g^{-1})	$H_{2,31}$ = 19.84*	<0.001	$H_{12,31}$ =7.78	0.802
BW-O_2	$F_{3,48}$ = 0.56	0.648	$F_{12,48}$ =1.00	0.469
BW-NH_4	$H_{3,48}$ = 1.56	0.669	$H_{12,48}$ =28.95*	0.004
BW-NO_3	$H_{3,48}$ = 3.80	0.284	$H_{12,48}$ =25.75*	0.012
BW-PO_4	$H_{3,48}$ = 3.01	0.391	$H_{12,48}$ =13.65	0.324
BW-$Si(OH)_4$	$H_{3,48}$ = 19.22*	<0.001	$H_{12,48}$ =10.51	0.572
Sediment water fluxes (µmol m^{-2} h^{-1})				
O_2	$H_{3,48}$ = 12.81*	0.005	$H_{12,48}$ =14.77	0.254
NH_4	$H_{3,48}$ = 1.98	0.576	$H_{12,48}$ =20.78	0.054
NO_3	$H_{3,48}$ = 8.15*	0.043	$H_{12,48}$ =11.43	0.492
PO_4	$H_{3,48}$ = 6.60	0.086	$H_{12,48}$ =14.33	0.280
$Si(OH)_4$	$H_{3,48}$ = 21.83*	<0.001	$H_{12,48}$ =3.63	0.989

Bottom water concentrations (BW) in µmol l^{-1}.

3.2 Sediment Oxygen Demand and nutrient fluxes

Sediment Oxygen Demand (SOD) showed high variation (Figure 7) with minimum respiration rates (mean 840 µmol m^{-2} h^{-1} (sd 440, n=51) measured at most stations in March 2009. Conversely, highest fluxes were recorded (mean 2750 µmol m^{-2} h^{-1}, sd 1720, n=52) in October 2009, during the wet season, whereas measurements in March 2010 and November 2010 showed intermediate SOD. The Kruskal-Wallis test confirmed a significant difference among sampling seasons but not sites ($H_{3.48}$= 12.81, p = 0.005). The maximum SOD were measured at station I in October 2009 (7400 µmol m^{-2} h^{-1}, sd 1600, n=4) and November 2010 (6400 µmol m^{-2} h^{-1} sd 840, n=3). These values were 4 times (and significantly) higher than the mean SOD measured over the whole period (1700 ± 395 µmol m^{-2} h^{-1} sd 1375, n=49). The results of the Kruskal-Wallis ANOVA test for NO_3 and $Si(OH)_4$ fluxes showed significant differences among seasons only (Table 2). This was due to nitrate fluxes in October 2009 (-5.0 ± 5.5 µmol m^{-2} h^{-1}) which were significantly lower (t=6.072, df 175, $p < 0.001$) and directed into the sediment, compared to the other periods when nitrate fluxed out the sediment (8.6 ± 2.6 µmol m^{-2} h^{-1}). Similarly, for $Si(OH)_4$, the March 2009 fluxes (19.5 ± 3.5 µmol m^{-2} h^{-1}) were significantly different (Mann-Whitney U = 34.00, $p < 0.001$) compared to the other periods (86.0 ± 12.9 µmol m^{-2} h^{-1}). According to Kruskal-Wallis tests, ammonium and phosphate fluxes did not show significant differences in space or time (Table IV.2) mainly due to the large variability encountered.

The correlation matrix in Table3 shows the relationships between the 17 main variables measured. Bottom water nitrates and $Si(OH)_4$ are negatively correlated to salinity. Taking salinity as an index of freshwater inputs, these nutrient levels seemed well related to river inputs. Porosity behaved similarly in response to the supply of silt and mud by the rivers. Organic contents in sediments (C, N and pigments) appeared positively related to porosity as did the sediment organic carbon to nitrogen ratio and pigments. Bottom water O_2 correlated with sediment organic matter (N and pigments), between NH_4 and NO_3 as did $Si(OH)_4$. Bottom water NH_4 and PO_4 were negatively related to O2 and sediment organic carbon, respectively. SOD related positively to sediment organic contents (C, N and pigments) and to bottom water phosphate. A negative relationship was shown between nitrate fluxes and bottom water ammonium and nitrate. Fluxes of nitrate and ammonium were positively correlated. PO_4 fluxes co-variate with bottom water NO_3, and silicate fluxes with sediment pigments, bottom water PO_4, $Si(OH)_4$ and SOD.

River inputs accounting for 95 % of freshwater inputs to Laguna de Términos (Fichez et al., in review) correlation with salinity could be used as an indicator of estuarine influence. Salinity was negatively correlated with porosity and bottom water nitrates and $Si(OH)_4$ and only positively correlated with the C:N ratio. Beside salinity, positive correlation between environmental descriptors was evidenced for porosity with organic carbon, nitrogen and chloropigment; organic carbon with nitrogen, chloropigment and C:N; nitrogen with chloropigment and oxygen; chloropigment with oxygen; NH_4 with NO_3; NO_3 with $Si(OH)_4$.

Significant negative correlations were revealed for organic carbon with PO_4 and NH_4 with O_2. Considering fluxes, SOD correlated positively with N, chloropigments, PO_4 and silicate flux; NH4 flux correlated positively with NO3 and DIN fluxes; NO_3 flux correlated negatively with NH_4 and NO_3 and positively with NH_4 and $Si(OH)_4$ fluxes; DIN flux correlated positively with NH_4 and NO_3; PO_4 flux correlated positively with NO_3; and finally $Si(OH)_4$ flux correlated positively with chloropigments, PO_4, $Si(OH)_4$ and SOD.

Table 3. Pearson Product Moment Correlation matrix.

Variables	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**
Salinity (1)	-																
Temperature (°C) (2)	0.171																
Porosity (3)	**-0.324**	0.156															
orgC ($\mu g.g^{-1}$) (4)	-0.059	0.164	**0.294**														
N ($\mu g.g^{-1}$) (5)	-0.237	0.098	**0.639**	**0.661**													
Sed Chla ($\mu g.g^{-1}$) (6)	-0.117	0.102	**0.374**	**0.670**	**0.845**												
C:N (molar) (7)	**0.301**	0.032	-0.146	**0.295**	-0.122	-0.081											
O_2 ($\mu mol\ l^{-1}$) (8)	-0.138	-0.154	0.062	0.140	**0.254**	**0.483**	-0.101										
NH_4 ($\mu mol\ l^{-1}$) (9)	0.014	0.158	0.058	0.060	0.035	-0.026	-0.108	**-0.269**									
NO_3 ($\mu mol\ l^{-1}$) (10)	**-0.561**	-0.058	0.061	0.027	0.036	-0.056	-0.137	0.035	**0.397**								
PO_4 ($\mu mol\ l^{-1}$) (11)	0.242	0.152	-0.157	**-0.320**	-0.164	-0.153	-0.166	0.080	-0.004	-0.059							
$Si(OH)_4$ ($\mu mol\ l^{-1}$) (12)	**-0.407**	0.013	0.148	0.082	0.026	0.016	0.030	-0.023	0.004	**0.470**	-0.015						
Flux O_2 (13)	0.188	0.052	0.086	0.125	**0.257**	**0.458**	0.158	0.154	0.024	-0.091	**0.269**	-0.081					
Flux NH_4 (14)	0.052	0.050	0.106	0.197	0.030	-0.111	0.067	-0.162	-0.230	-0.186	0.016	0.072	-0.192				
Flux NO_3 (15)	-0.224	-0.129	0.163	0.089	0.009	-0.036	-0.089	0.110	**-0.356**	**-0.257**	0.070	0.106	-0.150	**0.405**			
Flux DIN (16)	0.060	-0.042	-0.036	0.064	-0.140	-0.200	0.166	-0.159	-0.182	-0.233	0.015	0.026	-0.154	**0.829**	**0.513**		
Flux PO_4 (17)	-0.194	0.111	0.194	0.091	0.205	0.119	-0.190	0.018	0.324	**0.329**	0.121	-0.012	-0.066	0.183	0.106	0.189	
Flux $Si(OH)_4$ (18)	-0.140	0.063	0.161	0.085	0.146	**0.259**	0.055	-0.026	-0.224	0.078	**0.257**	**0.616**	**0.250**	0.221	0.165	0.144	-0.073

All data were compiled from the 4 surveys apart for Sediment chlorophyll. Values shown are the correlation coefficients between variables. Bold coefficient values were statistically significant ($p < 0.05$). Positive or negative coefficients indicate positive or negative correlations with 1 or -1 being the strongest positive or negative relationship. Fluxes are in $\mu mol\ m^{-2}\ h^{-1}$.

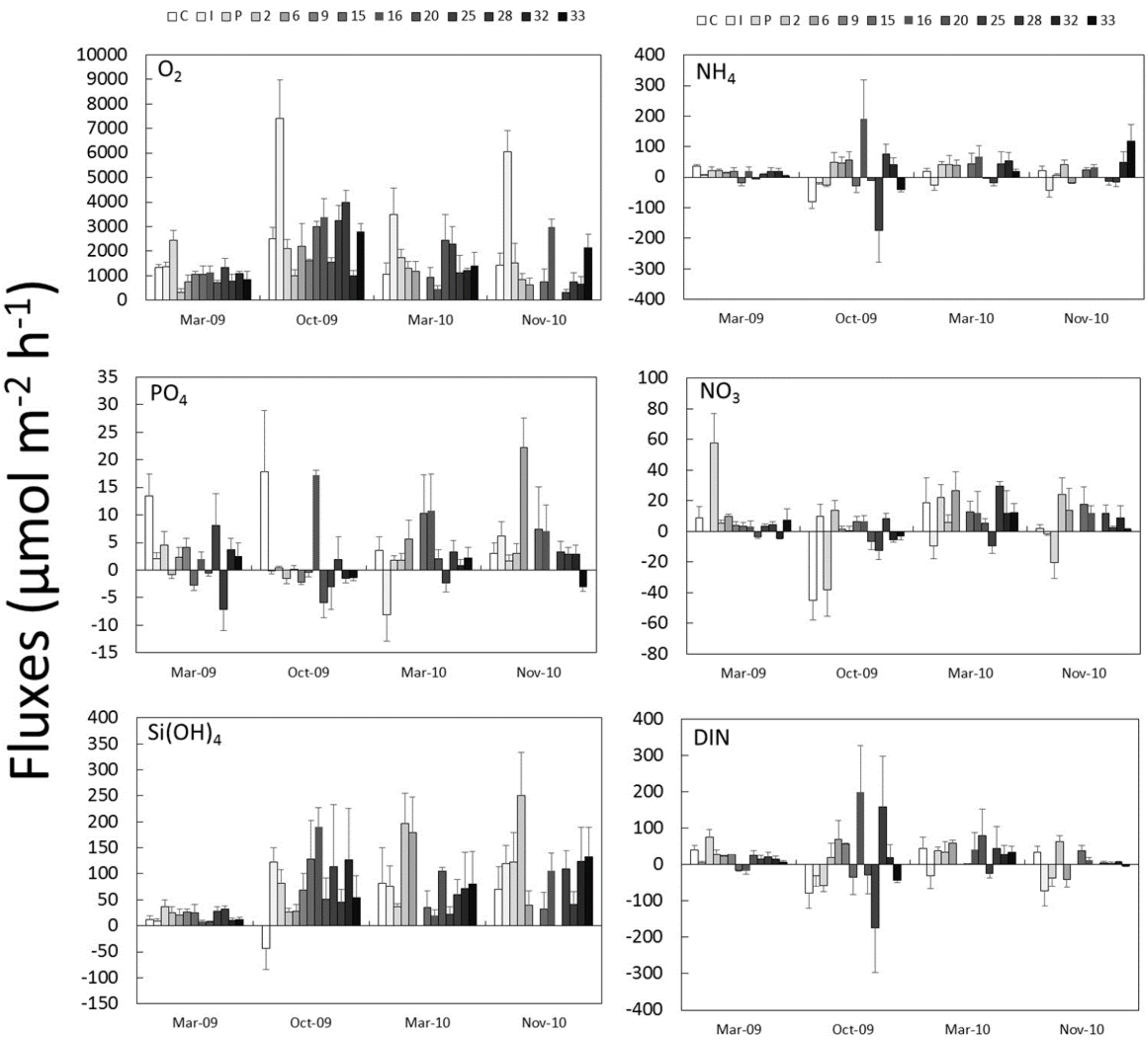

Figure IV.7 Seasonal variation of SOD and nutrient fluxes during dry (March 2009) and wet (October 2009 -November 2010) seasons (bars indicate sd for n=4).

4. Discussion

Even if Laguna de Términos is the most thoroughly studied lagoon in Mexico, to our knowledge, no published data are available regarding nutrient fluxes or SOD measurements at the sediment water interface. Compared to other (sub) tropical and more temperate aquatic systems, our SOD stand in the upper range of available measurements (Table IV.4). The highest values in temperate systems were reported from specific sediments in catfish aquaculture ponds (Berthelson et al., 1996), in Danish and Cypriote fish farms (Heilskov et al., 2006) and underneath shellfish cultures in Ria de Vigo (Forja et al., 2004) and Thau Lagoon (Thouzeau et al., 2007).

Table 4. Example of benthic oxygen fluxes (min max) measured in shallow aquatic systems.

Site	Latitude	O2 ($\mu mol.m^{-2}.h^{-1}$)		Author
Temperate systems				
Upper Waterway, Illinois	42°52N	723	4598	Butts, 1974
Eastern Michigan River	44°15N	129	3552	Bowie et al., 1985
Chesapeake bay	37°35N	2067	4068	Boynton & Kemp, 1985
Lake Ton-Ton (Uruguay)	34°51N	1163	2286	Sommaruga, 1991
Hiroshima bay	34°20N	129	904	Seiki et al., 1994
Tualatin River basin	45°19N	517	3358	Rounds & Doyle, 1995
NW Mississipi aquaculture pond	45°34N	3390	8728	Berthelson et al., 1996
Upper Klamath Oregon	42°23N	1421	4779	Wood, 2001
Neuse Estuary	35°13N	2822	3616	Borsuk et al., 2001
Golfe de Fos, France	43°22N	625	1958	Rabouille et al., 2003
Anacostia River, USA	38°50N	1291	4650	Machelor et al., 2003
Chester River, USA	39°4N	2067	4069	Boynton et al., 2003
Beach Haven Ridge, NW Atlantic	39°34 N	239	2819	Laursen & Seitzinger , 2003
Helsingør, Denmark	56°2N	2200	3800	Wenzhofer & Glud, 2004
Ria of Vigo, Spain	42°12N	667	8292	Forja et al, 2004
Thau lagoon, France	43°23N	3140	10980	Thouzeau et al., 2007
Tacan Bay, Korea	36°4N	317	1321	Kyung Hee Kim, 2007
Hauraki Gulf, New Zeland	36°25S	128	1222	Giles et al., 2007
Georgia Coastal plain, USA	31°14N	129	5813	Utley et al., 2008
Keelung River, Taiwan	25°6N	310	1330	Liu, 2009
Coombabah lake, Australia	27°54S	279	4736	Dunn et al., 2012
Derwent estuary	42°51S	532	1153	Banks et al., 2013
Oregon Shelf, USA	44°2 N	180	520	Fuchsman et al., 2015
Gulf of Valencia, W Med	39°26N	611	2306	Sospedra et al., 2015
(Sub)tropical systems				
Shing-Mun River, Hong Kong	22°23N	1188	18988	Chen et al., 2000
Tolo Habor	22°25N	607	1653	Chau, 2002
New Caledonia	22°22N	550	1570	Grenz et al., 2003
Nichupte, Mexico	21°7N	250	12875	Valdes-Lozano et al., 2006
Goa, W Coast India	15°27'N	1460	4120	Pratihary et al., 2009
Pompey Reef, Australia	21°0 S	821	3400	Alongi et al., 2011
Cochin Backwater System	9°49N	995	2267	Abhilash et al., 2012
Semariang Batu River, Malaysia	1°37N	982	14803	Ling et al., 2009
Terminos lagoon	**18°40N**	**305**	**7400**	**This study**

Temperature combined with organic matter influx to the sediments control benthic mineralisation logically driving coastal tropical lagoons in the upper range of SOD values as demonstrated by the maximum reported from shallow rivers in Hong Kong and Malaysia (Chen et al. 2000, Ling et al. 2009), and from coastal lagoons near Cancun (Valdes-Lozano et al. 2006). SOD reflects aerobic microbial respiration and reoxidation of reduced compounds (Hammond et al. 1985; Kaspar et al. 1985; Hopkinson 1987), but physical and biological mediated disturbance including the impact of macro- and meiofauna also affect the exchange rates between sediment and water column (Aller 1980, Andersen & Kristensen 1988, Kristensen et al., 1992). Quality and quantity of sediment organic matter also control nutrient fluxes and benthic respiration rates (Janhke et al., 2005, Burdige, 2006, Alongi et al., 2011).

The main picture that emerges from our data set from Laguna de Términos is the large heterogeneity. SOD in Laguna de Términos is highly variable in space and time with a minimum of 305±180 µmol m^{-2} h^{-1} at station 2 in March 2009, and a maximum of 7400±1590 µmol m^{-2} h^{-1} at station I in October 2009. Like all large estuarine ecosystems, the lagoon hosts highly diverse habitats such as mangrove swamps, seagrass beds, muddy or sandy sediments. Moreover the area is characterised by a tropical wet-dry climate with high freshwater outflows in summer. The inputs from Palizada River (9.08 10^9 m^3 y^{-1}) play an important role as this inflow represents between 75% and 80 % of the fresh water within Terminos (Smith et al. 1999; Fichez et al. in review), producing turbid, nutrient-rich and low salinity waters (Bach et al. 2005). On the seaside, both inlets exchange seawater from the Campeche shelf acting as a buffer maintaining high salinities and water transparency. David & Kjerfve (1998) showed that the lagoon behaves as a single hydrological unit with a net east-to-west flow-through, especially during the rainy season. The consequence is a South West to North East gradient in most of the hydro-biological variables.

As the rates of biogeochemical processes are likely to be limited by either the availability of organic matter or of terminal electron acceptors (Jorgensen 2000), microbial active zones are often limited to the top layer of sediments. We observed that organic matter distribution in the 4 cm top layer of sediment is variable in both time and space (Two-way ANOVA), sediments containing 0.5 to 3 % of organic carbon and 0.1 to 0.2 % of nitrogen with C:N molar ratios above 10, indicating preferential degradation of the nitrogen-rich component. The δ^{13}Corg values confirm a terrestrially dominated origin of carbon in the sediments from the western part (from -27 to -20 ‰) shifting to a more marine influence (from -20 to -7 ‰) toward the north-eastern part of the lagoon. This distinction of two end-members related to a mixing trend between terrestrial and marine/seagrass sources of OM has already been shown for estuarine systems (Thornton & McManus, 1994, Ogrinc et al., 2003). The least negative values of δ^{13}C were correlated with lowest stable nitrogen isotopes in the north eastern stations including station I on the lagoon side of the barrier island Isla de Carmen. For instance Peirera et al. (2010) found similar ranges in sediments from Mãe-Bá Lagoon in Brasil. Possible explanations include the presence of seagrass detritus mixture in the bulk sediments. Marguillier et al. (1997) showed a mean range of -10.02 to -19.8 ‰ for δ^{13}C and +1.11 and 1.51 ‰ for δ^{15}N seagrass leaves in a tidal creek in Kenya. The very specific values in δ^{13}C and δ^{15}N recorded at station 25 in October 2009 and March 2010 could be linked to the stable isotope signatures of some mangrove tree species such as *Rhizophora mangle, Avicenia germinans* and *Laguncularia racemosa* (Kuramoto & Minagawa 2001, Fogel et al. 2008) that has been reported as the main mangrove tree species in the area (Day et al., 1987) but the short temporality of those two occurrence is not consistent with the permanence of fringing mangrove forest. Of much more relevance is the stable isotope signature from microbial mat reported from the mangrove system of Twin Cays in Belize (Fogel et al. 2008) that if it varied in a wide range (-13 to 25 ‰) for $\delta^{13}C$ was much more definite (3 to -4 ‰) for $\delta^{15}N$. Therefore, the values of circa -23 ‰ $\delta^{13}C$ and 1.5 ‰ $\delta^{15}N$ observed at station 25 in October 2009 and March 2010 reasonably support the hypothesis of a microbial mat temporarily forming under sustained conditions of low river inputs consecutive to the 2009 drought period (Figure IV.8) and disappearing on the return of estuarine conditions in November 2010.

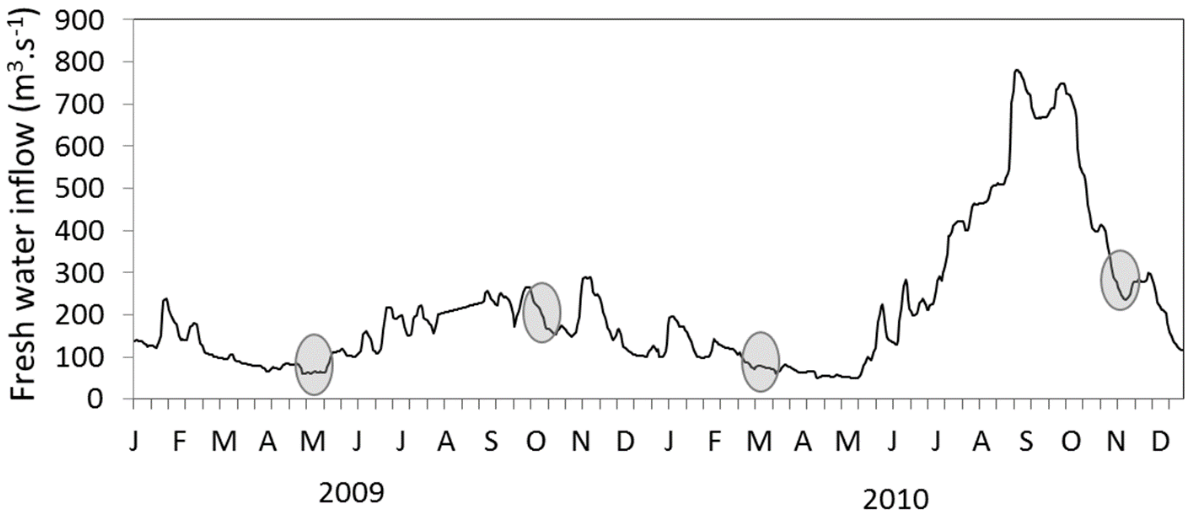

Figure IV.8 Daily freshwater inflows from Palizada River (m3 s^{-1}) from January 2009 to December 2010, filled circles depict the sampling periods (data from CONAGUA, http://www.conagua.gob.mx).

Chlorophyll pigments in sediments showed a seasonal trend (Kruskal-Wallis H=19.84, $p<0.001$) mostly because of the high values measured in the sub-surface layers during the rainy season, especially in November 2010 (t=3.004, df=189, $p<0.003$). The contribution of Chlorophyll a to total pigments fluctuated between 3 and 20 % showing that degraded pigments dominated. Pigment content was significantly higher in October 2009 than in March 2009 (t=6.170, df=207, $p<0.001$) but lower than in November 2010. The rain deficit in 2009 most certainly accounting for such a discrepancy. Sediments support productive microalgal communities (Sundback et al., 2000, McGlathery et al., 2001) in shallow and transparent waters like in the Northern and Eastern part of Laguna de Términos. SOD were positively correlated to organic matter and chloropigments in the sediments (N and Sed Chla, $p < 0.05$ in Table IV.3). This has already been shown in temperate and tropical systems (Lansard et al., 2008, Grenz et al., 2000, 2003, 2010). The highest SOD were observed at station I which is dominated by sediments composed of 50-75 % calcium carbonate (Yañez-Correa, 1963). These rates are comparable to the one measured by Alongi et al. (1996) in a sheltered lagoon containing mixed terrigenous-carbonate sediments where sulfate reduction accounted for a significant fraction of total organic carbon oxidation.

The dominance in NH_4 effluxes observed during the dry season indicated degradation of sedimentary organic N (Belias et al., 2007) while the negative values measured in October 2009 could be the consequence of intense nitrification. The significant correlation of Si fluxes with sediment chlorophyll could be the result of mineralisation of benthic diatoms or dissolution of freshly deposited frustules (Katamani, 1982, Yamada & D'Elia, 1984, Loucaides et al., 2012). Silica release from the sediments is often considered as a gradient-driven process (Willey, 1978). We found on one occasion a significant influx of silicate to the sediment (Station C in October 2009) which corresponded to a period when silicate concentrations in the bottom water were higher than in interstitial pore waters (data not shown). These unusual Si influxes related to high water column silicate were also recorded by Niencheski & Jahnke (2002) in Patos lagoon (Brazil). For all other observations Si fluxes were directed towards the water column. The high positive correlation between Si fluxes and $Si(OH)_4$ in bottom waters in general ($r=0.616$) shows a potential resupply of this nutrient in favour of the nutrient pool in the water column.

Although sediments are generally considered to be a significant internal source of nutrients in shallow coastal ecosystems, several studies have shown that they may be a net sink of dissolved nitrogen at least during certain times of the year (Sundback et al. 2000, Tyler et al. 2003). In our case Nitrate and Silicate fluxes seemed more variable during the wet season as confirmed by the ANOVA Kruskal-Wallis test.

To compare our flux data to riverine inputs, we considered the monthly freshwater inflows at the given dates (88.5, 189.9, 75.5 and 307.8 $m^3\ s^{-1}$, for March 09, October 09, March 10 and November 2010 respectively, data from CONAGUA). River nutrient concentrations were calculated from regressing nutrient data against salinity in the range of salinity 0-3 for each season (data from P. Salles UNAM Sisal, pers. comm., from Vera-Herrera & Rojas-Galaviz, 1983, from Medina-Gomez et al., 2015, and from our data at Palizada station). Based on our data, we calculated both minimum (Mean-CI) and maximum (Mean+CI) sediment-water fluxes for the total lagoon (2000 km^2). Finally we divided these lagoon-wide sediment-water exchange fluxes by the river inputs for each nutrient and season (Table IV.5) to compare the magnitude of sediment-water released with the river inputs for the entire lagoon. During both seasons, sediment-water nutrient fluxes for the total lagoon were always equal to or higher than the contributions from rivers. Benthic fluxes represented between 1 to 4 times the $Si(OH)_4$ river inputs during the wet season and 50 to 160 times the PO_4 river inputs during the dry season. Even when nutrients were consumed by the sediments, these uptakes were higher than the nutrient river inputs. This predictable relation results from the vast area of the lagoon compared to the proportional low river discharges. When adding the presumed high residence time of the water masses inside the lagoon (between 9 and 159 days, David and Kjerfve (1998), David (1999)), the contribution of benthic fluxes to biogeochemical cycling of nutrients becomes prominent.

Table IV.5 Ratio between benthic fluxes and River inputs of nutrients during dry and wet seasons (Fluxes ± C.I. in µmol m^{-2} h^{-1}, River Conc in µmol l^{-1}, Terminos Lagoon area 2 109 m2).

Season		NH_4	NO_3	DIN	PO_4	$Si(OH)_4$
	Benthic Fluxes	20.3±5.5	9.5±3.2	24.3±7.3	2.4±1.1	46.5±11.4
Dry	River Concentration	4.7	9.8	14.5	0.2	70
	F/R*	20 - 40	4 - 10	7 – 16	50 – 160	3 - 4
	Benthic Fluxes	10.0±16.3	0.2±3.7	2.9±18.8	3.2±1.5	89.4±15.9
Wet	River Concentration	4.1	23.8	27.9	0.8	120.2
	F/R*	(-3) - 12	(-1) – 4	(-2) - 2	4 – 18	1 – 4

* F: Benthic fluxes (min - max) x lagoon area, R: River Concentration x Flow x 10^3 (both units in µM h^{-1}).

A similar calculation could be performed to compare primary production to benthic carbon mineralisation rates. We used data from Day et al. (1987) and Gomez-Reyes et al. (1997) to calculate a mean primary production rate of 200 g C m^{-2} yr^{-1}. Considering a community respiration quotient (CRQ) of 1.1 (Denis, Univ. Lille, pers. comm.) and mean SOD of 1327±161 and 2248±359 µmol m^{-2} h^{-1} for dry and wet seasons respectively, we found that the sediments mineralized between 67 and 86 % of the carbon produced in the water column during the dry season and between 109 to 151 % during the wet season. These ranges are slightly higher to proportions calculated for sub-tropical lagoons in New Caledonia and Brazil (Grenz et al., 2010, Machado and Knoppers, 1988). The reduced precipitation as a consequence of the ENSO event in 2009 affected the magnitude of SOD with an increase in oxygen consumption by almost 50 %. These higher rates may influence the oxygen balance in Laguna de Términos and lead to hypoxic events, moreover in the context of global climate change and the potential increase in dryness under these latitudes (Mendoza et al. 1997, Brito et al. 2012).

Considering C mineralization rates as calculated previously (1206 and 2011 µmol C m^{-2} h^{-1}) and the Redfield stoechiometry (106/16), N removal was estimated to amount 182 and 308 µmol N m^{-2} h^{-1} during dry and wet season respectively. When considering our N/C ratio estimate, C mineralization is lower and corresponds to 47 and 80 µmol N m^{-2} h^{-1} (dry and wet season, respectively). Our DIN efflux measurements were 23 and 3 µmol N m^{-2} h^{-1} (dry and wet season, respectively), indicating that a substantial part of Nitrogen (between 50 and more then 95 % depending on the calculation) is removed by the sediment through denitrification or other N consuming process (Sørensen 1978, Seitzinger 1988, Kelso et al. 1999). The C/DIP ratio calculated from the effluxes (0.002) is well below Redfield indicating that P is removed from the sediment. Finally the mean flux ratio DIP/DIN over all periods (1/5) is well above Redfield (1/16) indicating that N is more efficiently removed than P.

5. *Conclusions*

Despite the fairly large variability associated with some of the SOD and nutrient flux estimates, several important conclusions can be drawn from the results. The seasonal variability exceeded the spatial variability, with peak rates of mineralization during the wet seasons significantly related to organic matter content in the sediments. In contrast, a strong SW-NE spatial gradient was found in the isotopic signatures of the sedimentary OM and this was constant over the studied period. The low $\delta^{15}N$ combined to heavier $\delta^{13}C$ in the easternmost stations and along the inshore of the barrier island was probably due to a higher fraction of seagrass debris in the sediments. High C/N ratio emphasized the refractory nature of the sediment mixture.

Benthic in- or effluxes of nutrients were always equal or higher than the river inputs, while benthic carbon mineralization rates, as inferred from SOD measurements, were equivalent to a significant proportion of the pelagic carbon production. This emphasizes the predominant role played by benthic processes in the biogeochemical cycles in tropical estuarine systems regularly submitted to high freshwater inflows.

Acknowledgments

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You cannot create experience. You must undergo it.

Albert Camus

Chapitre V.

Benthic mineralisation rates in contrasted sites in a shallow tropical lagoon (Campeche, Gulf of Mexico).

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Benthic mineralisation rates in contrasted sites in a shallow tropical lagoon (Campeche, Gulf of Mexico).

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Abstract

Sediment Oxygen Demand (SOD) and nutrient fluxes were measured between 2008 and 2010 in Laguna de Términos. During 2 years, three contrasted stations were visited every 3 to 4 month: a site nearby the Palizada river outflow (P), a sheltered area colonized by seagrasses (I) and a station close to an urbanized area (C). These stations were compared to a reference station located in the middle of the lagoon (St 9). SOD and nutrient exchange rates were measured through sediment core incubations under constant tropical temperature of around 28°C, supposed to favor benthic activity by increasing respiration rates. The highest SOD was observed at St. I (3187±569 $\mu mol.m^{-2}.h^{-1}$), twice the rate measured at the control station. SOD at St.C and St.P were lower but still high compared to literature flux data. DIN fluxes showed that St.C and St.I consisted as a net sink of nitrogen whereas St.C represented a net source of PO_4 for the water column. Our flux data showed spatial differences among stations and support the hypothesis that human impact or the presence of seagrasses determine benthic metabolism and that different environmental situations lead to different sedimentary behavior.

1. Introduction

Coastal lagoons are geomorphologically defined as coastal depressions below the mean maximal of high tides, always protected from the sea by physical or hydrodynamic barriers (Yáñez-Arancibia et al. 1993). The shallow nature of lagoons leads to a high ratio of surface area to water volume and the sediment compartment is usually within the photic zone (Tyler et al., 2003). These ecosystems are known to be important economic and ecological systems and, due to their sheltered nature, they represent potential accumulating sites for organic matter and pollutants (Rabalais et al. 2009, Zanchettin et al. 2007, Brito et al. 2012). The understanding of benthic dynamics in such systems is particularly important as they are usually subjected to major short-term oscillations in their physical and chemical characteristics (Fonseca & Netto 2006). Moreover in estuarine ecosystems, benthos has been recognized as a good indicator of environmental change (O´Reilly 2006, Hernandez-Guevara et al 2008). Freshwater discharge, tidal forcing, turbulent mixing of fresh and salt water can generate abrupt changes in temperature, salinity, turbidity, pH and bioactive element concentrations (Hedges & Keil 1999). At the sediment-water interface, highly variable chemical and biological activities increase with reduced water depth and impact over the water column processes (Smith 1974; Ståhlberg et al. 2006).

Tropical ecosystems are known to be characterised by a smaller amplitude in temperature related to their high-latitude, so the variability in physical characteristics of the habitats are supposed to be linked to weather seasonality (O´Reilly 2006; Hernandez-Guevara et al 2008). These systems are vulnerable to global changes, (such as sea-level rise, increased temperatures and storminess, floods and shoreline erosion) and they are exposed to human pressure, especially those submitted to freshwater inflows (Newton et al. 2012, Newton et al. 2014). The major problems faced in coastal ecosystems are land reclamation (Murray et al. 2006, Newton et al. 2014) and the loss of coastal vegetation (Ehrenfeld 2000; Newton et al. 2014) and habitats (Beck et al., 2001, Newton et al., 2014). Even though population exposure to water stress will increase substantially with climate change, climate prediction uncertainties at the regional to local scale are still to be considered (Met Office 2011; Fichez 2015).

Benthic primary production is often more important than pelagic production, and sediment mineralization of nutrients may drive overall biogeochemical cycling (Anderson et al., 2003; Newton, et al., 2014) Thus, understanding the biogeochemical processes at environmental redox interfaces is crucial for predicting and protecting water quality and ecosystem health

(Borch et al. 2010). Net ecosystem metabolism is an indicator of how a system process nutrients and organic material (Kemp & Boyton 1980, Gonneea et al. 2004, Giordano et al. 2012). The relative long residence time and penetration of light together with high freshwater and nutrient inflows make lagoons susceptible to eutrophication (McGlathery et al. 2007; Giordano et al. 2012), mostly because they have considerably elevated organic matter concentrations relative to adjacent water masses (Newton et al. 2014).

The Mexican coast is 11 122 km long, characterized by an estuarine surface of 16 000 km^2, and 12 000 km2 of coastal lagoons (Lara-Lara et al., 2008). Laguna de Términos (TL) is the largest coastal lagoon system in area (2000 km^2) and volume (6.0 10^9 m^3). This makes our study site the perfect open-air laboratory to investigate sediment and water dynamics.

Knowledge about systems functioning in coastal lagoons is still fragmentary despite the large effort put into research (Newton et al. 2014). Therefore the aim of the present study is to measure temporal variability in benthic respiration (SOD) and mineralisation rates over two years (2008-2010) by analysing four stations with contrasting influences (anthropogenic impact, macrobenthic communities, freshwater inputs compared to a reference station).

2. Materials and methods

2.1 Study site

Laguna de Términos is located at the southern part of Gulf of Mexico and presents diverse environments. Considering the principal physical and chemical features of TL four stations were sampled every two-four months from October 2008 to November 2010 in the Western part of the lagoon (Figure V.1). Station Palizada (st. P) is located at the entrance of the Palizada River which is a tributary of the Usumacinta River, the longest River in Mexico with the largest run-off, resulting by far the most significant source of freshwater inputs within TL (Yañez-Arancibia & Day. 2005). Station Isla (St.I) correspond to a seagrass area characterized for its high primary production and located in the North-East. In contrast to the other sites, station Ciudad del Carmen (st. C) was choosen because od the proximity of the largest city around TL. To compare these drivers a reference station has been selected in the middle of TL (st. 9). The lagoon is subjected to three distinct seasons: dry season (from March to May), rainy season (from September to October) and nortes (from October to February). The tides are mainly diurnal outside and inside the lagoon inlets (Contreras Ruiz Esparza et al. 2014).

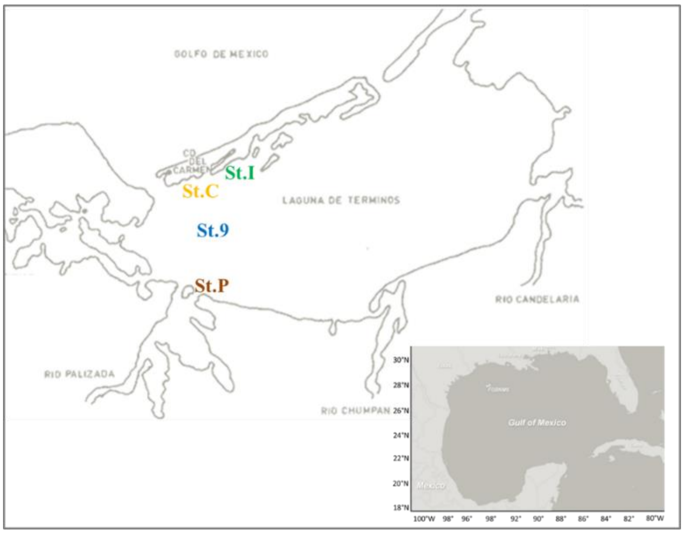

Figure V.1 Localisation of the four stations within Términos Lagoon considering the main differences among them (human activities St.C, seagrass mats St.I, fresh water inputs St.P and reference station St.9).

2.2 Sediment-water incubations

The study was conducted using sediment cores sampled at the different stations. The core sampling and incubation procedures are described in Origel et al. (submitted, Grenz et al. 2003). Briefly, acrylic cores of 45 cm length and 15 cm diameter containing 30 cm sediment with 15 cm overlying water were transported to the laboratory around 1 hour after sampling. These were sealed and placed under dark conditions and in situ temperature. Two stations per day with 4 replicate cores each were incubated during 15 hour periods. Pre- and post-calibrated mini-probes (UNISENSE) recorded oxygen concentration changes while nutrient changes were determined by regular water sampling (120 ml) in the stirred overlying water every 2 hours during the incubation periods. Oxygen consumption and nutrient exchange rates were calculated by regressing concentration changes over time (µmol m^{-2} h^{-1}). Chemical analyses consisted of Winkler titrations for oxygen and classical automated colorimetric analysis (Technicon AutoAnalyzer II) for nutrients (NO_3=NO_2^-+NO_3^-, PO_4 and $Si(OH)_4$, Denis & Grenz 2003, Clavier et al. 2005).

2.3 Sediment analyses

Subsamples of sedimentcores were freeze-dried and grinded for porosity and organic matter analyses. Particulate organic carbon and nitrogen were obtained using high combustion (900°C) on a CN Integra mass spectrometer and analyzed for stable isotopic composition ($\delta^{13}C$ and $\delta^{15}N$) (Kristensen & Andersen 1987, Raimbault et al. 2008).

Data analysis was carried out by SigmaPlot 12.0: One Way Analysis of Variance was used to test the variability of fluxes, Pairwise Multiple Comparison Procedure (Tukey Test) or non-parametric tests (Kuskal-Wallis, when normality assumption failed or when F-test determined unequal variances) were used to compare mean flux values among stations.

3. Results

3.1 Environmental conditions

Salinity varied from 0 to 4 at station P to 15 to 37 for all other stations (Figure V.2). Lowest salinities were recorded during wet months in October-November 2008 and July and November 2010, when freshwater inputs were highest. The year 2009 was exceptional with reduced precipitation and freshwater inflows in September and October 2009, due to an El Nino event (Figure V.3 Fichez et al. in review), (Tableau V.I)

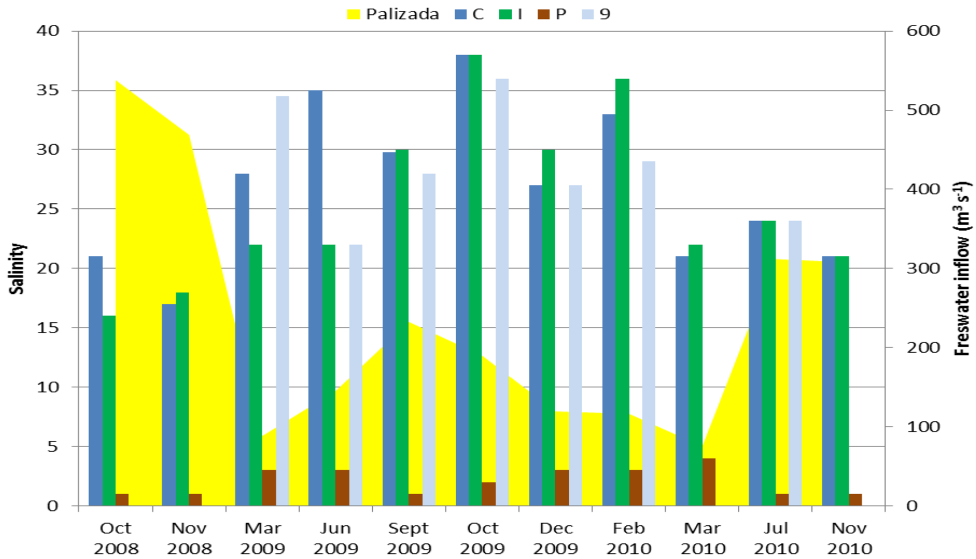

Figure V.2 Salinity measured at the different stations during the field survey and corresponding monthly means of freshwater inflows from Palizada River (data from CONAGUA http://www.conagua.gob.mx).

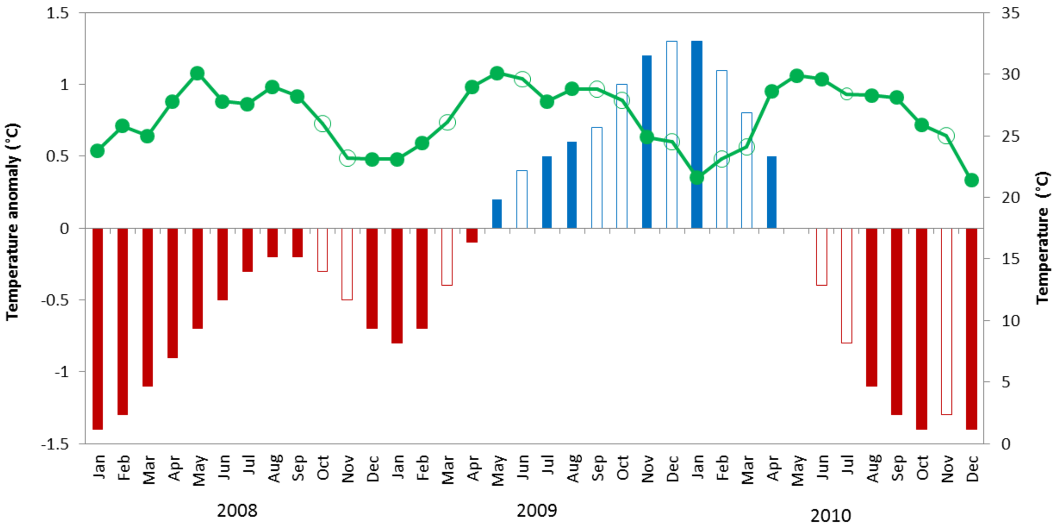

Figure V.3 Monthly temperature anomaly based on ONI (Ocean Niño Index: warm (red) and cold (blue) periods) and air temperature (green) during 2008, 2009 and 2010 where empty bars and dots represent the sampling dates (air temperature data from Sistema Metereologico Nacional Mexico (2012) and ONI from NOAA, Niño 3.4 region).

Table V.1. Descriptive statistics and Shapiro-Wilks normality test (W and p) for all variables and fluxes during the sampling periods.

Parameter	n	Mean	SE	W	p
Salinity	39	20.01	1.92	0.895	0.001
T°C	42	28.55	0.39	0.957	0.112
Porosity	42	0.68	0.02	0.983	0.802
Sed. organic matter ($\mu g\ g^{-1}$)					
C	36	23.87	2.10	0.967	0.358
N	36	1.44	0.2	0.681	<0.001
C:N (M/M)	36	20.26	1.49	0.873	<0.001
Bottom water (µM)					
O_2	41	191.5	7.43	0.971	<0.001
NH_4	39	2.24	0.51	0.648	<0.001
NO_3	40	1.90	0.42	0.680	<0.001
DIN	40	3.70	0.64	0.802	<0.001
PO_4	40	0.34	0.06	0.758	<0.001
$Si(OH)_4$	40	8.86	1.06	0.857	<0.001
Benthic fluxes ($\mu mol.m^{-2}.h$-1)					
SOD	40	2503.97	204.67	0.802	<0.001
NH_4	40	10.21	6.89	0.972	0.406
NO_3	38	-4.89	5.73	0.766	<0.001
DIN	42	5.31	9.70	0.929	0.012
PO_4	39	4.76	1.46	0.683	<0.001
$Si(OH)_4$	38	56.44	5.78	0.924	0.013

Small values of W (or $p< 0.05$) indicate a departure from normality

3.2 Sediment organic matter

During the course of the sampling period, the range of organic carbon and nitrogen content in the sediments varied between 2.04 - 60.6 µgC g^{-1} and 0.28 – 7.25 µgN g^{-1}. C/N molar ratios ranged from 6.86 to 47.27, always over the Redfiel ratio (Figure V.4). St.I showed the highest temporal variability whereas st.P showed lowest organic carbon contents (Table V.I).

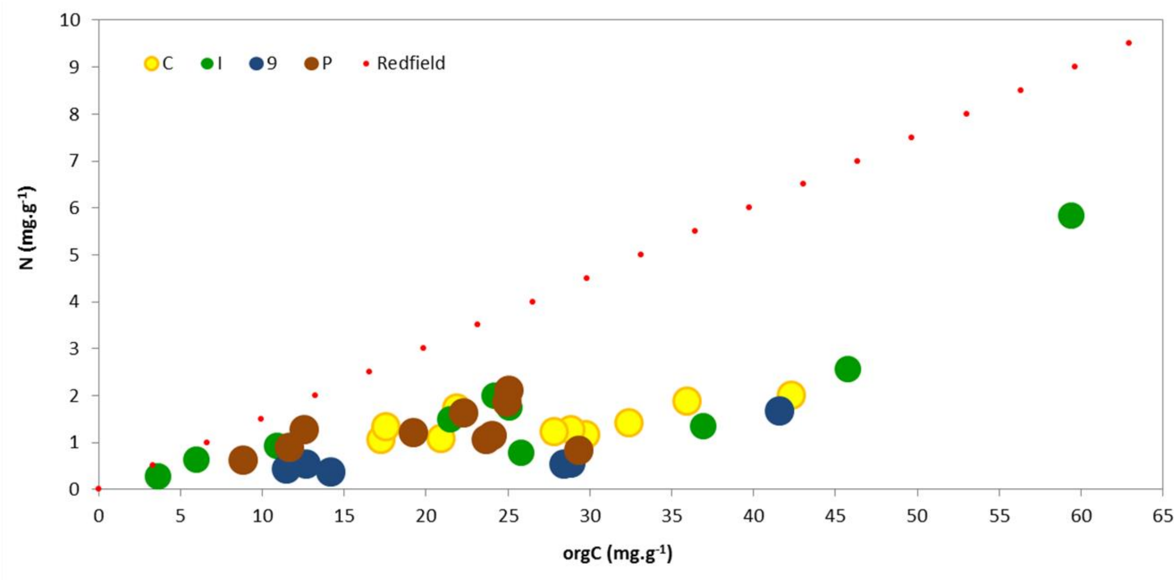

Figure V.4 Carbon and Nitrogen distribution within the first 4cm of the sediment for all stations during sampling periods from October 2008 to November 2010.

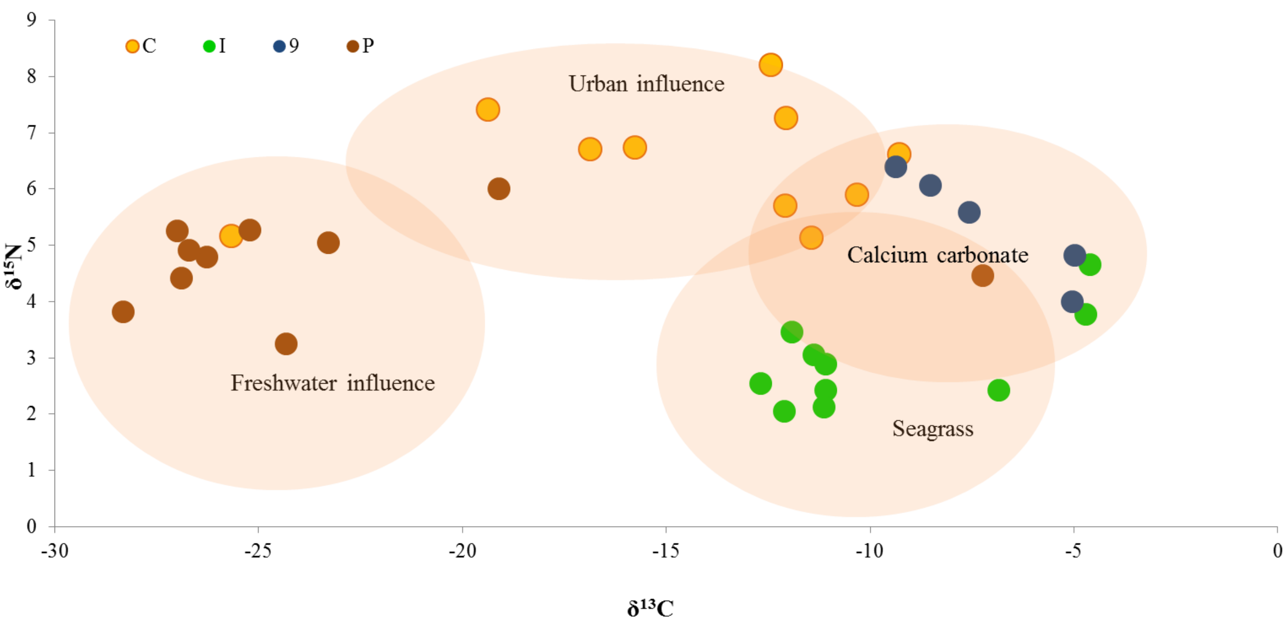

Figure V.5 Distribution of δN15/δC13 (molar) ratio within the first 4 cm in the sediment for all stations during sampling periods from October 2008 to November 2010.

High organic carbon and nitrogen contents in the sediments were related to porosity (R=0.458, df 35, F=9.011, p=0.005). Stable isotopic composition ($\delta^{13}C$ againts $\delta^{15}N$) in Figure V.5 showed a clear distribution of stations between terrestrial domain for St.P and marine domain for St.I and St.9. Most of the stations located in the marine domain portion of the lagoon correspond to samplings performed between September 2009 and March 2010, a period of reduced precipitation (Figure V.3).

3.3 Benthic fluxes

The mean values of SOD grouped by stations (Figure V.6) showed significant differences (F=21.760, p<0.001). Highest SOD were measured at St.I (3187±569 µmol m^{-2} h^{-1}) and lowest at St.9 (1479±355 µmol m^{-2} h^{-1}). St.I is significantly different from the others (p<0.05) (Table V.I). Bottom water oxygen concentrations were slightly below or close to saturation levels most of the time.

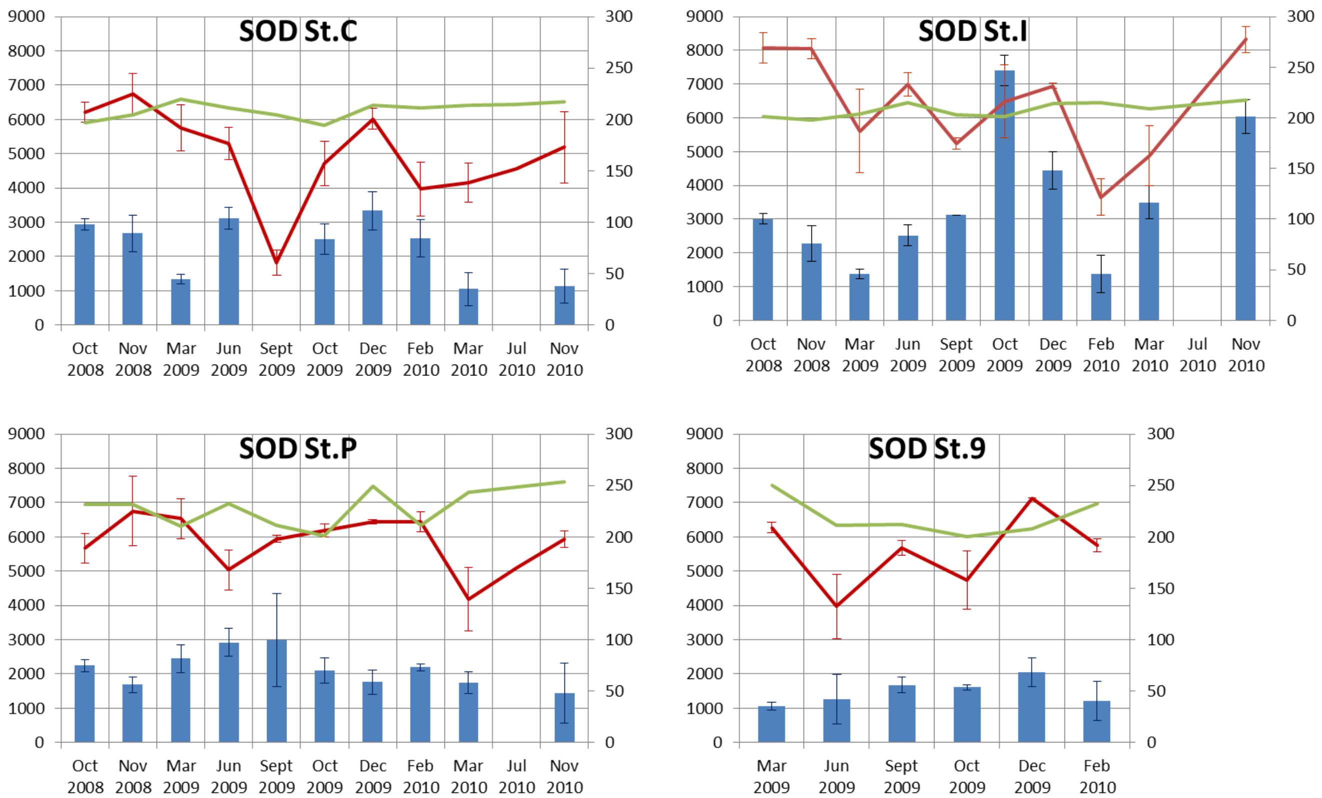

Figure V.6 SOD (in µmol m^{-2} h^{-1}, left scale) during the different periods at stations C, I, P and St.9 and corresponding oxygen contents in bottom waters (red compared to green at 100 % saturation, both expressed in µM right scale). Bars represent S.E. of replicate measurements (4 for fluxes and 8 for concentrations).

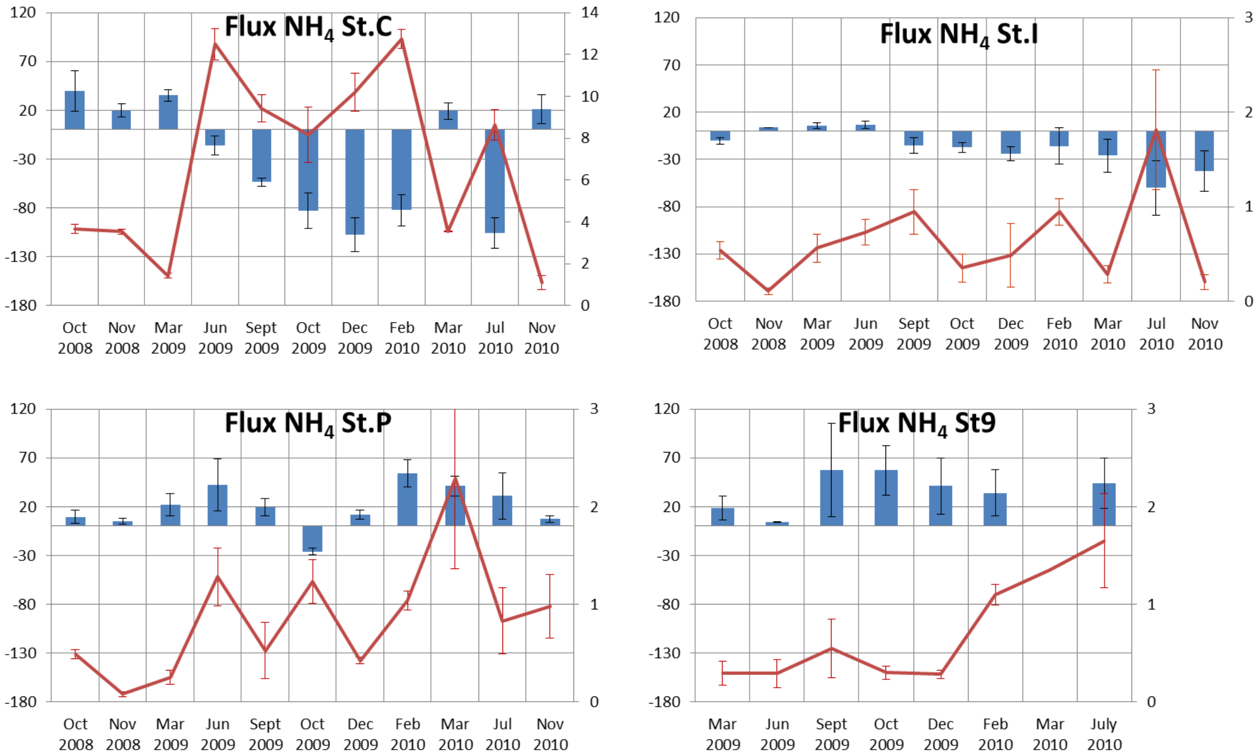

Figure V.7 Ammonium fluxes (in µmol m^{-2} h^{-1}, left scale) during the different periods at stations C, I, P and St.9 and corresponding NH_4 contents in bottom waters (red, right scale: 0-14 µM for St.C and 0-3 µM for the other stations). Bars represent S.E. of replicate measurements (4 for fluxes and 8 for concentrations).

Ammonium fluxes varied both between sampling periods and stations (Figure V.7). St.I is characterized by an influx of NH_4 whereas St.9 showed an efflux from the sediment. The consequence is a significant difference between mean ammonia fluxes ($p<0.05$). At St.C, the first period is characterized by an efflux while the 2009 period showed an influx. During that period the concentrations of NH_4 in bottom waters were high (8-10 µM) compared to the other periods and even stations.

Nitrate + Nitrite fluxes and ammonium fluxes showed high variability in direction and intensity (Figure V.8). Mean fluxes per stations were significantly different ($p<0.001$) and highest effluxes were measured in July 2010 in St.I and St.P. during periods of highest bottom water NO_{2+3} contents.

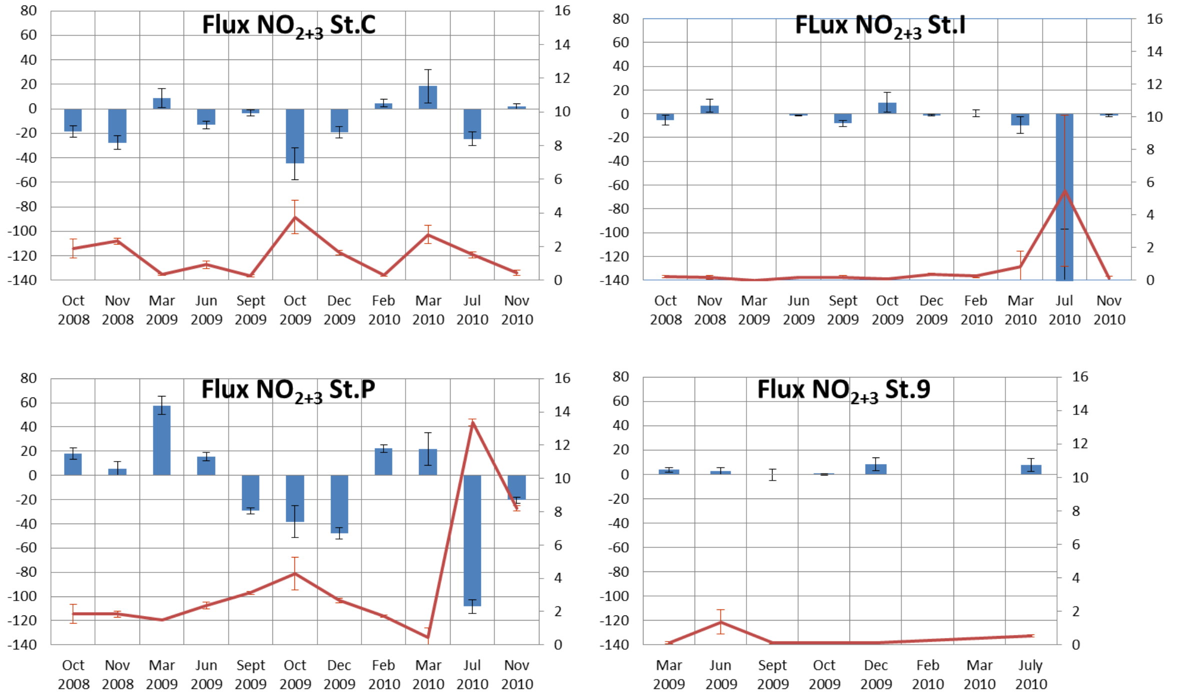

Figure V.8 Nitrate + Nitrite fluxes (in µmol m^{-2} h^{-1}, left scale) during the different periods at stations C, I, P and St.9 and corresponding NO2+3 contents in bottom waters (red, right scale in µM). Bars represent S.E. of replicate measurements (4 for fluxes and 8 for concentrations).

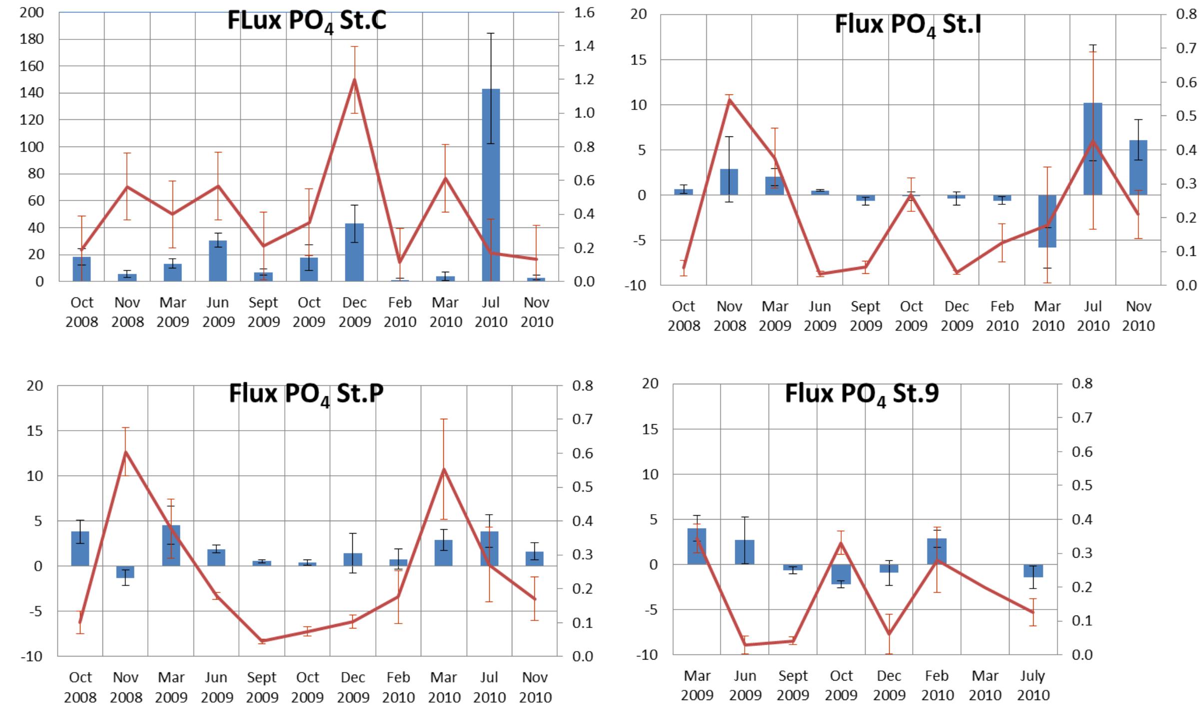

Figure V.9 Phosphate fluxes (in µmol m^{-2} h^{-1}, left scale) during the different periods at stations C, I, P and St.9 and corresponding PO4 contents in bottom waters (red, right scale: 0-1.6 µM for St.C and 0-0.8 µM for the other stations). Bars represent S.E. of replicate measurements (4 for fluxes and 8 for concentrations). (St.C scale for fluxes is ten times higher than the others scales).

Phosphate fluxes and bottom water concentrations (Figure V.9) again showed high variability with around 10 to 40 µmol PO_4 m^{-2} h^{-1} up to 140 for St.C and lower values between -5 and +10 µmol PO_4 m^{-2} h^{-1} for the other stations. Bottom water PO_4 was twice as much higher in St.C as at the other stations.

Silicate fluxes variability (Figure V.10) is less pronounced than the other nutrient fluxes, but there is still a statistically significant difference between stations ($P = 0.029$).

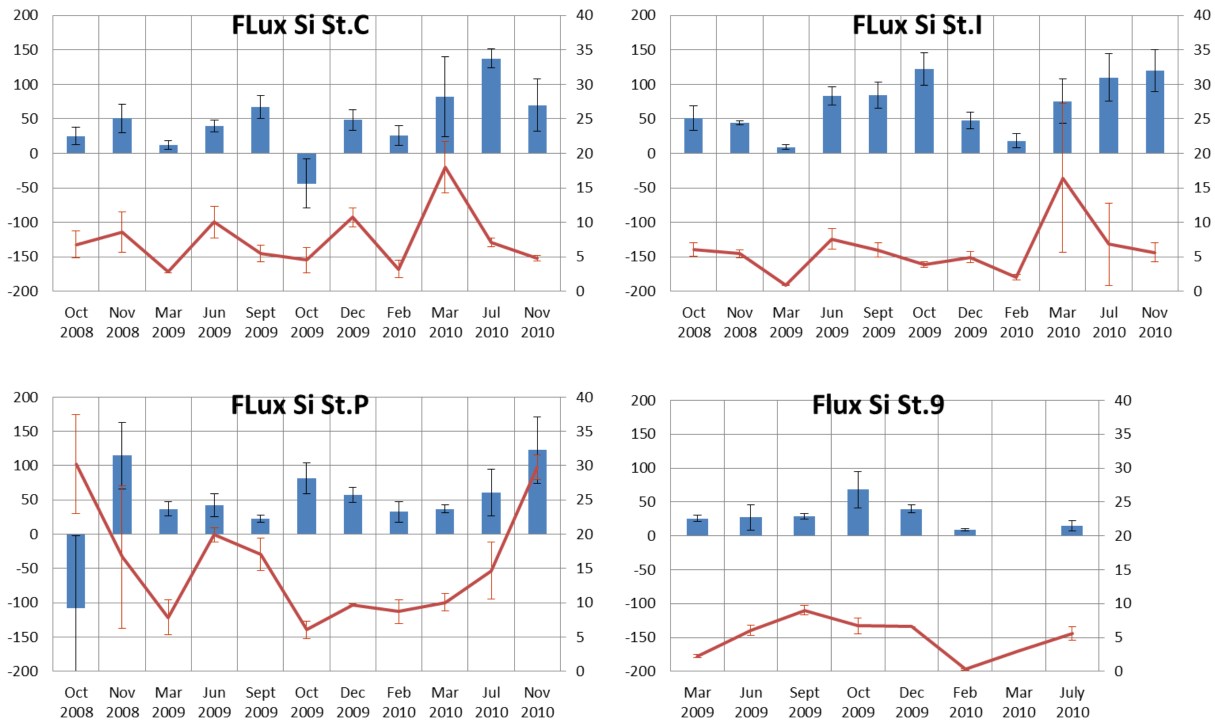

Figure V.10 Silicate fluxes (in µmol m^{-2} h^{-1}, left scale) during the different periods at stations C, I, P and St.9 and corresponding Si(OH)4 contents in bottom waters (red, right scale in µM). Bars represent S.E. of replicate measurements (4 for fluxes and 8 for concentrations).

At two occasions (St.C Oct-2009 and St.P Oct-2008) the fluxes were oriented towards the sediment while in all other instances they were effluxes. Again during that periods, the variability between replicates was high. Bottom water silicates were highest at St.P (around 5 to 30 µM) compared to the other stations (5-15 µM for St.C and St.I, and 0-10 for St.9).

4. Discussion and conclusions

Laguna de Términos is characterized by its diversity of environments ranging from areas continuously impacted by riverine inflows to areas largely influenced by seawater. The goal of this study was to estimate benthic respiration rates and nutrient fluxes in contrasted sites submitted to different degrees of natural and anthopogenic pressure, in order to infer the drivers that control the variability and intensity of the fluxes. Averaged results showed highest SOD at St.I, followed decreasingly by St.C, St.P and St.9.

St.I is characterized by a *Thalassia testudinum* dominated seagrass meadow and these systems are known to show enhanced mineralization rates due to increased carbon input under the seagrass canopy (Gacia et al. 2002) and an intensification of the mineralization processes related to enhanced bacterial activity (Moriarty et al. 1990). Eelgrasses export high amounts of organic carbon into the sediments through a combination of direct DOC exudation and remineralization of detrital plant material wirthin the seagrass bed (Kaldy et al. 2006). The carbon and nitrogen stable isotopes measured in the sediments of St.I revealed the presence of seagrass detritus mixture as indicated by Marguillier et al. (1997) and Pereira et al. (2010) for other lagoons. Moreover, we observed black (reduced) sediments with numerous micro zones, which released a strong odour of hydrogen sulphides. High levels of sulphide may in fact be found in St.I because of low iron contents in carbonate sediments, which prevent sulphide from binding to iron and subsequently form pyrite, a dominant Fe–S storage compound in marine sediments (Koch and Erskine 2001, Deborde et al. 2008). However, the organic carbon content measured in the same period did not exhibit significant differences between St.I and the other stations; a high temporal variability was instead measured and it could be explained by the seasonal decomposition of seagrass leaf litter (Peduzzi & Herndl 1991) as shown by the relative high $\delta C^{13}$and low δN^{15}isotope ratios. Nitrogen fluxes at St.I were dominated by NH_4 effluxes while NO_{2+3} fluxes were smaller or extremely variable. Ziegler & Benner (1999) showed similar fluxes measured in the dark by means of chambers placed over un-vegetated sediments in Laguna Madre (southernmost estuary located on the Texas coast). Negative NH_4 fluxes could be related to gradient driven diffusion when overlying water content is high compared to interstitial concentrations. In our case, low ammonium contents were measured in the bottom waters at St.I. As the presence of sulphide is known to inhibit both nitrification and denitrification (Dedieu et al 2007), the ammonium influx cannot be directly related to bacterial mediated consumption. Some studies suggested that manganese oxides could consume the potential pool of available NH_4 (Luther et al. 1997, Anschutz et al. 2000). Seagrasses decomposition is a faster process compared to mangrove litter remineralization, due to their low fibre content and the high nutrient contents lead to high mineralization rates producing nutrients in excess (Eyre et al. 2010).

Fluxes of PO_4 were highly variable but positive when detectable. The PO_4 efflux was similar to fluxes measured in Arcachon bay in a *Zostera noltii* meadow. This was related to an oxic layer thickness drop and release of PO_4 from the DIP pool and during the seasonal decay period of *Z. noltii* biomass (Deborde et al. 2008). Desorption from iron oxides associated with more reduced conditions are known to enhance PO_4 effluxes (Conley et al. 2002, Tucker et al. 2014, Khalil & Rifaat 2013). Silicate efflux was highest at station I compared to the other stations and showed temporal variability independent of bottom water Si content.

SOD at St.C and St.P behaves similarly and contributed probably to the undersaturation in bottom water oxygen. SOD of about 2200 µmol m^{-2} h^{-1} are still high compared to other temperate and tropical systems (Origel et al., submitted). Sediments from both sites have distinct sources of OM as shown by the isotope data. The content and range of sediment OrgC and N were higher for St.C than for St.P. Fluxes of NH_4 in St.C were negative when ammonia concentration in bottom water were high which underlines the probable high contribution of gradient driven processes. In St.P the bottom water concentrations in NH_4 are lower and the mean flux always oriented towards the water column. PO_4 effluxes in St.C are higher than in the other stations around 26 µmol m^{-2} h^{-1} (up to 140 in July 2010) compared to 1-2 µmol m^{-2} h^{-1}. Bottom water PO_4 in St.C is twice the phosphate content measured at the other stations, underlining, as for NH_4, the impact of the main city on local nutrient budgets probably related to non-point sources of wastewater discharges. Silicate fluxes for St.C and St.P are similar and comparable to St.I. Compared to St.9 all fluxes were largely enhanced even if the organic load in the sediments of this station was not significantly different.

Table V.2 Mean oxygen and nutrient fluxes (± S.E.) measured at each station (data in µmol m-2 h-1).

Station	SOD	NH_4	NO_{2+3}	DIN	PO_4	Si
C	2294±367	-28±12	-11±6	-44±26	26±8	47±22
I	3187±569	-18±11	-14±7	-20±21	1±2	70±18
P	2155±457	20±11	-9±11	10±21	2±1	45±29
St.9	1479±355	37±24	4±3	35±26	1±1	42±10

The results present differences between stations under contrasted influences (Table V.2). The 2 years survey covered different climatic situations from dry to wet periods including a special signal during El Nino related dryness in 2009. Benthic metabolism in the seagrass dominated ecosystem showed a clear difference since SOD was twice as high as that measured for the rest of the lagoon, underlining the complex but active mechanism of organic carbon remineralization process. Urban influence was highlighted through higher nutrient loads in the water column, proportional high SOC and DIN influxes. DIP was released by the sediment at a high rate, which underline active mineralization processes and/or release of Fe-bound DIP from anoxic layers in the sediment. River influenced stations, in our case submitted to low salinities (< 4), and showed highest silicate contents in the water column and DIN release exclusively attributable to ammonia effluxes. These results showed the complexity of the processes involved in benthic metabolism even in a system where temperature plays a minor role compared to temperate systems.

Acknowledgments

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Experience is the name that
everyone gives to their mistakes.

Oscar Wilde

Chapitre VI.

Sediment nitrogen recycling in a large and shallow tropical lagoon (Campeche, Gulf of Mexico).

Montserrat Origel Moreno [1], Christian Grenz [1], Karline Sotaert[3], Lionel Denis[2], Renaud Fichez[1].

Sediment nitrogen recycling in a large and shallow tropical lagoon (Campeche, Gulf of Mexico).

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1. Introduction

Estuarine sediments play a significant role in the transformations of nitrogen compounds in coastal systems (Fenchel and Blackburn, 1979; Sloth et al., 1995). Moreover, a significant amount of the dissolved inorganic nitrogen (DIN) required to support benthic and pelagic primary production in these systems, is regenerated by decomposition of organic matter within sediments and recycled to the overlying water (Nixon 1981). Effluxes of $NH4^+$ from sediments following ammonification have been implicated as a cause of elevated $NH4^+$ concentrations on continental shelves (Whitledge et al. 1986, Rowe and Phoel 1992). Denitrification and anammox are the major microbial processes removing fixed N from the sediments through the production of dinitrogen gas (N_2). During denitrification, nitrate (NO_3^-) is reduced to nitrite (NO_2^-), nitric oxide (NO) and nitrous oxide (N_2O), before eventually being converted to N_2. Anammox directly removes fixed N and couples NO_2^- reduction with ammonium (NH_4^+) oxidation to produce N_2 (Emerson & Hedges 2003). Denitrification and anammox are important for the removal of N from natural system such as tropical mangroves (Fernandes et al. 2012), intertidal flats (Nicholls and Trimmer 2009), marsh sediments (Koop-Jakobsen and Giblin 2009), and sediments from the continental shelf and slope (Trimmer and Nicholls 2009; Horak et al. 2013).

The overall regulation of this ammonification-nitrification-denitrification pathway is relatively complex, due to the involvement of both aerobic and anaerobic microbial processes and consequently, the relative importance of N_2 as a product depends strongly on the environmental conditions (Castine et al. 2012). The aim of our study is to gain some new insights into N cycling processes related to the mineralization of organic matter in shallow tropical marine systems, in particular where rising N inputs, consecutive to urbanization and increased fertilizer production and use in tropical regions, hampers N proper management.

2. Methodology

Laguna de Terminos has been subjected to intense research and monitoring since mid-1960. Its large extension (around 2000 km^2) and its shallow waters (mean depth 4 m) are richly endowed with seagrass beds, oyster reefs and mangrove wetlands. Considering the hydrologic characteristics, the lagoon can be separated in two areas; the western part, well-mixed portion of the lagoon receiving the bulk of the river flow, with muddy sediment and low salinity, productive, and, the central- eastern part of the lagoon which is very shallow with greater abundance of calcareous sediment (Bach et al. 2005). The seasonal variation of fresh water inflows to the lagoon depends mainly on precipitation events generated during the alternating of wet and dry periods: the first dry season from March to May, the rainy season from June to September, and the second dry season from October to February. This last period is marked by intermittent storms (Bach et al. 2005). A total of 13 stations were visited each time during March 2009 and 2010 (first dry season) and during October 2009 and November 2010 (wet season, Figure VI.1). In order to evaluate the benthic mineralisation rate through the different seasons, sediment oxygen demand (SOD) and nutrient fluxes at the sediment–water interface were measured on intact sediment cores (15 cm diameter, ca. 30 cm sediment depth; 4 per station).Cores were collected from a small boat using a coring device equipped with a core cylinder and a one-way check valve, to preserve core and overlying water integrity (Grenz et al., 2010). Each core was incubated at near *in situ* temperature and in the dark. Sediment–water oxygen and nutrient fluxes were calculated regressing concentrations against time and were corrected for cross-sectional area of the cores (as detailed in Denis and Grenz 2003). Nutrient were analyzed by Auto-Analyzer according to Tréguer & Le Corre (1975) and oxygen by recording mini-electrodes (UNISENSE) calibrated by Winkler titration.

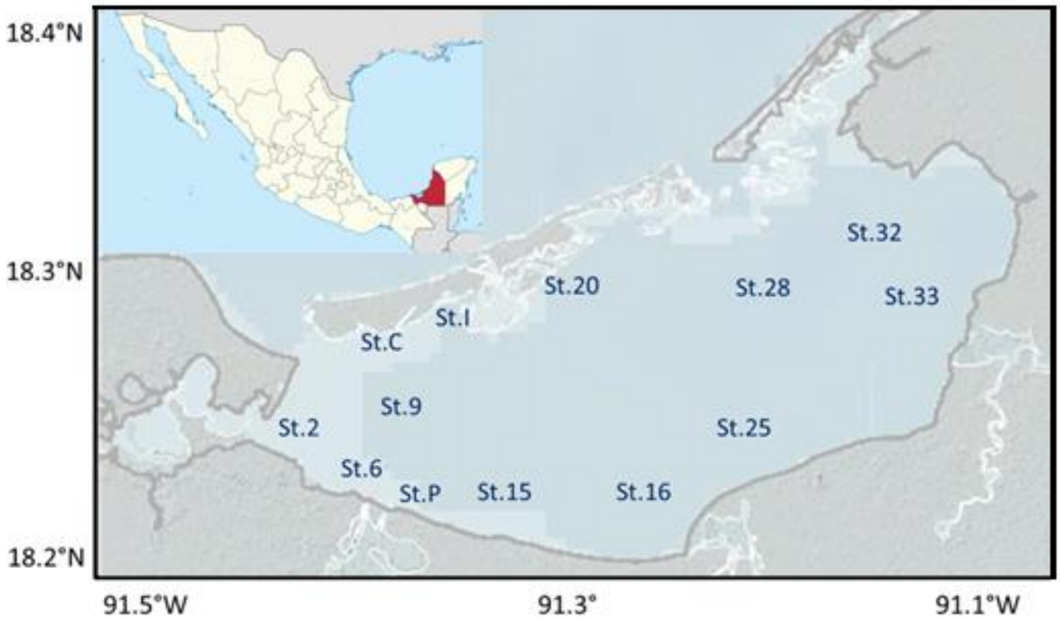

Figure VI.1 Localisation of sampling stations in Laguna de Términos

2.1 Mass balances for oxygen, nitrate and ammonium.

The model is based on the work of Braeckman et al. (2010). Oxygen consumption is linked to mineralization (O2MIN) or to nitrification (NITRIF). The first term comprises oxygen consumed directly for carbon oxidation and oxygen linked indirectly to carbon anoxic mineralisation, by reoxidising reduced substances produced during the anoxic mineralization. There are no assumptions as to how important this last process is compared to total anoxic mineralization. It can be in between 0% (none of the reduced substances reoxidised) or 100 % (all reduced substances reoxidised). In the former case, the O2MIN equals the oxic mineralization; in the latter case O2MIN equals the sum of oxic and anoxic mineralization.

$$\frac{dO2}{dt} = 0 = O2flux - O2MIN - 2(NITRIF)$$

Nitrate is produced during nitrification and consumed by denitrification, DENITRIF:

$$\frac{dNO3}{dt} = 0 = NO3flux + NITRIF - 0.8(DENITRIF)$$

Ammonium is consumed by nitrification and produced by all mineralization processes, proportionally to the NC ratio of the organic matter. The mineralization processes include oxic mineralization, anoxic mineralization and denitrification. For consistency with the oxygen model, we made a further distinction: the mineralization that also consumes oxygen, O2MIN, the denitrification, DENITRIF, and the part of the anoxic mineralization in which the reduced substances are not reoxidised, but either flux out of the sediment (H_2S, methane, reduced Fe, Mn), or are buried in the sediment, ANOX_escape.

$$\frac{dNH3}{dt} = 0 = NH3flux - NITRIF + (O2MIN + DENITRIF + ANOX\_escape)(NC)$$

Basic assumption is that the changes in ammonium, nitrate and oxygen integrated concentration (dNH3/dt, dNO3/dt, dO2/dt) are sufficiently small, in comparison to the other rates, (O2MIN, DENITRIF, NITRIF) to be negligible and therefore ignored – set to 0.

The unknowns in this equation are NITRIF, O2MIN, DENITRIF and ANOX_escape; the data are the three fluxes, and the NC ratio of the organic matter. In cases where the latter is lacking, Redfield ratio is assumed.

In the model as used by Braeckman et al. (2010), O2MIN is set equal to the sum OxicMin + AnoxicMin, i.e. all reduced substances are reoxidised, and hence ANOX_escape is equal to 0. However, one then obtains a model that cannot be solved, which indicates that not all reduced substances can be reoxidised, given the observed fluxes.

By explicitly accounting for the escape of some reduced substances, solution becomes possible. The caveat is that one then obtains an underdetermined system, with 4 unknowns and 3 observations, i.e. there are an infinite amount of solutions. The indeterminacy is then solved by minimizing ANOX_NoO2, using linear programming. This then gives the *minimal* amount of reduced substances that escape reoxidation that are consistent with the data. The model is solved in R, using the R-package LimSolve (Soetaert et al. 2009)

In cases where the estimated minimum for ANOX_NoO2 equals 0, the new model gives the same result as in Braeckman et al. (2010).

The Minimal total mineralization equals:

$$Min\ (TOTALMIN) = O2MIN + DENITRIF + \min(ANOX_{escape})$$

3. Results

Mean salinity of the bottom waters fluctuated between the two periods, spatially depending on freshwater inputs. An example is shown in figure VI.2: high salinities all over the lagoon but near the river outflows in March 2010 (during the dry season) and low salinities in half of the lagoon on the continental side (< 22) in November 2010 (during the wet season). The only part of the lagoon showing typical seawater values is the area around Puerto Real inlet in the North East.

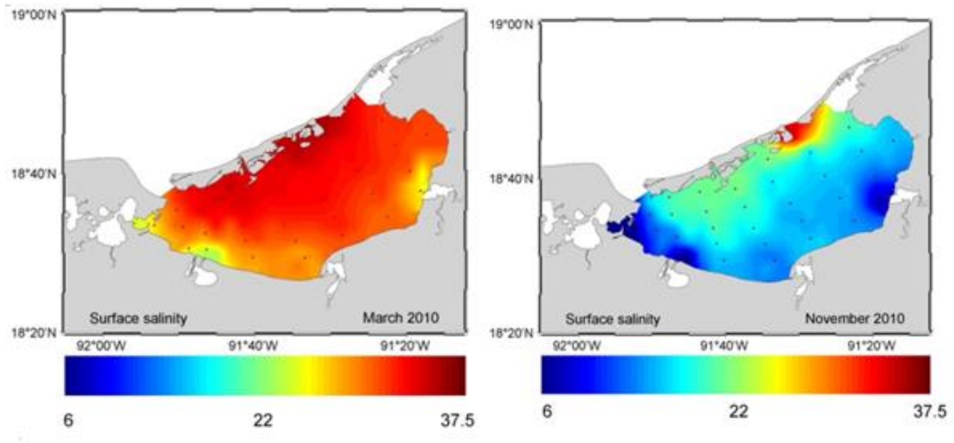

Figure VI.2 Salinity distribution in bottom water from Laguna de Términos during dry (March) and wet (November) seasons in 2010.

Particulate organic matter sediment content in Laguna de Términos were less variable than those of the water column, both for carbon and nitrogen (data not shown). The stations located near the major river outflows and the stations located nearby Puerto Real under marine influence, showed the lowest $\delta^{13}C$ and low C/N ratios. Conversely, sediments from stations poorly influenced by rivers (mixed source) showed higher $\delta^{13}C$ and C/N ratios (Figure VI.3).

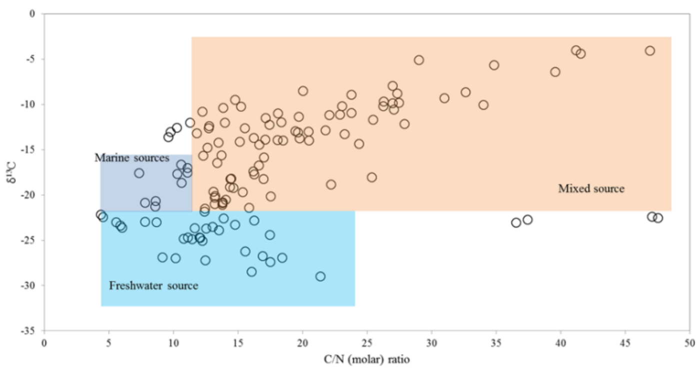

Figure VI.3 δ13C versus C/N (molar) ratio in the sediments considering all values per stations and seasons from March 2009 and 2010 as well as October 2009 and November 2010 samples (grouping based on Lamb et al. (2006)).

The mean SOD within the lagoon was 1775 ± 103µmol m^{-2} h^{-1}, but fluctuated over the sampling periods. October 2009 SOD were highest (2775 ± 239 µmol m^{-2} h^{-1}), 2.5 times than in March 2009 (1101 ± 239 µmol m^{-2} h^{-1}), whereas the SOD in March and November 2010 were mostly the same. NH_4 fluxes ranged from 3 to 28 µmol N m^2 h^{-1}, while NO_3 fluxes varied from -6 to 11 µmol N m^2 h^{-1} and NO_3^-+NO_2^- from -3 to 41 µmol N m^2 h^{-1} (Figure VI.4).

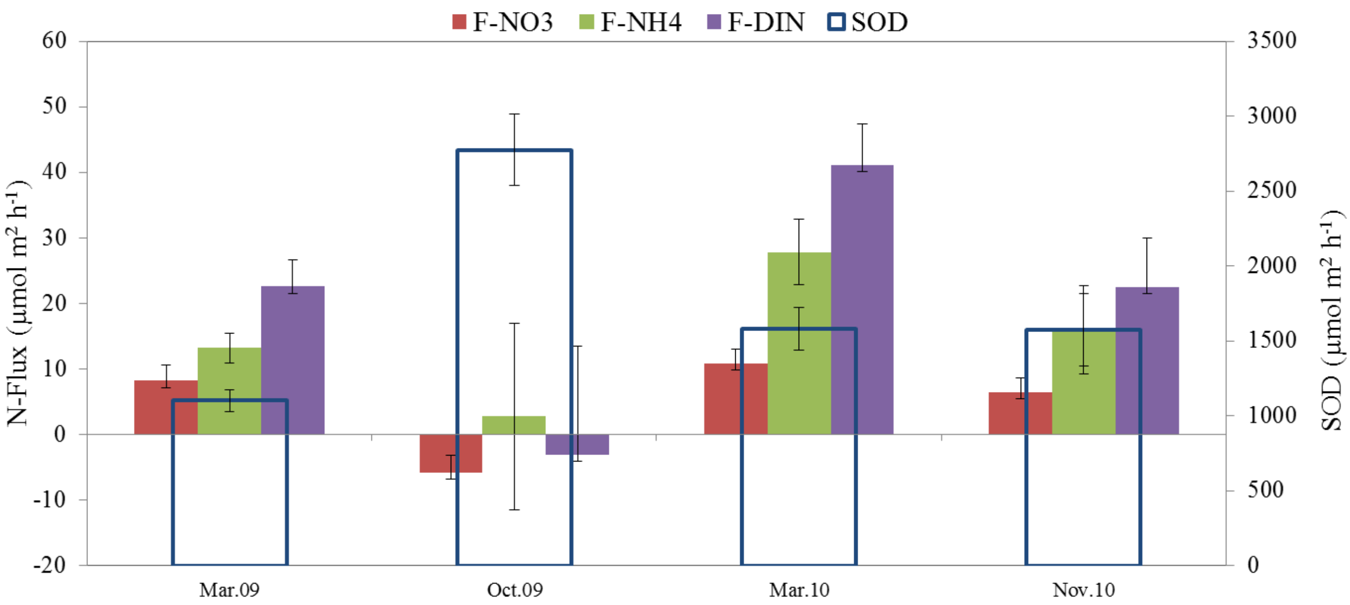

Figure VI.4 Benthic fluxes during the four sampling periods in 2009 and 2010 where empty bars represent SOD and filled bars N fluxes (NH_4, NO_3, DIN).

In October 2009 nitrification and denitrification were twice as high as in the rest of the sampling periods (156 ± 24 and 204 ± 30 µmol m^{-2} h^{-1}, respectively) and the fluxes for NH_4 (2.7 ± 14 µmol m^{-2} h^{-1}) and NO_3 (-5. 8 ± 2.7 µmol m^{-2} h^{-1}), were the lowest creating a DIN flux of$^-$ -3 ± 17 µmol m^{-2} h^{-1}. On the contrary, March 2010 showed the highest fluxes for ammonium (28 ± 5 µmol m^{-2} h^{-1}), for nitrate+nitrite (11 ± 2 µmol m^{-2} h^{-1}) and DIN (41 ± 6 µmol m^{-2} h^{-1}). Considering the mean for the oxygen mineralization estimation (O2MIN.est) of 1550 ± 94 µmol m^{-2} h^{-1} and the mean of the oxic-anoxic mineralization of 330 ± 124 µmol m^{-2} h^{-1}, the total estimated mineralization was 2000 ± 170 µmol m^{-2} h^{-1}) (Figure VI.5).

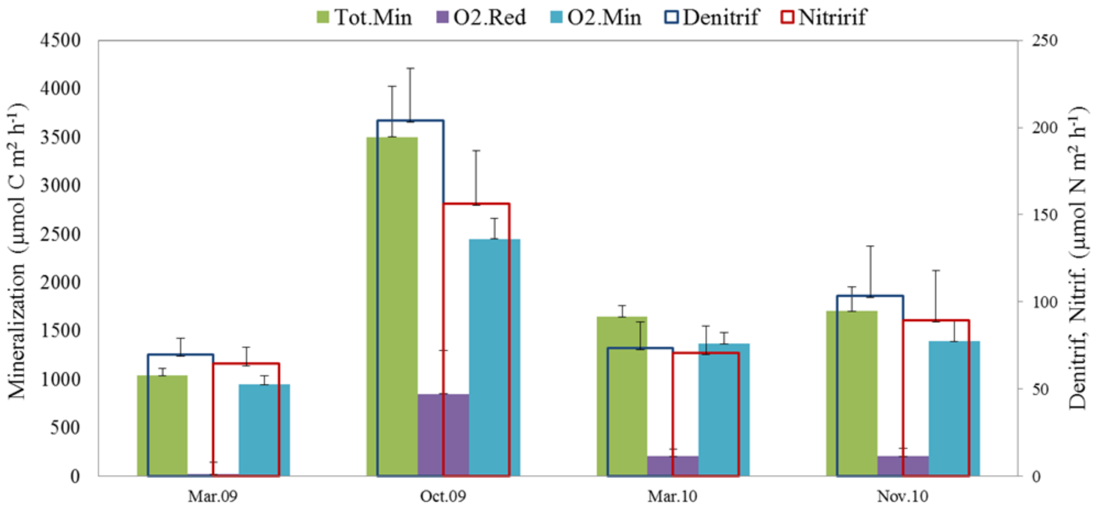

Figure VI.5 Benthic mineralization processes for the four sampling periods during 2009 and 2010, where empty bars represent denitrification (Denitrif.) and nitrification (Nitrif) and, filled bars symbolize the estimation of total mineralization (Tot.Min), the oxic-anoxic mineralization (O2.Red) and the oxic mineralization (O2.Min), all expressed in µmol m^{-2} h^{-1}.

4. Discussion

Benthic nitrogen fluxes can be used as a net measure of the individual processes involved in sediment nitrogen turnover (Herbert 1999). In an estuary, sediment can act as either a nitrogen source or sink (NO_3 in October 20009), depending on many biogeochemical parameters (Burton-Ewans 2005), and denitrification rates in continental shelf sediments are highly variable (Devol et al., 1997; Rysgaard et al., 1998). In Laguna de Términos estimated denitrification rates were high (114 µmol N m^2 h^{-1}) compared to measurements from the Baltic region (42 µmol N m^2 h^{-1}) or the New York Bight (38 µmol N m^2 h^{-1}) (Laursen and Seitzinger, 2002). Similar or higher denitrification rates were foundin St. Leonard Creek (106 µmol N m^2 h^{-1}) or Long Island Sound (125 µmol N m^2 h^{-1}) (Jenkins and Kemp 1984).

Based on the coupling of denitrification and SOD, through Organic Matter (OM) regenerated ammonium oxidation (Laursen and Seitzinger, 2002), we calculated the relationship between denitrification and SOD on our data set (Figure VI.6). We found a significant linear correlation ($r=0.84$, $p < 0.001$) of DENIT = 0.083 * SOD, comparable to the one calculated over various continental shelf regions (DNF=0.105 * SOC, Laursen and Seitzinger, 2002) and slightly higher than the relationship given for Boston Harbour (between 0.04 and 0.09*SOD) by Tucker et al. (2014).

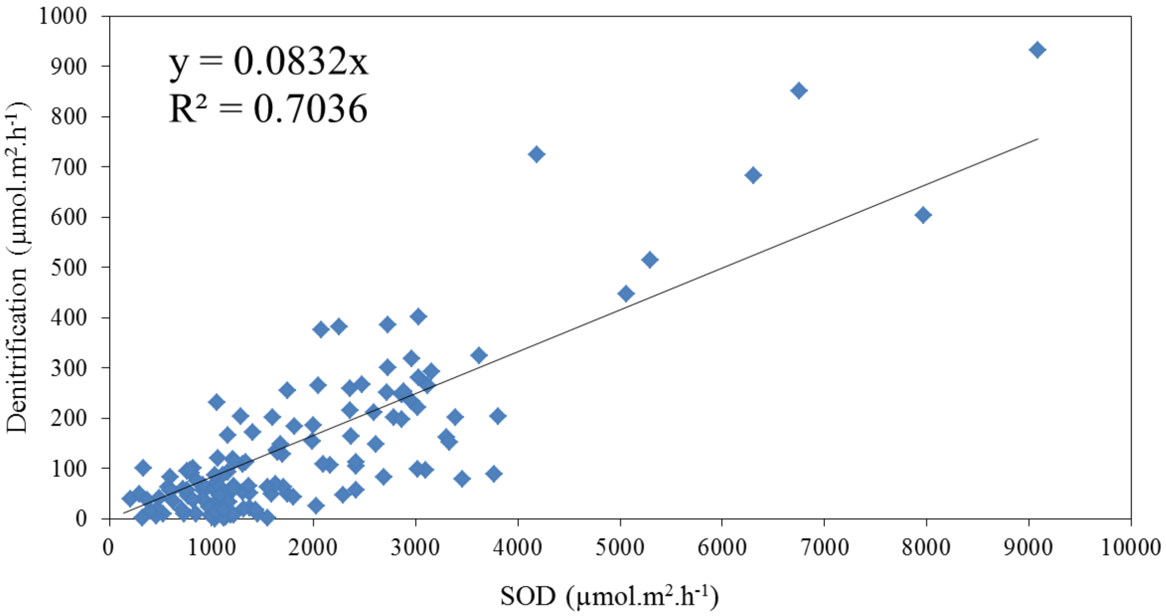

Figure VI.6 Relation between SOD and denitrification coupled with nitrification (data from March 2009 and 2010, October 2009 and November 2010)

Respiratory reduction of nitrate (denitrification) is recognized as the most important process converting biologically available (fixed) nitrogen to N2 (Hulth et al., 2005). Denitrification rates are more important than nitrate reduction to NH_4 (Koike and Sorensen 1988), since nitrate reduction can be broken down into 60% for N_2 production and 40% for NH_4 production and nitrogen loss by denitrification may account for 25 % of total mineralized nitrogen (Billen and Lancelot, 1988; Chapelle 1994, Herbert 1999). Denitrification may be enhanced by the lack of sulfides and mineral sulfide formation, as denitrifying bacteria are inhibited by sulfides and sulfate-reducing activity (Koch and Erskine, 2001). Denitrification has been proposed as a 'natural control' in marine coastal systems that receive large quantities of nitrogen from anthropogenic sources, since it provides a mechanism to remove excess nitrogen and therefore helps controlling the eutrophication rate of these environments (Herbert 1999).

Nitrification rates decrease as a consequence of reduced oxygen penetration into the surface sediment layer, resulting from stimulated respiratory demand. In addition to nitrification, other sediment processes create an oxygen demand, in particular sulfide oxidation and oxidation of other reduced chemical species (Fe_2^+ and Mn_2^+), while nitrifying bacteria consume oxygen and use the ammonium regenerated by organic matter decomposition as a substrate. Thus, SOD is related to nitrification and therefore coupled to denitrification (Laursen and Seitzinger, 2001). The re-oxydation of reduced species takes place at oxic-anoxic interfaces, which separate aerobic from anaerobic processes in virtually all environments (Zhu et al. 2010).

In Laguna de Términos, the oxic mineralization represents 70-90 % of the total mineralization (in October and March 2009, respectively), anoxic mineralization around 2-24 % (March and October 2009), and denitrification only 4 to 6% (Figure VI.7).

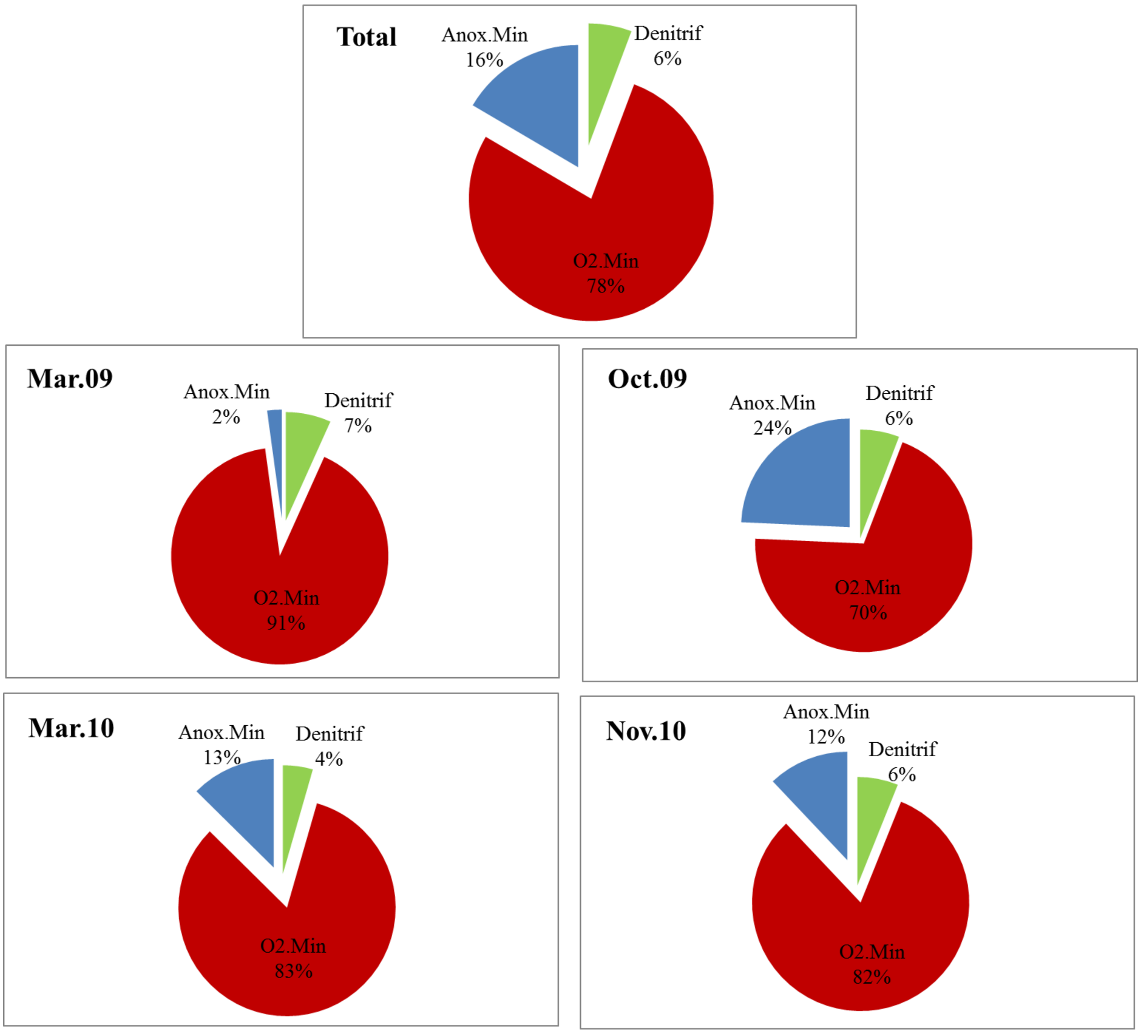

Figure VI.7 Oxygen mineralization (O2.Min), anoxic mineralization (Anox.Min) and denitrification (Denitrif) contribution within Laguna de Términos, considering the mean fluxes (µmol m^{-2} h^{-1}) from the four cores per station (13 stations) during March 2009 and 2010, as well as October 2009 and November 2010.

Benthic microalgae are commonly found in shallow environments acting as filters to control the release of inorganic nitrogen from sediment to water column and they contribute to benthic remineralization (Burton-Ewans 2005, Alongi et al. 2007). Changes in water salinity can play an important role in regulating sediment nitrification (Santoro & Enrich-Prast, 2004). This may explain the particular behavior of October 2009, which showed the highest SOD, mineralization estimation and nitrification-denitrification rates with the lowest DIN efflux, although this period corresponds to rainy season (Fichez et al., in review).

Remineralization increases with the amount of labile organic matter and benthic-pelagic fluxes are dependent on the nutrient concentration in the water column. In Laguna de Términos most of the particulate organic matter sources are a mixture of terrestrial and oceanic carbone. In an organic-rich sediment, the most important factor controlling microbiological activity is probably the availability of oxidants (Vanderborght et al., 2013).

Modelling can be used for understanding the benthic role of nutrient cycling related to biological, physical and chemical processes at the ecosystem level (Lancelot and Billen 1985). The upper layer of the sediment (few cm) hosts most of the remineralization processes, more than the entire overlying water column and it is a hotspot for biogeochemical function (Paraska et al. 2014). Incubation procedures have serious limitations, since pore water advection driven by current flow over rough sediment surfaces (Marinelli et al., 1998) and turbulent mixing of surficial sediments (Gehlen et al., 1995; Lohse et al., 1996) can affect solute mass transfer leading to an underestimation of fluxes within the cores. Nevertheless, our modeling results showed that oxic processes were the main pathways of organic matter mineralisation and that denitrification contributed to less than 10%. We are aware that the assumptions used for the model are not always satisfied, so future direct measurements of denitrification may to be considered as well as the other anoxic processes consuming oxygen, in order to improve these estimations.

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Honest disagreement is often a good sign of progress.

Gandhi

Chapitre VII.

Synthèse et Conclusion

L'objectif de ce travail étant la quantification des flux d'Oxygène et de nutriments à l'interface eau-sédiment de la laguna de Términos, nous avons réalisé un total de 285 incubations individuelles afin d'évaluer la variabilité spatio-temporelle de ces flux au cours de 11 campagnes couvrant la période 2008 – 2010. La période suivante 2011-2012 a permis d'aborder les mesures de production primaire benthique au cours de 3 campagnes supplémentaires sur un réseau de 4 stations (PI Prof. Lionel DENIS Univ Lille1 et Centro de Ciencias de la Atmosfera-UNAM). Faute de temps ces données n'ont pu être intégrées dans le manuscrit. Seules les mesures couplées de flux O2/CO2 à l'obscurité ont été utilisées pour calculer les coefficients respiratoires permettant ainsi d'exprimer la consommation d'O_2 en production de CO_2 lors de la minéralisation.

Néanmoins, les données acquises au cours de ce travail de thèse sont novatrices dans le sens où aucune mesure de ce type n'avait été acquise jusqu'alors avec ce degré de résolution spatiale et temporelle. Nous développerons dans ce chapitre les points essentiels en rapport avec le questionnement annoncé en introduction compte tenu des spécificités de notre site d'étude.

Ces spécificités que nous résumons brièvement ici sont :

- La lagune de Terminos représente un Ecosystème de très faible profondeur (3-4 m), un des plus vastes de la zone des Grands Caraïbes, représentative d'une zone côtière sub-tropicale soumise à des régimes météorologiques caractérisés par des successions de périodes sèches et humides.
- Cette zone estuarienne subit les apports de 3 rivières en particulier le long de son flanc continental, créant des zones saumâtres chargés en particules, contrebalancées par des apports d'eaux marines plus claires pénétrant la lagune par les passes de part et d'autre de l'Isla del Carmen. Les apports de la rivière Palizada représentent environ 90 % des apports d'eau douce de la lagune.
- La partie ouest de la Isla del Carmen abrite la zone urbaine et portuaire de Carmen où se côtoient une population d'environ 150 000 habitants et les industries liées aux exploitations pétrolières du plateau de Campeche. Cette partie est donc sous pression anthropique croissante (Chapitre II).
- Les zones situées sur les rives sud de l'Isla del Carmen ainsi que celle à l'est de la lagune abritent des vastes herbiers dominés par *Thalassia testudinum* implanté sur des fonds de

sédiments carbonatés alors que le centre et les zones sud en sont dépourvus en raison des dessalures intermittentes et des fortes turbidités.

1. *Quel est le niveau de variabilité spatiale et temporelle des taux de minéralisation benthique et les facteurs de contrôle de ces flux dans la Lagune de Términos ?*

Pour tenir compte des différentes situations rencontrées dans la lagune du point de vue des conditions météorologiques et des particularités biogéographiques, notre stratégie a permis de quantifier le niveau de variabilité de la demande en O_2 du sédiment (SOD) et des flux de nutriments au cours des différentes saisons climatiques. La station représentant la zone des herbiers est de loin celle présentant les plus forts taux de minéralisation, surtout lors des saisons des pluies. Cette zone est caractérisée par des consommations significatives de NH_4 et de NO_{2+3} par les sédiments. Ces consommations sont probablement liées aux forts taux de denitrification rencontrés généralement dans ces zones et/ou une consommation directe par les végétaux en raison des faibles concentrations dans la colonne d'eau (Iizumi et al., 1982, Short & McRoy, 1984). La station C, la plus proche de la zone urbanisée de Ciudad del Carmen présente des taux intermédiaires de SOD avec une nouvelle fois de fortes consommations de DIN et un relargage de PO_4 (Figure VII.1). Ceci souligne l'intensité de la reminéralisation de la matière organique et probablement l'existence de processus de désorption des phosphates liés aux hydroxydes de fer. En effet, dans les sédiments le phosphore biodisponible est en partie lié au fer et peut être libéré par réduction des espèces oxydées réactives lorsque le sédiment devient anoxique (Froelich, 1988).

Un point intéressant concerne l'impact de la ville sur les concentrations en ammonium de la colonne d'eau qui sont entre 1 et 7 fois plus fortes à la station C qu'aux autres stations avec une corrélation significative entre flux et concentration négative ($r=0,79$, $p<0,01$, $dl=9$). Dans ce cas, le flux serait contrôlé également pas la concentration de l'ammonium présent dans la colonne d'eau surnageante.

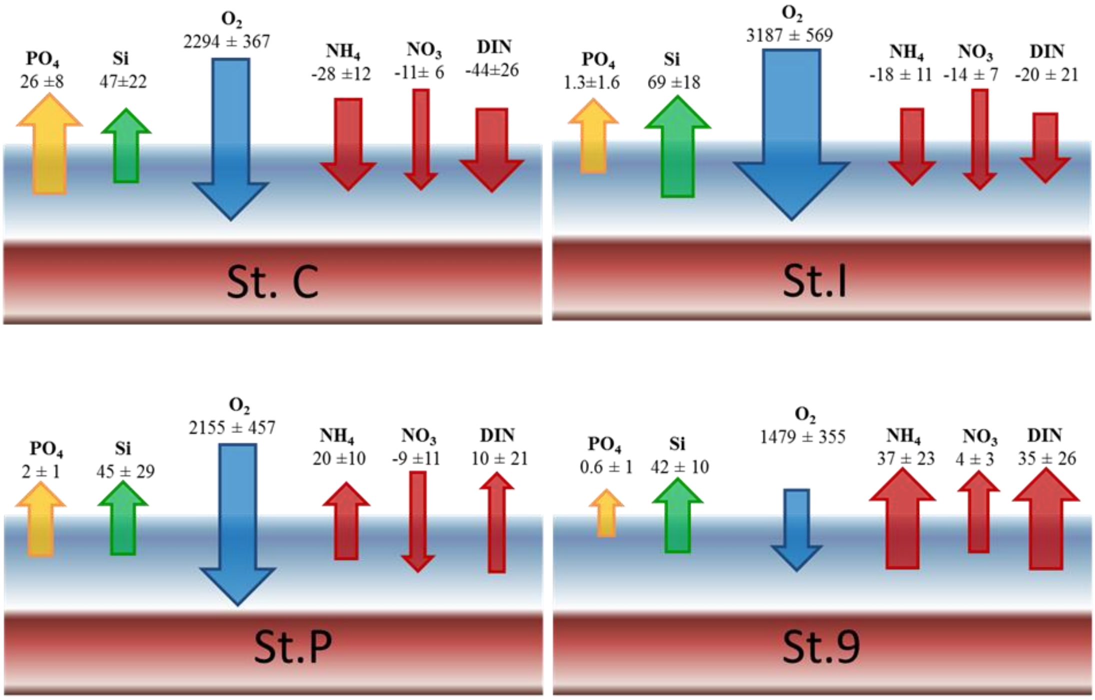

Figure VII.1 Bilan des flux benthiques à l'interface eau-sédiment (µmol m^2 h^{-1}) aux 4 stations de référence visitées entre 2008 et 2010.

De façon plus générale, nous avons pu démontrer que la variabilité saisonnière du métabolisme benthique était supérieure à la variabilité spatiale (Chapitre IV). Les conditions environnementales rencontrées lors des saisons sèches et humides contraignent donc le métabolisme benthique avec des flux significativement plus élevés pendant la saison des pluies, corrélés avec une matière organique des sédiments plus abondante.

2. Sont-ils différents de ceux des systèmes tempérés compte tenu de l'alternance de saisons sèches et humides et du faible gradient thermique ?

Un rapide aperçu des données de la littérature (Chapitre IV, Tableau 4) indique que les flux mesurés font partie des plus forts taux rencontrés en zone estuarienne. En zone tempérée, seuls des sites particuliers comme les zones conchylicoles ou de pisciculture, voire de rivières fortement eutrophisées, toutes caractérisées par de fortes concentrations en matière organique dans les sédiments, présentent des SOD du même ordre que ceux mesurés dans la lagune de Términos.

Les processus biogéochimiques étant limités par la disponibilité de la matière organique et probablement aussi de son état de dégradation, il est intéressant de noter que nous n'avons pas trouvé de corrélation significative entre les flux et le rapport C/N des sédiments (Chapitre IV Tableau 3). Seule la quantité de chlorophylle des sédiments dans les premiers niveaux de sub-surface a montré une augmentation très importante en novembre 2010 pendant la saison humide.

Enfin la température rencontrée dans notre site d'étude (moyenne de 27,7°C sur les deux années de suivi) est largement supérieure à celle rencontrée en zone tempérée et joue probablement un rôle important dans le métabolisme, en raison des conditions thermiques optimales rencontrées pour les processus bactériens.

3. Quel est la contribution de ces flux benthiques dans les bilans biogéochimiques de la lagune et varie-t-elle saisonnièrement ?

Plusieurs calculs ont été effectués à partir des données spatiales afin de comparer les flux par rapports aux apports par les rivières. Comme on pouvait s'y attendre, la contribution des flux benthiques dépasse de loin les apports terrestres pendant la saison sèche (Chapitre IV, Tableau 5). Les flux représentent entre 7 et 16 fois les apports de DIN, entre 50 et 160 fois ceux de PO_4 et entre 3 et 4 fois ceux de $Si(OH)_4$. Pendant la saison humide, les différences sont moins évidentes avec 1 à 4 fois pour $Si(OH)_4$ et 4 à 18 fois les apports de PO_4. Pour l'azote la différence est encore moins importante. Néanmoins, compte tenu de l'étendue de la lagune, ce calcul souligne l'influence des flux de nutriments issu des sédiments dans la dynamique et le recyclage des minéraux. Un calcul similaire a été effectué en comparant en termes de carbone la production primaire pélagique (données de la littérature) avec les productions de CO_2 des sédiments (moyennant un coefficient respiratoire mesuré). Il s'avère que les sédiment minéralise une quantité équivalente à 70 à 140 % du carbone produit dans la colonne d'eau, soulignant une nouvelle fois l'influence prépondérante du métabolisme benthique et probablement des apports de sources allochtones de matière organique venant alimenter les sédiments, surtout pendant la saison humide.

Pour synthétiser les résultats, la figure VII.2 présente les différents flux mesurés (Chapitre IV) et les taux de nitrification et de dénitrification estimés par le modèle des 'bilans de masse' (Chapitre VI). Concernant le modèle, son application dépend d'un certain nombre d'hypothèses qui ne sont pas forcément satisfaites. Mais compte tenu de la corrélation robuste que nous avons pu établir entre la dénitrification simulée et nos SOD, dont la pente est du même ordre que celle trouvée dans la littérature, les résultats nous permettent de tirer quelques leçons sur la variabilité saisonnière et la prédominance de certains processus dans le recyclage biogéochimique.

Une certaine constance semble se dégager dans le fait que la minéralisation oxique représente de loin la voie métabolique privilégiée dans le cycle de la matière et ce, quelle que soit la saison (Figure VI-7). Parallèlement la dénitrification estimée par le modèle fluctue entre 4 et 7 %.

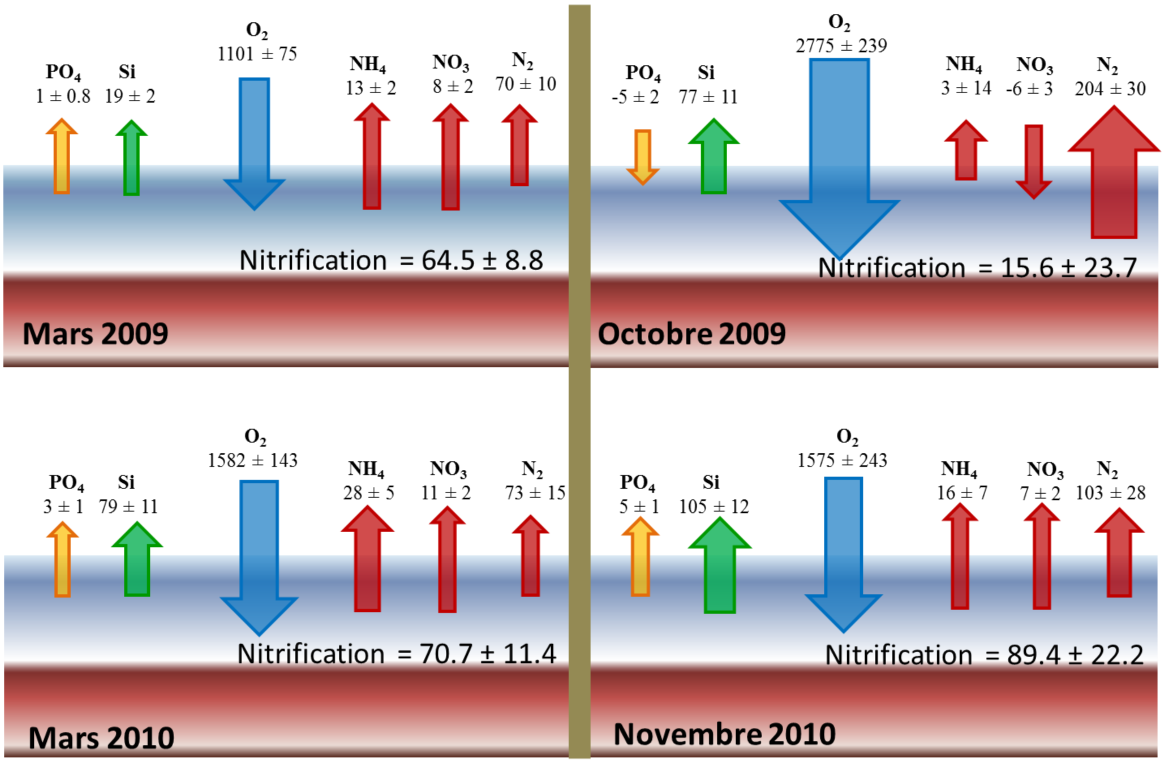

Figure VII-2. Bilan des flux benthiques à l'interface eau-sédiment mesurés aux 13 stations visitées au cours des 4 campagnes saisonnières de 2009 et 2010. Les termes de Nitrification et de dénitrification (N_2) sont issus du modèle (unités : µmol m^2 h^{-1} ± SE).

Un dernier point concerne l'évènement El Nino qui a eu lieu en 2009 et qui vient 'parasiter' quelque peu le signal saisonnier puisque la période d'octobre 2009 ne représente plus réellement une saison humide, comme l'atteste les salinités élevées rencontrées à cette période.

Par contre la matière organique des sédiments n'a pas subi d'impact lié à cet évènement puisque les concentrations en Corg et en N ne sont pas significativement différentes y compris les teneurs en isotopes stables ($\delta^{13}C$ et $\delta^{15}N$). Au stade actuel de nos connaissances, nous ne pouvons définitivement trancher si les variations observées en matière de flux benthiques d'octobre 2009 sont représentative d'une saison des pluies à rapprocher à la période de novembre 2010.

Cet exercice de bilan saisonnier même s'il lisse les fluctuations spatiales, permet de fixer les ordres de grandeur des flux à l'interface eau-sédiment de la lagune de Terminos. Les résultats de ce travail permettront notamment de compléter les exercices de bilan type LOICZ pour tenir compte des échanges d'azote et de phosphore des sédiments de la lagune.

Enfin, un certain nombre de questions reste en suspens et demanderait des travaux supplémentaires notamment pour ce qui concerne les métabolismes anaérobiques qui n'ont pas été abordés dans ce travail. Il s'agit notamment de la sulfato-réduction qui probablement joue un rôle majeur dans la zone des herbiers et des métabolismes azotés qui n'ont que brièvement été abordés par le modèle de 'bilan de masse'.

Les mesures de respiration pélagique effectuées dans les nourrices pendant les incubations avaient pour vocation de corriger éventuellement les biais liés aux remplacements des volumes d'eau prélevés. Des expériences plus ciblées autour de ce processus de minéralisation pélagique devraient être poursuivies afin de comparer les résultats avec le métabolisme benthique.

En raison de l'éclairement et de la faible profondeur de la colonne d'eau, les processus de production primaire benthique, dont quelques mesures ont été effectuées en 4 stations mais non exploitées dans ce travail, requièrent également une attention spéciale pour arriver à un bilan métabolique complet de la lagune.

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C'est lui qui nous a fait découvrir la beauté de notre planète océan, qui nous a amenés à prendre conscience du rôle déterminant de la mer, de son impact sur l'environnement et le climat. C'est lui qui nous a suggéré de modifier nos comportements

Jean-Michel Cousteau

ANNEXE A.

Publications

Origel Moreno M., C.Grenz, K. Sotaert, L.Denis, D. Douillet, R. Fichez. (Soumis). (Spatio-temporal variability in benthic exchanges at the sediment water interface of a shallow tropical coastal lagoon (south coast of Gulf of Mexico).

Origel Moreno M., C.Grenz, K. Sotaert, L.Denis, R. Fichez. (à soumettre). Benthic mineralisation rates in contrasted sites in a shallow tropical lagoon (Campeche, Gulf of Mexico).

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ANNEXE B.

Environmental status of Terminos Lagoon (Mexico): a review and intercomparison with major Gulf of Mexico coastal lagoons.

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

ABSTRACT

Terminos Lagoon, the largest tidal lagoon located at the base of the Yucatán Peninsula, is part of the largest hydrographic river basin in Mexico. The ecosystem is a nutrient rich coastal lagoon approximately 2000 km^2 large connected by two channels to the Gulf of Mexico. Offshore the lagoon, the Bay of Campeche is one of the most important fishery areas in the western central Atlantic region. In parallel, the Cantarell oil field, located on the Campeche bank, is one of the largest oil fields in the world, making Mexico - as a major non-OPEC oil producer - the sixth-largest oil producer in the world in 2006. The economic importance of this ecosystem, exposed to threats related to the petroleum industry, led the Mexican government to designate the lagoon as a federally protected area for flora and fauna in 1994. As a very large and shallow subtropical system potentially exposed to environmental change, Terminos Lagoon is receiving increasing political and scientific attention and there has been a clear need for a

review paper compiling the existing knowledge of this lagoon, a large part of which comes from grey literature in Spanish. This ecosystem was chosen as an example of a subtropical Marine Ecosystem characterized by small temperature fluctuations but with two distinct seasons (dry and wet) which exert control over the biological, geochemical and physical processes and components. Intercomparison with other coastal lagoons in the Gulf of Mexico was undertaken in order to position Terminos Lagoon clearly within a general ecological context.

1. INTRODUCTION

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

Marine ecosystems are highly diverse, considering their biogeographical characteristics on a global scale. While using a classification based on the ratio between the surface and the mean depth of each systems (S:D), three different pools of systems can be described. The first one has S:D ratios in km^2/m from 45,000 to 1000 and includes the oceans and most of the marginal seas. The second is characterized by much smaller ratios from 900 to 100, and the remainder have ratios of less than 100 (Figure 1). As coastal ecosystems, these last two pools are strongly exposed to local anthropogenic impacts that combine with global climate change. Interestingly, most of these ecosystems lie in the subtropical region (Figure 1, box b), where fewer studies have been conducted than in temperate regions. Indeed, a search on ScienceDirect conducted on the 17th of February 2015 over the 1822 to 2014 period, yielded 25,841 articles dealing with “temperate coastal ecosystems” and only 14,665 dealing with “subtropical coastal ecosystems”. The pool of medium S:D ratio systems comprises semi-enclosed coastal systems including open, leaky and choked lagoons (Newton et al., 2014 and references therein) and transitional waters for most of them (EU, 2000). Most of the systems described in Figure B.1 are shallow

(91% less than 10 m depth). Because of the physical proximity of the benthic layer to the majority of the water column, the geochemical and biological dynamics depend extensively on benthic pelagic interactions. Terminos Lagoon in the southern Gulf of Mexico is one of the largest lagoons situated in the subtropical zone and is characterized by a medium S:D of 500 (2000:4), which positions this system in the intermediate pool of lagoons. Due to its ecological importance and potential exposure to environmental change Terminos Lagoon is receiving increasing political and scientific attention. That raised a strong need for a review of existing knowledge of this lagoon, especially as a large part of this knowledge comes from grey literature in Spanish and as Terminos Lagoon represents a major subtropical marine ecosystem study site with seasonal signals distinct from those in temperate regions

The following chapters present an overview of the general features of Terminos Lagoon. These include land-use in watersheds, hydrodynamic characteristics and coastal erosion processes, benthic habitats with special attention paid to seagrass communities, and finally, trophic status and contaminant level. Considering the great variability in the numerous factors that control coastal lagoon environmental status, intercomparison between very diverse sites may be considered as being of debatable scientific pertinence, but we nevertheless tried to compare Terminos Lagoon other major coastal lagoons of the Gulf of Mexico (GoM).

2. GENERAL FEATURES

Terminos Lagoon borders the southern Gulf of Mexico in the state of Campeche and is the second largest estuarine system of Mexico in terms of area and volume. It was recently defined as pertaining to the terrestrial ecological region 15.1 “Gulf of Mexico humid coastal plain and hills”, and corresponding to a typical habitat of “River dominated systems, coastal processes dominated by high freshwater inflow, important estuarine plume, broad coastal wetlands, low to medium salinity variability at yearly time scale” (Yañez-Arancibia et al., 2013). The lagoon borders two geologic provinces: to the east, the Yucatan Peninsula (low rainfall, calcareous soils, and no significant surface drainage) and to the west and south, the lowlands of Tabasco and the highlands of Chiapas and Guatemala, characterized by high rainfall and fluvial soils. Three main rivers discharge into the lagoon and into the Gulf: the Candelaria, the Chumpan, and the Palizada (a tributary of the Grijalva-Usumacinta) with a catchment area amounting to a total of 49 700 km^2.

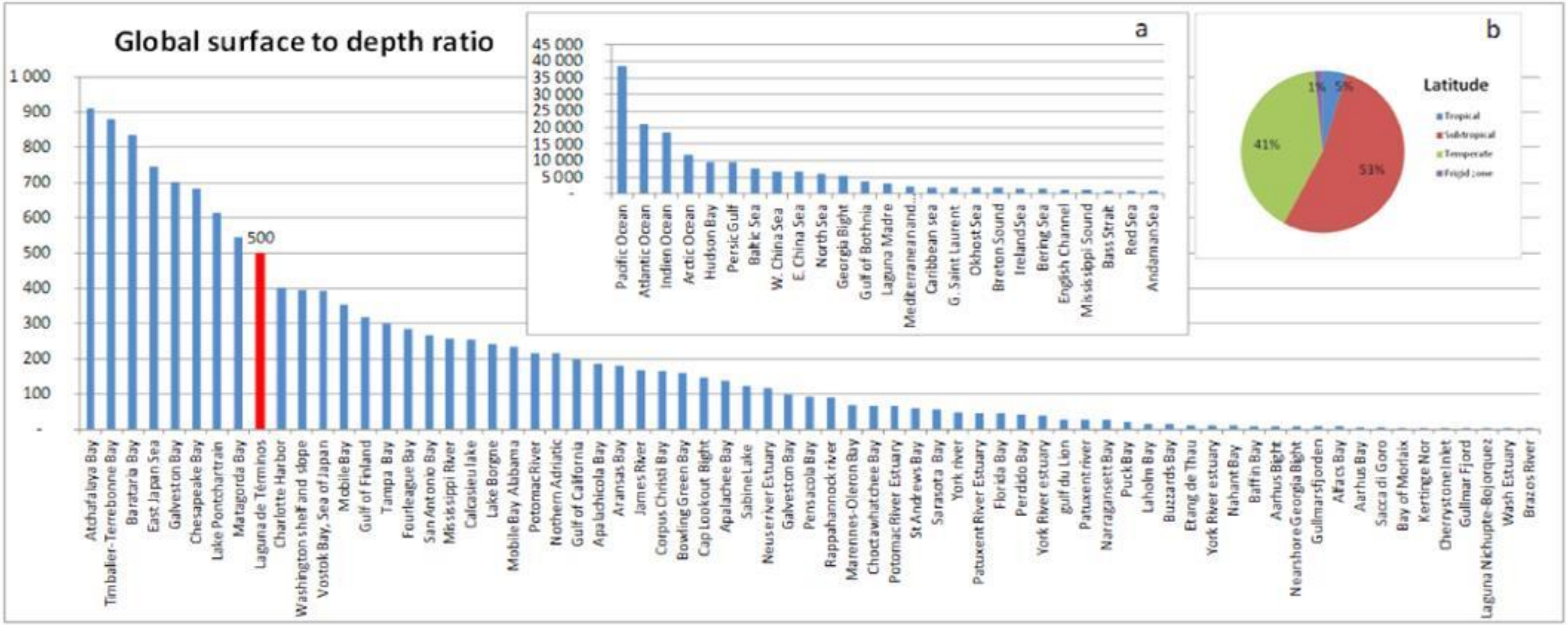

FIGURE B.1| Examples of surface to depth ratios (km^2 : m) calculated for estuaries and bays (main figure) versus ocean and marginal seas (box a) and latitudinal distribution of the systems (box b) - Terminos Lagoon in red (Data compiled from Wikipedia)

The average freshwater flow rate reaches roughly 12 10^9 m^3 yr^{-1}, the Palizada River catchment area in the western coast of the lagoon accounting for most of the fresh water inputs. Satellite images clearly show green plumes of sediment, likely mixed with phytoplankton cells, spilling out of Terminos Lagoon and along the western coast of the Yucatán Peninsula (**Figure B.2**).

FIGURE B.2 | Satellite image of Terminos Lagoon (altitude 650 km NASA)

As a probable consequence, the continental shelf (Campeche Sound) is one of the most important fishery areas in the western central Atlantic region. Campeche Sound (Tabasco/Campeche) contributes 34% of the total Mexican fishery yield in the Gulf and Caribbean coasts, including penaeid shrimp, mollusks, demersal and pelagic fishes (Arenas-Fuentes and Jimenez-Badillo, 2004; CONAPESCA, 2008).

Parallel to fisheries, crude oil extraction in the Gulf of Mexico represents an important economic activity. Since 1938, Petroleros Mexicanos or PEMEX, a major state-owned company and non-OPEC oil producer (top 10) has extracted approximately 2 million barrels per day from the Campeche continental platform (Cantarell oil field). More significantly, earnings from the oil industry (including taxes and direct payments from PEMEX) accounted for about 32% of total government revenues in 2013. Locally, this has generated the urban development of Ciudad del Carmen, the largest town located on the western tip of the island and led to a large degree to the classification of Laguna de Terminos as a Protected Area of

Flora and Fauna (APFFLT) in 1994. Ten years later, the lagoon was listed among the RAMSAR sites and is today the largest in Mexico, measuring 705,016 hectares (www.ramsar.org). Unfortunately, PEMEX operations within the protected area potentially threaten the ecosystem through accidental oil spills and leaking pipelines (e.g. Ixto-1 in 1979-1980).

The vast wetlands surrounding the area is a suitable place for migration and breeding of various species such as sea bass, shellfish, shrimp, manatees and dolphins, among others, and is home to the highest concentration of dolphins in the Gulf. This protected area is one of the most important bird wintering areas in the Gulf of Mexico, and as is the case for most areas with strong gradients in environmental conditions, its level of marine and terrestrial flora and fauna diversity is considered as very high (Yañez-Arancibia and Day., 1988). The coastal fringe is occupied by vast areas of mangroves and the lagoon hosts various habitats including sizeable oyster and seagrass beds (Moore and Wetzel, 1988).

The area presents three climatic seasons; the rainy season (Jun-Sep); the season of Nortes, or winter storms (Nov-Mar), and the dry season (Feb-May). Prevailing winds are from the southeast and strong winds blow from the North and North-East in winter (Yáñez-Arancibia et al., 1983). Average evaporation is 1512 mm yr^{-1} and average rainfall is 1805 mm yr^{-1}, the majority of which falls during the wet season (Yáñez-Arancibia and Day, 1988).

Terminos Lagoon stretches over more than 2000 km^2 (Figure A.3). The lagoon is connected to the sea by two inlets: ‘Carmen Inlet’ on the western side (4 km long) and ‘Puerto Real Inlet’ on the eastern side (3.3 km long). They are separated by Carmen Island, a carbonated sandbar (30 km in length and 2.5 km wide). The system is shallow with an average depth of 3.5 m, with the exception of the tidal flats and a deep channel on the eastern part of each inlet. The eastern entrance is affected by relatively clear marine waters forming an interior delta; the western inlet is affected by the Palizada River with suspended terrigeneous materials, generating high turbidity and contributing to the formation of an exterior delta.

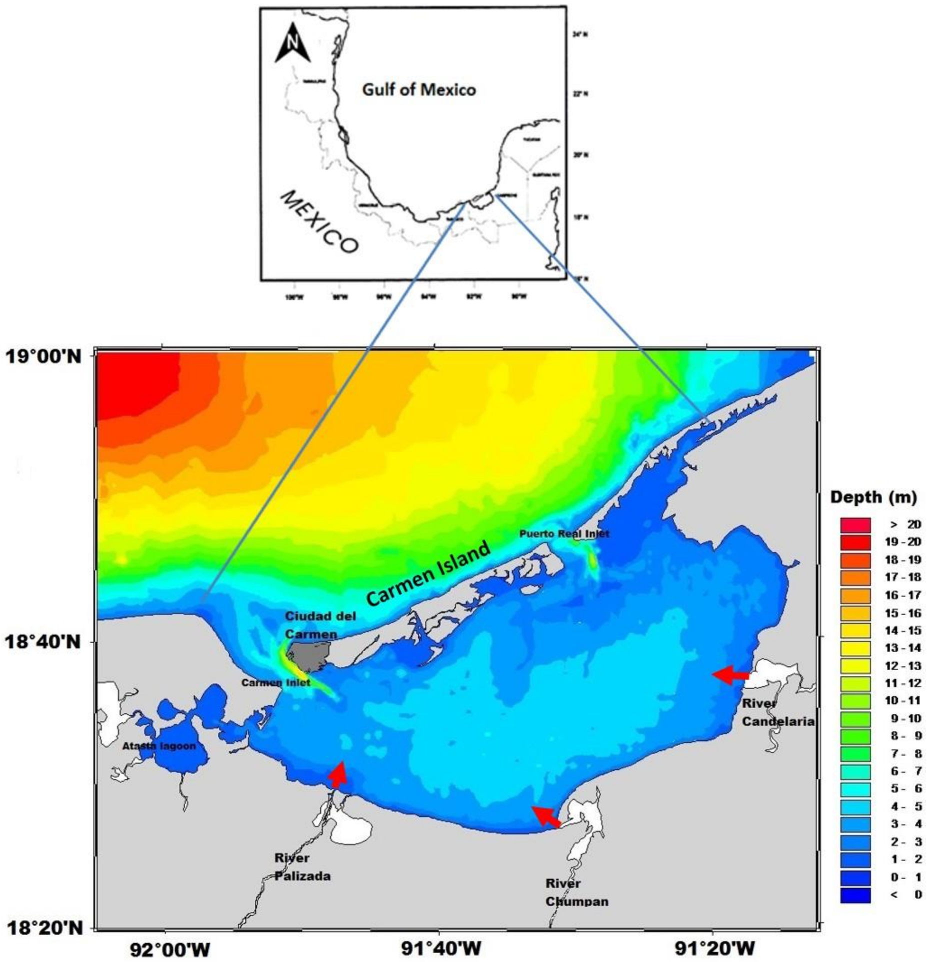

FIGURE B.3 | Depth distribution in Terminos Lagoon and location of the main river outflows (red arrows). Cuidad del Carmen is located at the western tip of Carmen Island (dark grey).

Fringing vegetation is composed mainly of brackish to freshwater mangroves, with the exception of the leeward side of the barrier island, which is essentially fringed by marine mangroves. Predominant sediments are silt and clay; only calcareous sands (shells and shell fragments) are present in the eastern part and close to the barrier island. The sediments of the western part are silty-clay (Yáñez-Arancibia et al., 1983). All these characteristics enable the definition of different subsystems or lagoon-estuarine habitats structuring highly complex nektonic communities as a function of diversity, distribution, abundance, trophic webs and biological strategies developed in connection with Campeche Sound (Yáñez-Arancibia et al., 1983; Sánchez, 1997; Sánchez and Raz-Guzman, 1997). Satellite image analysis has shown that changes in land cover in the region since the mid-70s include extensive loss of tropical forest and mangroves, while urban areas and induced grassland have increased considerably

(Challenger, 1998; Estrada and Coates-Estrada, 1995). According to the SEMARNAT (2002) report on the Environment in Mexico, there was a net loss of 7,119,300 hectares of jungle and 2,432,100 hectares of forest during the 1976 to 2000 period. According to Velázquez et al. (2001), more than half of the ecosystem area showed changes in its original land cover, and a third of it was deteriorated. The main causes of deforestation were both the increase in grassland and the growth of urban areas. Deforestation was, however, attenuated by natural reforestation and plant canopy recovery. Studies of coastal dynamics carried out in the littoral zone of Ciudad del Carmen (Márquez-García, 2010) showed strong erosion processes in the littoral zone along Carmen island and the Atasta Peninsula. According to different studies performed in the state of Campeche, erosion rates averaged 7 m yr^{-1} in the littoral zone (Ortiz-Pérez, 1992). In some sectors of the littoral, coastal erosion has reached considerable rates such as, for example, 19 m yr^{-1} along the Atasta Peninsula. This erosion is mainly related to long-term factors such as terrigeneous sediment inputs, sea level rise, waves and currents, which are all amplified during occasional extreme events such as hurricanes and north winds. Indeed, the fluvial-lagoon systems of Terminos Lagoon are disturbed, and according to EPOMEX (2002), the zones that encounter the most change are the river-mouths of the three main rivers (the Palizada, Chumpan and Candelaria) due to excessive inputs of terrigeneous materials and growth of oyster reefs. A study by Yañez-Correa (1963) comparing the sediment structures of both inlets showed that sediment accumulation outside Carmen Inlet in the west contributed to the formation of a small alluvial delta outside of the lagoon, due to predominant seaward-oriented currents. Conversely, the presence of a submarine alluvial delta made up of coarse sediment fraction of marine origin stretching inside the lagoon at eastern Puerto Real Inlet, reveals an inward component of the currents. Salinity signatures confirm the general circulation pattern from east to west, with a net westward transport of the water masses entering the lagoon through Puerto Real Inlet and leaving the lagoon by Carmen Inlet. This was shown by Dressler (1981) and Kverfje et al. (1988), especially during the dry season. During the wet period, these same authors described different patterns with a residual circulation leading to an export of water masses out of the lagoon through both inlets (Jensen et al. 1989). Based on tidal current measurements, David and Kjerfve (1998) calculated a mean 50% flushing time of nine days around the inlets, and, depending on seasonal conditions, estimated water residence time for the whole lagoon to range between 1 and 5 months. Tidal effects in conjunction with high freshwater inputs tend to generate a cyclonic circulation inside the lagoon with a vortex core located in the northeast part, while predominant winds from the east tend to push the river flows towards Carmen Inlet

(Contreras Ruiz Esparza et al., 2014). Based on meteorological data from Ciudad del Carmen airport, winds from 45° to 135° are the most frequent (67 %).

2.1 Gulf of Mexico lagoons

Intercomparison with 10 coastal lagoons spread along the GoM coast (Figure B.4) has been based on a multiparameter database provided as additional material. In terms of lagoon morphology, a majority of the considered systems are classified as Barrier Island protected lagoons even though some of them stretch farther inland in the form of margin deltaic basins or buried shelf valleys. Terminos Lagoon, with its open water surface of 1,936 km^2, is one of the largest lagoons in the GoM together with the Mexican Laguna Madre (2,010 km^2). All systems studied are very shallow, with a minimum average depth of 0.7 m in the Mexican Laguna Madre and a maximum average depth of 3.7 m in Lake Pontchartrain. As a direct result of extension and mean depth, Terminos Lagoon, with a volume of 2.4 km^3, ranks second behind Lake Pontchartrain (6.03 km^3). The Alvarado Lagoon system, with a total volume of only 0.19 km^3, ranks last. With a 7 km wide permanent connection to the GoM, Terminos Lagoon significantly interacts with coastal marine waters, as do Tampa Bay and Charlotte Harbor with their 9 km and 5 km large openings, respectively.

FIGURE B.4 | Location of the coastal lagoons used for the intercomparison.

According to the updated Köppen-Geiger classification (Peel et al., 2007), climate is mostly tropical monsoonal (Am) and tropical wet and dry (Aw) along the eastern to central Mexico coast, subtropical dry semiarid (Bsh) close to the USA-Mexico border and mostly humid subtropical (Cfa) along the US coast.

Yearly river discharge is a strong environmental factor driving salinity as well as nutrient inputs. Terminos lagoon, with an average yearly river discharge of 12 km^3 yr^{-1}, ranks second to Galveston Bay (13.7 km^3 yr^{-1}). As a direct function of river discharge versus lagoon volume, Terminos Lagoon displays a lagoon flushing time by river inputs of 141 days. Based on the criteria of size, volume and riverborne water flushing time, Matagorda Bay and Galveston Bay are the two lagoon systems most similar to Terminos Lagoon. Combining the lowest volume with a large yearly river discharge, the Laguna Alvarado system strongly differs from all other lagoons, standing as a river-dominated lagoon with a rapid flushing time of 16 days. At the other end of the spectrum, Corpus Christi Bay, Laguna Madre Tamaulipas, Lower Laguna Madre Texas and Laguna Tamiahua with riverborne water flushing times in the range 500 to 800 days are more typical of tide-dominated systems.

The bibliographic search using the ISI Web of science does not claim to be exhaustive but can be used as a comparative indicator of the level of scientific knowledge available for each site considered. There was a strong discrepancy between sites, ranging as low as 26 and 27 references for the Tamiahua and Alvarado Lagoon systems, respectively, to a maximum of 705 references for Tampa Bay. In Mexico, Terminos ranked first, closely followed by Laguna Madre. In general, the level of knowledge appeared slightly higher in the US, with Galveston Bay and Tampa Bay high publication level being most likely linked to their proximity with major scientific. Similarly, the high level of knowledge pertaining to Terminos Lagoon may be related to the proximity of research institutions (Universidad Nacional Autonoma de México-Instituto de Ciencias del Mar y Limnologia, El Carmen University, University of Campeche-EPOMEX Center).

Despite significant efforts to synthesize information on coastal ecosystem health, some essential information on numerous coastal processes, such as nutrient cycling, primary productivity or hydrodynamic patterns are sparse, or totally lacking (Ortiz-Lozano et al., 2005; Camacho-Ibar and Rivera-Monroy, 2014).

The field of hydrodynamics has been very unevenly represented, despite playing a major role as environmental driver. Terminos Lagoon is one of the rare Mexican sites to benefit from significant investigation in hydrodynamics, including current measurements and 2D and 3D modeling. Hydrodynamic studies have been much more developed in US lagoons, especially in Tampa Bay, Charlotte Harbor and in all Texas lagoons, the latter benefiting from an exemplary state-wide joint initiative to address coastal lagoon hydrodynamics in a coordinated way (Texas Water Development Board).

As a consequence of longshore currents, hurricanes and sea level rise, most lagoons are exposed to coastal and lagoon shoreline erosion, and are thus highly to very highly vulnerable, especially on the seaward side of their protecting barrier islands. Coastal vulnerability assessment showed that the three areas most affected by erosion on the Mexican coast were: (i) the delta complex of the Grijalva-Mexcalapa-Usumacinta and the Laguna de Terminos in the east, (ii) the Laguna Madre system and the delta plain of the Rio Bravo at the Mexico-USA border, and (iii) the mouth of the Rio Papaloapan and Laguna del Alvarado in the central west (Martinez et al, 2014). Along the northwestern Gulf Coast, sand supply is insufficient to sustain shorelines, baylines are experiencing erosion rates that are faster than the late Holocene average, and bay head deltas are at the tipping point of catastrophic retreat (Anderson et al., 2014). Considering that the rate of coastal submergence exceeds the rate of lagoon sediment filling, it is also predicted that the Texan Laguna Madre will maintain its general form and gradually shift landward (Morton et al., 2000).

3. SEAGRASS

Seagrass meadows are known to play a number of important ecological roles in estuarine and shallow-water coastal ecosystems: they enhance primary production and nutrient cycling, stabilize sediments, elevate biodiversity, and provide nursery and feeding grounds for a range of invertebrates and fish. (Fonseca, 1989; Orth et al., 2010; Unsworth and Cullen, 2010; Cullen-Unsworth and Unsworth, 2013). Seagrass meadows account for 15 percent of the ocean's total carbon storage (Duarte et al., 2010; Kennedy et al., 2010). As they have high light requirements and are highly productive, meadows are responsive to environmental changes, especially those that alter water quality, including nutrient and sediment inputs (Koch, 2001). In Terminos

Lagoon, seagrass beds were estimated to cover 229 km^2 (Mas Caussel, 2006), corresponding to 12 % of the open water surface, and their distribution coincided with key environmental factors such as water movement, water clarity and salinity. Seagrasses develop denser meadows along the lagoon shoreline of Isla del Carmen and, in particular, in the delta of Puerto Real where high water clarity and salinity, as well as a high percentage of calcium carbonate in the sediments, occur (Figure B.5, Moore and Wetzel, 1988; Cruz-Ábrego et al., 1994).

The seagrass meadows are dominated by the turtle grass *Thalassia testudinum* and, in lower density, by *Halodule wrightii* and occasionally *Syringodium filiforme* (Yáñez-Arancibia and Day, 1982; Raz-Guzmán and Barba, 2000). *Halodule* grows in the shallowest areas while *Thalassia* extends to depths of 3 m (Ortega, 1995). Day et al. (1982) established a range of 1.8 to 12.7 g DW/m^2 per day of biomass production of *Thalassia* (0.7 to 5.1 g C/m^2 per day) with maximum productivity during the dry season when water clarity peaked (February-May). The area has high crustacean abundance and diversity and serves as a nursery ground for immature stages of penaeid shrimps (Sánchez and Raz-Guzman, 1997). Epifauna associated to the seagrass meadows is abundant and includes epibenthic amphipods and their predators, i.e. crustacean species of Zostera shrimp (*Hippolyte zostericola*) and Pink shrimp (*Farfantepenaeus duorarum*) (Negreiros-Fransozo et al., 1996, Sánchez 1997; Corona et al., 2000).

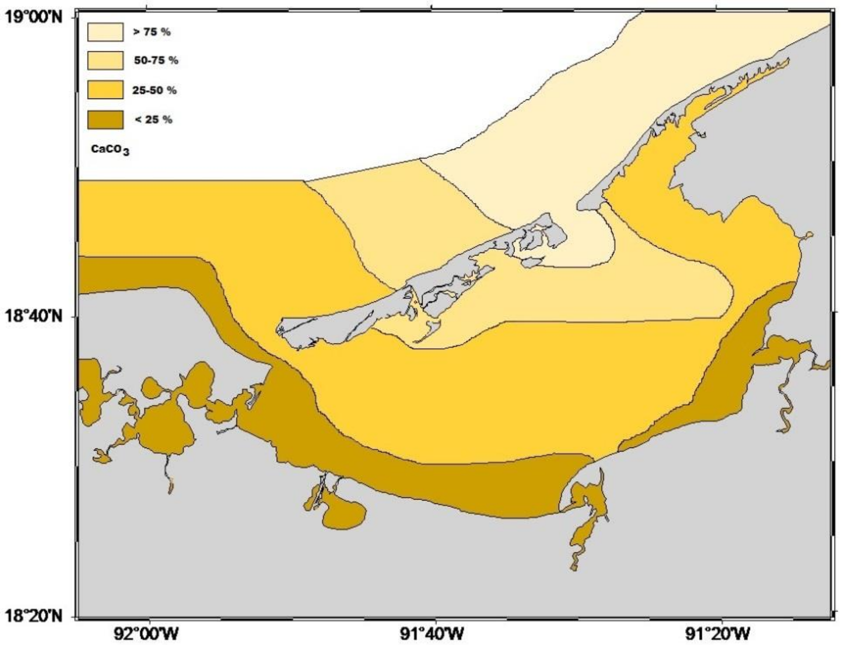

FIGURE B.5 | C 1969)

Terminos Lagoons sea-grass cover compared to those of Laguna Tamiahua and Tampa Bay. Seagrass cover was predictably low in lagoons such as Alvarado and Pontchartrain where oligohaline conditions favored the seasonal development of freshwater benthic algae, but it was also very low in Corpus Christi, Matagorda and Galveston Lagoons as a consequence of direct anthropogenic impacts and watershed mismanagement. High seagrass cover ratios were recorded in the Laguna Madre de Tamaulipas, in Charlotte Harbor and culminated in the Lower Laguna Madre, where seagrass stretched over 52 % of the entire lagoon surface. Additionally, it has been reported that in the northwestern Gulf of Mexico, historically dominant shoal grass (*Halodule wrightii*) cover is decreasing, while manatee grass (*Syringodium filiforme*) and turtle grass (*Thalassia testudinum*) covers are increasing, most likely as a consequence of global climate change (Ray et al., 2014).

4. BENTHO-PELAGIC FAUNA

Several descriptive studies of the benthic compartment were performed in Terminos Lagoon between the 60s and the 80s, dealing for the most part essentially with the taxonomy of a given group. 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 production, probably consecutive to high river runoffs. This distribution is clearly linked to the amount of calcium carbonate in surficial sediments and reflects the circulation in the lagoon. Open-gulf foraminifers were close to Puerto Real Inlet and along the southern side of Isla del Carmen, while lagoon foraminifers occurred close to Ciudad del Carmen Inlet. A mixed fluvial assemblage also occurred in and near the river mouths.

In parallel, Morales (1966) described the ostracods, with up to 39 mainly euryhaline species. Half of them were located in transitional areas from clear waters rich in vegetation to turbid waters. Solis-Wolfowitz (1973) described the ascidians, Núñez (1978) the sponges, while Caso (1979) described the echinoderms. As these groups are mainly marine fauna, they occurred only in those parts of the lagoon characterized as having large and persistent marine influence (i.e. Puerto Real Inlet and the lagoon side of Isla del Carmen). Most sponges were found in association with seagrasses and macroalgae, while epibenthic animals were reported frequently on mangrove roots (Espinoza, 1980).

A total of 60 crustacean species have been identified in Terminos Lagoon (Yañez-Arancibia et al., 2007). Gracia and Soto (1990) described the parameters governing the abundance and distribution of shrimps and Sánchez (1993; 1997) established that densities were about 13 times higher in seagrasses than on unvegetated soft substrata. He also recommended taking into account both spatial (seagrass beds) and temporal (day/night) scales in future analysis. The distribution of decapods was reported in different areas of Terminos Lagoon before publication of a synthesis (Román-Contreras, 1988). Apart from the two communities identified close to the marine inlets, the author identified three subsystems inside the lagoon: 1- the southern part of the lagoon under the influence of river inputs (and associated lagoons), 2- the central part of the lagoon, and 3- the northern area located in the direct vicinity of Isla del Carmen which has marine characteristics. Crustacean species ranged from a maximum of 205 in Charlotte Harbor to a minimum of 36 in Laguna Alvarado System with a separation into two groups: (i) a first group of five lagoons with a range of 115 to 205 crustacean species (Lower Laguna Madre, Matagorda Bay, Galveston Bay, Tampa Bay and Charlotte Harbor) and (ii) a second group of 6 lagoons with a range of 36 to 64 crustacean species (all Mexican lagoons plus Matagorda Bay and Lake Pontchartrain).

Based on current knowledge, the annelids are represented by a total of 190 species (Hernández-Alcántara et al., 2014). Marrón-Aguilar (1975) and more recently Hernández-Alcántara et al. (2014) described the diversity and abundance of polychaetes in the whole lagoon, while Reveles (1984), Ibáñez-Aguirre and Solís-Weiss (1986), and Solís-Weiss and Carreño-Lopez (1986) focused on species associated with beds of *Thalassia testudinum* seagrass, and Hernández-Alcántara and Solís-Weiss (1991) concentrated on *Rhizophora mangle* mangroves. In the seagrass beds and mangroves, polychaetes dominated both in abundance and in species diversity, with up to 73 species found by Cruz-Ábrego et al. (1994). Their distribution was closely linked to the salinity gradient, turbidity and sediment types and three assemblages were identified: a first group was localized in the eastern part of the lagoon and was mainly composed of Spionidae and Cirratulidae. The second group was located in the central part and the south of the lagoon, with Cirratulidae and Lumbrineridae while the third group located close to Isla del Carmen was characterized by Capitellidae and Nereididae. Annelid species composition is unknown for Laguna Alvarado System but ranged from a maximum of 355 species in Corpus Christi to an obviously underestimated minimum of 13 in Laguna Madre Tamaulipas, the latter reflecting a low level of scientific knowledge, especially when compared with Lower Laguna

Madre (242 species). Between 100 and 250 annelid species were identified in the other lagoons, including Terminos Lagoon, with the exception of Laguna Tamiahua (64 species) and Lake Pontchartrain (72 species).

The mollusks have received extensive attention due to the exploitation of two bivalve species, the estuarine clam *Rangia cuneata* and the eastern oyster *Crassostrea virginica*. García-Cubas (1963) described the micro-mollusks of Terminos before publishing a review of all the mollusks encountered in this lagoon (García-Cubas, 1988), amounting to 173 species including 95 gastropods, 74 bivalves, 2 cephalopods and 1 polyplacophora (Yañez-Arancibia et al., 2007). Moreover, several studies have been conducted on commercially exploited bivalves such as the estuarine clam *Rangia cuneata* and the eastern oyster *Crassostrea virginica*, and have mainly concerned their distribution (Ruiz, 1975), the physiology of their reproduction (Rogers-Nieto and García-Cubas, 198la; 1981b) and the behaviour of larval stages (Chávez, 1979). Moreover, the level of contamination in the lagoon has been estimated more recently by using oysters as bioindicators (Norena-Barroso et al., 1999; Rendon-von Osten et al., 2006; 2007; Gold-Bouchot et al., 2007; Benitez et al., 2012). Based on the earlier of these reports, García-Cubas (1988) identified four typical subsystems in Terminos Lagoon: 1- the river dominated western inland part of the lagoon with limited connections to Terminos Lagoon (salinity less than 10 in summer periods) characterized by three bivalve species that make up a commercially significant community (*Rangia flexuosa*, *R. cuneata* and *Polymesoda caroliniana*); 2- the inland lagoons connected to the southwest part of Terminos Lagoon (salinity in the range of 0-15) where naturally occurring reefs of *Crassostrea virginica* and their typically associated communities are found; 3- the central basin of the main lagoon (salinity in the range of 10-36) where eight species of gastropods and nine species of bivalves dominate the mollusk community; and 4- an area of strong marine influence located close to Isla del Carmen (salinity in the range of 28 to 38) where a broad community of eight gastropods and nine bivalves are dominant and mainly associated with *Thalassia testudinum* beds. Maximum mollusk species numbers were reported from Charlotte Harbor and Tampa Bay (359 and 399 species, respectively), a probable consequence of their proximity with the coral reef systems of Florida. Between 114 and 222 species were reported from Laguna de Terminos, Lower Laguna Madre, Matagorda Bay, Corpus Christi Bay and Galveston Bay, with less than 100 species observed in Laguna Madre Tamaulipas, Lake Pontchartrain, Laguna Tamiahua and Laguna Alvarado system.

Extensive studies have been conducted on Terminos Lagoon fishes, yielding a total of 214 identified species, most of which have a direct trophic link with benthic macrofauna (Yañez-Arancibia and Day, 1988), even if only 10% of the species are permanent residents in the lagoon (45% use the lagoon as a nursery, and 45% are occasional visitors). While half of the fishes are classed as primary carnivorous, a quarter are higher carnivorous and the last quarter is composed of herbivorous, detritivorous or omnivorous fishes. A maximal juvenile flow into the lagoon was recorded in September-November, mainly via Puerto Real Inlet. Based on habitat (water column) characteristics, cluster analysis resulted in the identification of five groups of stations. Sosa-Lopez et al. (2005) evidenced changes in the structure of fish communities in Terminos Lagoon, with a re-allocation of biomass from the intermediate trophic level to carnivorous and herbivorous-detritivorous species. The authors attributed these changes to the loss of submerged vegetation (due either to intensive shrimp trawling in the 80s or to pollutants) and to the increased influence of marine conditions in the eastern part of the lagoon (long-term trend). High numbers of fish species were reported from Galveston Bay (278), Laguna de Terminos (214) and Matagorda Bay (201), whereas only 126 to 198 fish species were identified in Corpus Christi Bay, Lake Pontchartrain, Tampa Bay and Charlotte Harbor, and less than 100 species were identified in the Laguna Alvarado system, Laguna Tamiahua, Laguna Madre Tamaulipas and Lower Laguna Madre, with a minimum of 48 species for the latter.

5. BENTHIC METABOLISM

Dissolved and particulate exchanges between sediments and the water column remain poorly documented and most budgets are based on the assumption that the benthic boundary layer is in balance (Gomez-Reyes et al., 1997; David, 1999). Studies of sediment-water exchanges of nutrients remain poorly documented, with the exception of mangrove forest (Rivera-Monroy et al., 1995; Day et al., 1996) or *Thalassia testidinum* seagrass bed (Yañez-Arancibia and Day, 2005) systems.

In a fringe mangrove, sediment and nitrogen exchanges at the sediment-water interface have been estimated using a 12m-long flume stretching from a tidal creek to a basin mangrove forest. Rivera-Monroy et al. (1995) demonstrated that the tidal creek was the main source of ammonium (0.53 g m^{-2} yr^{-1}) and nitrate + nitrite (0.08 g m^{-2} yr^{-1}), while the basin forest was the principal source of total suspended sediments (210 g m^{-2} yr^{-1}). On the contrary, net export of particulate nitrogen occurred from the fringe forest to the tidal creek (0.52 g m^{-2} yr^{-1}), while less particulate nitrogen was exported to the basin forest (0.06 g m^{-2} yr^{-1}). They also demonstrated that the exchanges were highly variable with seasonal weather forcing, as salinity (hence nutrient concentrations) in the creek was influenced by inputs from rainfall and river discharge into the lagoon. Moreover, as the C/N ratio of particulate matter exported during ebb tides was generally higher than particulate matter imported into the forest during flooding, they suggested that there is a greater nitrogen loss during ebb tide, caused by the export of nitrogen deficient detritus from fringe and basin mangroves.

Seagrass beds stretch over an estimated surface of 229 km^2, representing 12 % of the open water lagoon surface. Several studies describing nutrient dynamics have been published concerning the *T. testudinum* seagrass beds located off the inner littoral of Carmen Island (Stevenson et al., 1988; Hopkinson et al., 1988; Kemp et al., 1988). Rates of NH_4 regeneration in sediments of *T. testudinum* beds were ten times higher in surficial sediments (0 to 2 cm) than at depth (18 to 20 cm). Turnover time for ammonium pools in the surface sediments was about one day. Both anaerobic decomposition and denitrification are important biogeochemical processes in Terminos Lagoon seagrass beds, and rates of ammonium regeneration were sufficient to supply >70% of the nitrogen required for seagrass growth in this system (Kemp et al., 1988). Nitrogen fixation rates measured in intact cores showed low rates ranging from 0.8 µmol $N.m^{-2}.d^{-1}$ in February ('Nortes') to 50 µmol $N.m^{-2}.d^{-1}$ in August (rainy season). Separate fixation rates by leaf, root, rhizome, and sediment components measured in small serum bottles suggest that N fixation provides 10 to 40% of the nitrogen demand of the seagrasses. Roots and rhizomes exhibited variable rates of up to 30 nmol N m^{-2} d^{-1}, or greater than 100% of demand (Stevenson et al., 1988). The highest fixation rates occurred just prior to the *T. testudinum* production peak in February (Rojas-Galaviz et al., 1992). Measurements of stocks of organic and inorganic nitrogen in the sediment, water and biota indicate that biotic stocks of 13,320 mmol m^{-2} dominated abiotic stocks of 19 mmol m^{-2} of nitrogen in the Thalassia system, with less than 0.2% of the nitrogen being in the inorganic form (Hopkinson et al., 1988). A large percentage of the total organic nitrogen pool (94%) is contained in dead material (746 versus 12,610 $mmol.m^{-2}$, living and dead material, respectively). Approximately 75% of the inorganic nitrogen and 97% of the organic nitrogen is in the sediments, as opposed to the water column (Hopkinson et al., 1988). Inorganic nitrogen uptake requirements are 7.5, 2.5, and 4.0 mmol $N.m^{-2}.d^{-1}$ for phytoplankton, epiphytes and Thalassia, respectively. The nitrogen turnover times ranged from less than 1 day for inorganic nitrogen in the water column to over 3,000 days for sedimentary organic nitrogen (Hopkinson et al., 1988).

6. WATER COLUMN

An abundance of literature can be found in books, reports or in grey literature written for the most part in Spanish. One of the most extensive synthetic studies published (Yáñez-Arancibia and Day, 1988) provides some insight into the environmental status of Terminos Lagoon and focuses essentially on biological issues. Several gaps concerning sources and distribution of pollutants and nutrients, as well as terrigeneous inputs, sediment flux and primary production have been underlined in a tentative LOICZ budget initiative (Reyes et al., 1997; David, 1999). The attempted budget concluded that Terminos Lagoon was slightly autotrophic on a yearly basis with a net production rate of +0.2 mol C m^{-2} yr^{-1}, even though the authors themselves underlined that such results should be considered with great caution due to the evident gaps in available datasets.

6.1 Salinity

As a semi enclosed lagoon which is subject to significant fresh water inputs, salinity in Terminos Lagoon is strongly variable at spatial and temporal scales as a function of precipitation and subsequent river discharge, sea level changes and wind patterns, as documented in Fuentes-Yaco et al. (2001) and Bach et al. (2005). Lower salinities were generally measured in the vicinity of the Palizada River and to a lesser extent the Atasta Lagoon entrances in the West, with the Candelaria and Chumpan Rivers contributing to a lesser extent to freshwater inputs to the lagoon in the south and the east. Highest salinities in the range of 33 to 37 - hence fairly similar to those of adjacent marine waters - were measured close to the Puerto Real Inlet and, in agreement with the general hydrodynamic pattern, these more marine water bodies tend to travel to the south-west along the coast of the main island.

Temporal variability is driven exclusively by the succession of dry and wet seasons which characterizes the tropical marine climate. Ranges of variability in temperature and solar radiations are lower than in temperate systems where shifts from winter to summer time prevail. As a consequence, Terminos Lagoon behaves like a brackish system during the wet season with salinities lower than 25 and a marine-dominated one during the dry season, with salinities higher than 25 associated with the freshwater inflow (Figure B.6).

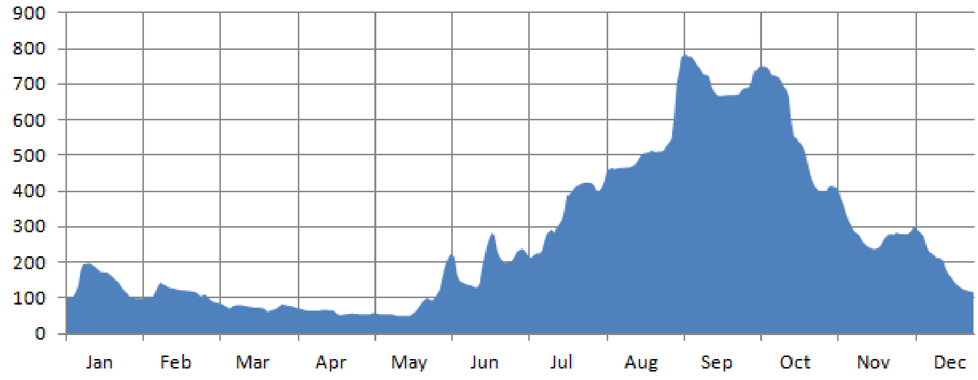

FIGURE B.6 | Freshwater inflow from the Palizada River measured in 2010 (m^3 s^{-1}, data from CONAGUA).

However, results from a recent survey (October 2008 to September 2010) conducted within the framework of the JEST project showed seasonal variability to be significantly impacted by ENSO related drought episodes (Fichez et al., 2010). Average salinity was significantly lower in October 2008 (13.7 ± 5.7) or in September 2010 (17.0 ± 5.4) than it was in September (34.4 ± 2.0) and October (32.6 ± 4.3) 2009 during a significant El Niño Modoki event. Therefore it appears that the salinity in Terminos Lagoon may be influenced by ENSO, a climatic factor that will have to be ascertained in future analysis of temporal data series. Furthermore, the consequences of such drastic changes in salinity evidently reflect changes in hydrologic regimes that most certainly affect trophic status and river-borne inputs to the lagoon. Long- term studies of such impacts are therefore strongly needed to fully understand the environmental sensitivity of the system to global change.

As stated earlier, there have been claims that a significant salinity increase from the 1980-1981 period (mean = 24.67; SD = 7.74) to the 1998-1999 period (mean = 26.8; SD = 8.09) in Terminos Lagoon resulted in a shift in fish population (Ramos-Miranda et al., 2005; Sosa-Lopez et al., 2007). Whereas a shift in salinity might exist on a long-term basis, it is essential to understand the limits of such short-term comparison. As stated above, coastal lagoons in general, and Terminos Lagoon in particular, are characterized by strong spatial and temporal variability. Considering the high level of variability and comparing average salinity between the 1998-1999 period and the 2008-2010 period, it appears difficult to conclude in favor of such a salinity increase, which thus underlines the urgent need to develop long-term monitoring efforts.

Due to their estuarine versus marine polarity and to the various potential sources of interactions (precipitation, evaporation, exchanges with benthic boundary layer and mangroves) GoM coastal lagoon water masses are strongly heterogeneous in space and time. Compiled environmental parameters must hence be interpreted with caution and their use limited to the analysis of global similarities and dissimilarities. Salinity, for example, is regarded as a relatively simple environmental parameter from which a general classification can be derived, but the average values used for this purpose must not veil the strong variability in salinity gradients encountered in coastal lagoons. From available average salinity values, Pontchartrain Lake (average salinity = 4) and the Alvarado Lagoon System (average salinity = 9) classify as oligohaline (below 5) and low mesohaline (5 to 10 range), respectively, whereas Galveston Bay (average salinity = 15.4) and Laguna Tamiahua (average salinity = 18) classify as high mesohaline (10 to 18 range). In the upper range, Laguna Madre Tamaulipas (average salinity = 41) and Lower Laguna Madre (average salinity = 35) classify as hyperhaline (over 30). Terminos Lagoon together with Corpus Christi Bay, Tampa Bay and Charlotte Harbor with average salinity ranging from 25 to 30 classify as polyhaline (18 to 30 range). Temperature also varies seasonally, with a predictable yearly average decrease toward the most northern latitudes, while remaining within the subtropical range. Water transparency is generally low (less than 1 m) with the exception of Charlotte Harbor and Tampa Bay, two sites which are largely open to the ocean, thus allowing for significant inflows of clear marine waters. Despite its temporal and spatial variability, dissolved oxygen is a strong indicator of eutrophication, of either natural or anthropogenic origin, and Terminos Lagoon is the only system where no hypoxic events have yet been reported. Hypoxia events of variable magnitude have been reported from all other sites, representing a major issue for most environmental management agencies.

6.2 Nutrients

Quite surprisingly, the trophic status (dissolved inorganic and organic material and particulate organic material) of Terminos Lagoon has been poorly documented, although the synthetic studies published by Yáñez-Arancibia and Day (1988) do provide some data on nutrients for the lagoon.

Nitrates + nitrites concentrations generally stand 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 and the Atasta Lagoon mouth. Concentrations in the middle lagoon are, in most cases, significantly below

1 µM. Nitrates + nitrites concentrations are higher during the wet season than during the dry season. Considering ammonium, it must be stated that the recent development of micromolar analytical techniques allowing for fluorometric detection (Holmes et al., 1999) demonstrated previous use of spectrophotometric detection (Hansen and Koroleff, 1999) to overestimate concentrations, hence rendering comparison with historical data dubious. Recent applications of this new fluorometric method to determine ammonium concentration in Terminos Lagoon yielded results that strongly diverged from previous results obtained by the older, photometric detection (Fichez, 2010). Results from past studies typically reported values in the range of 1 to 12 µM, whereas those obtained with the new micromolar technique stand within a 0.01 to 3.7 µM range with an average of 0.2 µM, with maximum concentrations being measured essentially in the southwest part of the lagoon close to the Palizada River and Atasta Lagoon system. Considering the clear overestimation of ammonium by the spectrophotometric method, future analysis of this essential nutrient will have to be conducted using the micromolar technique.

Phosphate (orthophosphate) concentrations stand within the 0 to 1 µM range with an average value of 0.13 µM. When averaged over the whole lagoon, dissolved inorganic N:P ratio ranges from 3:1 to 18:1 with an average value of 6:1, thus suggesting that nitrogen is the most probable element to limit pelagic primary production. However, ratios well over the 16:1 Redfield Ratio and as high as 353:1 were occasionally measured, mostly close to the Palizada River and the Atasta Lagoon mouth, demonstrating that such a paradigm must not be applied uniformly to the whole lagoon system.

Silicate concentrations generally correlate with salinity as fresh water transports huge quantities of silica originating from soil leaching. In the Gulf of Mexico, marine offshore waters have silicate concentrations of around 2 µM whereas coastal waters are generally closer to 20-40 µM. Concentrations in the lagoon were around 70 µM on average, with strong temporal and spatial variability, as was observed for salinity.

On average, concentrations in dissolved organic nitrogen and phosphorus were around 15 and 0.6 µM, respectively. Some strong spatial variation could be observed with occasional high concentrations in the northeast part of the lagoon, possibly due to export of organic compounds from the mangrove. On average, concentrations in particulate organic carbon, nitrogen and phosphorus were around 70, 10 and 0.5 µM, respectively.

Nutrient data intercomparison with GoM lagoons must also be considered with great caution due to extreme spatio-temporal variability and technical biases. Nutrient (ammonium, nitrate+nitrite and phosphate) average concentrations generally fell in a very similar 0.2 to 1 µM range for most lagoons, Terminos Lagoon included, with the exception of Charlotte Harbor and Galveston Bay on the lower side and of Lake Pontchartrain and Tampa Bay on the higher side. High nutrient concentrations were also reported from Laguna Tamiahua and Mexican Laguna Madre, but available data were altogether sparse and dated, thus requiring a significant effort in clarifying nutrient levels in these two systems which are considered as environmentally important at the national level. A key point to nutrient intercomparison is that, on a global scale, nitrogen is seen to be the limiting nutrient for primary production in all lagoons, with occasional large-scale phosphorus limitation being reported from Lake Pontchartrain, but only when exceptional Mississippi runoffs were diverted into the Lake.

6.3 Chloropigments and pelagic primary productivity

As a robust indicator of trophic status (Fichez et al. 2005) Chlorophyll a concentrations in Terminos lagoon have been more extensively documented. Concentrations in the Atasta Lagoon averaged 20 µg l^{-1} during the dry season and 3 µg l^{-1} during the wet season (Barreiro-Guemes and Aguirre-Leon, 1999). Average concentration in Terminos Lagoon as reported by various authors ranged between 1 and 10 µg l^{-1}, the lower values generally being measured in Puerto Real and the highest close to the Palizada estuary. Chlorophyll a versus total chloropigment ratios were very regularly recorded as being close to 0.75, demonstrating a relatively healthy population of pelagic primary producers. The few available assessments of net phytoplankton primary production in Terminos Lagoon yielded values of 200 g C m^{-3} yr^{-1} in the open lagoon and 333 to 478 g C m^{-3} yr^{-1} in mangrove channels (Day et al., 1988; Gomez-Reyes et al., 1997; Rivera-Monroy et al., 1998); the former value is thus considered to be the more globally representative of lagoon pelagic primary production.

Average concentration of 3.7 µg l^{-1} in Terminos Lagoon ranked as the lowest reported for all the GoM lagoons considered. Average chlorophyll a concentrations over 10 µg l^{-1} were recorded in the Laguna de Alvarado system, Laguna Tamiahua, Lower Laguna Madre and Corpus Christi Bay.

Phytoplankton primary production data were sparse, and historical data prior to the use of ^{14}C methodology can be judged as strongly biased (Johansson, 2010), thus necessitating once again that comparative approaches be practiced with great caution. Much attention has been given to seagrass primary production even though phytoplankton often account for a large part of open lagoon global primary production (Johansson, 2010), except for very shallow lagoons such as the Lower Laguna Madre where seagrass and macroalgae beds are the main primary producers (Kaldy et al., 2002). Based on the few available data, Terminos Lagoon pelagic primary production of 200 g C m^{-2} yr^{-1} stood within the 100 to 200 g C m^{-2} yr^{-1} range, corresponding to most of the lagoons considered. Tampa Bay and Charlotte Harbor exceeded that range with values of 385 g C m^{-2} yr^{-1} and 258 g C m^{-2} yr^{-1}, whereas the low phytoplankton primary production of 55 g C m^{-2} yr^{-1} in Lower Laguna Madre could be related to the joint impact of shallowness, sea-grass competition and hypersaline conditions. Comparatively, the reported value of 600 g C m^{-2} yr^{-1} for Laguna Madre Tamaulipas (Ibarra-Obando and Contreras-Espinosa, 1997) was considered as strongly overestimated and was not retained. In comparison to reported lagoon phytoplankton primary production, annual carbon production in the offshore Louisiana-Texas (LATEX) continental shelf region averaged 159 g C m^{-2} $year^{1}$ (Chen et al., 2000).

7. TROPHIC STATUS

Using the TRIX index, Herrera-Silveira et al. (2011) classified the trophic status of Terminos Lagoon as Oligotrophic for the eastern part, Mesotrophic for the central part and Meso-eutrophic for the western part. According to Rojas-Galaviz et al. (1992), this system, unlike most temperate estuarine systems, exhibits high levels of primary production throughout the year, maintained by sequential pulses caused by different functional groups of primary producers. While the highest seagrass biomass generally occurs during the dry season when water clarity is highest, phytoplankton primary productivity and chlorophyll-a levels increase through the rainy season (Yanez-Arancibia and Day, 2005). This leads to high food availability and high secondary production, and probably also explains the low risk of hypoxia in Terminos Lagoon related to high replenishment of biological mediated oxygen.

8. POLLUTANTS

Total Polycyclic Aliphatic Hydrocarbons (PAH) concentrations in oyster tissues ranged from 0.7 to 5.7 µg g^{-1} (Gold-Bouchot et al., 2007). The predominance of low and medium molecular weight alkylated compounds over their parent compounds indicated the petrogenic source of these PAHs, thus pointing to offshore oil activities as a source of PAH inputs (Norena Barroso et al., 1999).

Chlorpyrifos was detected in the water at concentrations of up to 72 pg l^{-1} and amongst organochlorine compounds, PCB averaged 1,177 pg l^{-1} and DDT 279 pg l^{-1}, respectively (Carvalho et al., 2009a). Residues of chlorinated compounds were present in sediments and biota, with DDT averaging 190 pg g^{-1} in sediments and 9 ng g^{-1} in oysters (Gold-Bouchot et al., 2007). Concentrations of residues were not considered as having reached an alarming level and were even lower than was reported for other coastal lagoons of the region (Carvalho et al., 2009b).

The Palizada River is by far the major contributor of riverborne metal inputs to Terminos Lagoon (85 % to 99 % depending on the metal considered) (Paez-Osuna et al., 1987). Reported concentrations of total metals were higher in the lagoon waters than in pristine environment waters (Vazquez et al., 1999), but close to concentrations measured in other coastal waters. The authors linked the highest metal concentrations in the lagoon to anthropogenic inputs from rivers, as well as to more diffuse atmospheric input from the proximate petroleum industry, but no direct evidence was provided. Comparisons between metal concentrations in the oyster *Crassostrea virginica* with previous data (Vazquez et al., 1993) showed that whereas zinc concentrations had remained approximately constant since the mid-70s, the levels of cadmium had decreased and concentrations of copper and lead had increased significantly, reaching 0.18 µg g-1 for the latter (Benitez et al., 2012).

Biomonitoring using fixed marine invertebrates such as oysters has been widely used within the framework of the Mussel Watch Program, but some significant gaps remain, especially for Mexican lagoons. Additionally, factors favoring heterogeneity such as spatial distribution, individual variability, contaminant species, and interactions between contaminants result in a rather confused panorama, demonstrating the need for considerable progress to reach an acceptable level of scientific knowledge. Contaminant levels are considered as low to moderate in Terminos Lagoon, with the main contaminants being Polycyclic Aromatic Hydrocarbons (PAH) mainly resulting from petroleum extraction related activities (Gold-Bouchot et al., 1995). Corpus Christi Bay, Galveston Bay and Lake Pontchatrain are more severely exposed to contaminants and, despite a relative paucity of quantitative data, it has been stressed that the Laguna Alvarado System and Laguna Tamiahua are chronically exposed to more specific contamination issues. In Laguna Tamiahua, for example, Cd concentrations exceeded permissible limits for consumption of bivalve mollusks as established by the sanitary regulations, indicating a risk to human health (Lango-Reynoso et al., 2010).

9. MANAGEMENT ISSUES

All four Mexican lagoons are considered as important to very important in terms of national conservation priority and benefit from strong conservation status as national protected areas as well as RAMSAR sites. The situation of the US lagoons considered is much more heterogeneous, with high (Lower Laguna Madre, Tampa Bay and Charlotte Harbor) to low (Matagorda Bay, Corpus Christi Bay, Galveston Bay and Lake Pontchartrain) priority and conservation status levels. In terms of global environmental status, Terminos Lagoon is the only lagoon generally considered as having fair status (García-Ríos et al., 2013) with the very local exception of the small area close to the city of Ciudad del Carmen. All the other lagoons are considered as having moderate to poor environmental status.

In terms of Harmful Algal Blooms (HABs), there have been numerous accounts of *Karenia brevis* red tides all along the Mexican GoM coast, yet no precise reports exist concerning HABs in the coastal lagoons or their deleterious effects on fauna and mankind (Band-Schmidt et al. 2011). On the contrary, HAB events in US coastal lagoons of the GoM, such as *Karenia brevis* red tides all along the coast, *Aureoumbra lagunensis* brown tides in the central and western parts and *Pyrodinium bahamense* red tides in Florida, are much more fully-documented (Magaña et al., 2003; Badylak and Philips, 2008), which casts some doubt on the pertinence of available information in Mexico. Efforts are currently being made to operate a binational GoM-wide HABS monitoring and forecasting system.

All watersheds are severely impacted by upstream anthropogenic impacts due to agriculture, pasture, urban development and river management. Urbanization ranges from very low to moderate around the Mexican lagoons and from very low to very high around the US lagoons with a maximum in Galveston Bay where the total resident human population is estimated at 7.6 M. Finally, and despite some differences due to local specificities, management issues are strongly convergent focusing principally on: (i) climate change with its potential impacts on sea level rise and ensuing coastal erosion and storm surges, (ii) watershed management and subsequent pollutant delivery and changes in river discharge regimes, and (iii) living resources management as a function of the two previous factors combined with human exploitation.

10 CONCLUSIONS AND RECOMMENDATIONS

According to the analysis of national forest inventories for the watershed area surrounding Terminos Lagoon, the rate of change from forests to grazing and agricultural uses is consistent with the period of livestock exploitation of the humid tropics in Mexico since the 1970s (Challenger, 1998). Landscapes surrounding complex lagoons have been significantly modified. Wetlands have lost roughly 13,000 hectares, while forests, which in the 70s represented 49% of the surface area analyzed, had decreased to 33% by 2000. Nonetheless, further studies need to be conducted at larger scales in order to more precisely capture the dimensions and the nature of the changes produced, as well as their effects on the structure and function of the landscape. In addition, it is important to explore the history of land use more thoroughly to better evaluate the causes of changes that have occurred in the area. The regional trend of the past 30 years of replacing forests with pastures calls attention to the need to channel financial resources and materials so as to generate sufficiently detailed information that would permit to focus efforts on sites with greater degradation, to apply conservation policies through paid environmental services, and to strive towards prevention of deforestation in less impacted zones.

According to Márquez-García (2010), about 30% of the lagoon is in the process of sediment deposition to such a degree that the lagoon as a whole faces a major problem of sediment accumulation. The formation of an internal delta at the mouth of Puerto Real leads to the retention of sandy sediments in Terminos Lagoon due to the decrease in current velocity within the system. On the other hand, the processes of erosion-deposition in the lagoon generate changes in the depth of the system and affect the erosive morphology of some parts of the coastal area. This can lead to various problems such as the siltation and death of seagrasses. These changes, localized mainly in the east part of the lagoon, have probably transformed the biogeochemical characteristics of the sediments and impacted the distribution of benthic species and lagoon biodiversity.

The common consensus from models studied is that currents in Terminos Lagoon are primarily wind-driven river flows that are expected to be of a second or lower order of influence upon hydrodynamics (if not upon salinity). Changes in the hydraulics of either inlet would certainly affect lagoon circulation, and hence water quality. Despite the large number of measurements and the numerical models applied to Terminos Lagoon, information is still lacking to correctly determine the residence time of the water masses, a key driving factor to geochemical and biological features.

If several compartments of the benthic ecosystem have been studied, a number of topics have still to be assessed, such as sediment-water exchanges of nutrients and benthic carbon mineralization in the lagoon, as well as processes related to microphytobenthic productivity. Such information may be of prime importance to understanding the functioning of the lagoon and in calculating accurate budgets with the goal of preserving this protected but threatened ecosystem.

Three main points can be extracted from the intercomparison exercise.

1. The literature review on the selected lagoons of the GoM revealed a significant lack of data on some important ecological parameters and processes. Data on phytoplankton primary production are sparse and a large number of the recent publications have focused on the study of specific processes. Furthermore, many of these studies have been based on experimental bio-assays whereas background information on spatial and temporal variability of *in situ* primary production is missing or partial. Due to the emblematic status of seagrass beds, benthic metabolism studies have mainly focused on these communities while sediment oxygen consumption (SOC) studies have been extremely rare, even though bare sediments generally cover most of the surface of the lagoons considered.
2. Every coastal lagoon is unique and it may appear unrealistic to attempt to establish a tight parallel between two such systems. However, it must be said that the most similar system to Terminos Lagoon would be Corpus Christi Bay, in particular when taking in

consideration some major driving factors such as geomorphology, salinity and pelagic primary production.

3. Terminos Lagoon is a major conservation site benefiting from a rare historical record of scientific studies which is currently the object of renewed interest from the scientific community and which, among other noteworthy attention, was selected as a "pilot site" within the framework of the Global Environment Facility (GEF) of the Gulf of Mexico-Large Marine Ecosystem (GoM-LME) Program (Garcia Rios et al., 2013).

The paucity of information on salinity, trophic status and pollutant concentrations in Terminos Lagoon, the apparent relative sensitivity of the system to climatic drivers such as ENSO, and the existence of some methodology issues which weaken the potential interest of historical data comparison make a clear call for the development of a long-term environmental survey strategy.

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Additional material

TABLE 1 | Intercomparison of Gulf of Mexico coastal lagoons based on various environmental parameters. Referenced data sources (Ref column) are provided at the end of the table.

		Laguna de Términos	Laguna Alvarado system	Ref	Laguna Tamiahua	Ref	Laguna Madre Tamaulipas	Ref
General setting	Lagoon morphology	Barrier island lagoon	Differential erosion lagoon protected by an external sand barrier		Barrier island lagoon		Barrier island lagoon	
	Open water surface (km^2)	1,936	85	1	634	9	2,010	9
	Mean depth (m)	2.4	2.2	1	2.0	16	0.7	22
	Volume (km^3)	4.65	0.19		1.27		1.41	
	Connection to the GoM	Permanent large (7 km)	Permanent narrow (0.4 km)		Permanent narrow (0.22 km)		Permanent medium (2 km) + temporary (approx. 5 km)	
	Köppen-Geiger Climate Classification	Tropical wet and dry (Aw)	Tropical wet and dry (Aw) to (Am)		Tropical wet and dry (Aw)		Subtropical Dry Semi-arid (Bsh) to Humid Subtropical (Cfa)	
	Yearly river discharge (km^3 yr-1)	12	4	1	0.74	17	0.90	22
	Lagoon flushing time by river inputs (d) = (Volume : yearly river discharge)*365	141	16		623		571	
	ISI Web of science search (November 2014) Topic « key words » = nb of references	« Terminos Lagoon » = 112	« Alvarado lagoon » = 27		« Tamiahua Lagoon » = 26		« Laguna Madre Mexico » = 87 « Laguna Madre » = 235	
	Hydrodynamics	Measurements and modeling	One recent first study including tidal currents and water level modeling	1	No		No	
	Coastal erosion vulnerability	High to very high seaward (7 to 19 m yr^{-1} erosion on the western side) High on the lagoon shores	High seaward (from slow progradation on the northern and southern sides to fast erosion in the central part) High on the lagoon shores	2	Moderate seaward (progradation on Punta de Cabo Rojo and erosion everywhere else) Moderate on the lagoon shores	2	High seaward Low on the lagoon shores	2
Water mass	Salinity - Average (minimum to maximum)	26.1 (0.3 to 38)	9 (0.1 to 39) Highest salinities in remote Laguna Camaronera	3	18 (14 to 38)	3	41 (33 to 63)	3
	Temperature	29 °C (23 to 33)	29.5 (22 to 33 °C)	3	29.5 °C (23 to 34)	3	26 °C (15 to 28)	3
	Turbidity - Average (minimum to maximum)	Secchi = 0.5 m (0.2 to 4) Turbidity = 7.9 NTU (1 to 24)	Secchi = 0.4 m (0.6 to 0.2) Turbidity = (2.5 to 32 NTU)	4	Secchi = 0.5 m (0.1 to 1)		Secchi = 0.3 m (0.05 to 1)	23
	Dissolved oxygen - Average (minimum to maximum)	6.5 mg l^{-1}(4.0 to 8.2) (Oxic)	5.2 mg l^{-1}(2 to 7.4) (Potential hypoxia in summer)	3	6.0 mg l-1 (2 to 8) (Potential hypoxia in summer)	3	5 mg l^{-1}(4 to 9.2)	3
	NH4 - Average (minimum to maximum)	0.2 µM (0 to 3.7)	8.9 µM (0.2 to 84)	3	6.7 µM (0.7 to 32)	3	3.6 µM (0.8 to 21)	3
	NO3+N02 - Average (minimum to maximum)	0.6 µM (0 to 17)	1.8 µM (0.3 to 62)	3	2.6 µM (0.7 to 12)	3	2.4 µM (0.4 to 6)	3
	PO4 - Average (minimum to maximum)	0.13 µM (0.1 to 1)	2 µM (0.2 to 25)	3	2.5 µM (0.1 to 7)	3	2.1 µM (0.1 to 7.6)	3
	N:P (molecular)	Mean = 6 (N limited)	Mean = 5.4 (N limited)		Mean = 3.7 (N limited)		Mean = 2.9 (N limited)	
	Chlorophyll a - Average (minimum to maximum)	3.7 µg l^{-1}(0.3 to 15)	13 µg l^{-1}(0 to 175)	5	10.1 µg l^{-1}(0.02 to 64)	3	5.3 µg l^{-1}(0.01 to 55)	3
	Phytoplankton primary productivity	200 g C $m^{-2}yr^{-1}$	200 g C $m^{-2}yr^{-1}$	6	105 g C $m^{-2}yr^{-1}$	18	Considered as strongly overestimated (600 g C $m^{-2}yr^{-1}$)	24
Fauna and Flora	Seagrass (most important, in decreasing order of abundance)	229 km^2 = 12 % *Thalassia testudinum* *Halodule wrightii* *Syringodium filiforme*	Only 3 km^2 = 3.5 % *Ruppia maritima*	7	106 km^2 = 14 % *Ruppia maritima* *Halodule wrightii*	7	480 km^2 = 24 % *Halodule wrightii* *Ruppia marítima* *Halophila engelmannii* *Thalassia testudinum* *Syringodium filiforme*	22
	High commercial value species (artisanal, industrial and recreative resources)	Fishery : Shrimp (*Litopenaeus setiferus, Farfantepenaeus duorarum*), oyster, blue crab, mollusks algae, octopus and fish (snappers, groupers, snook) Aquaculture : very low, Tilapia	Fishery : Clam, blue crab and fish (snook,*Tilapia castarrica)* Aquaculture : very low, Tilapia and clam *(Rangia sp.)*		Fishery : Shrimp (*Farfantepenaeus aztecus, Litopenaeus setiferus*), blue crab (*Callinectes* sp.), fish (snapper, drum, snook, etc.) Aquaculture : very low, oyster (*Crassostrea virginica*), Tilapia		Fishery : Shrimp (*Farfantepenaeus aztecus*) blue crab (*Callinectes sp.*), fish (*Mugil cephalus* , Pompanos, drum, snapper, sea bass). Aquaculture : non-significant	
	Invasive species	Plant : water hyacinth *Eichhornia crispes* Fish :*Tilapia rendalli, Orechromis mossambicu* and *O.niloticus*	Plant : water hyacinth *Eichhornia crispes* Fish :*Tilapia spp*	8	Unreported		Tilapia	11
	Fishes (reported number of species)	214	90	9	80	9	132	23
	Annelids (reported number of species)	123	Unavailable		64	19	13 (strongly underestimated)	25
	Mollusks (reported number of species)	173	62	3	67	9	89 (Gasteropods + bivalves)	23
	Crustaceans (reported number of species)	60	36	9	32	9	112	23
	Contaminant concentrations in oyster *Crassostrea sp* . dry weight	Low to moderate PAH = 4.6 µg g^{-1}(0.7 to 5.7) ΣDDTs = 9 ng g^{-1}(0.1 to 45) Pb = 0.18 µg g^{-1}(0 to 1.3)	Allegedly high but few available quantitative data Pb = 9 µg g^{-1}	10	Moderate with serious issue regarding Cd, representing a potential public health risk Pb = 0.8 µg g^{-1}, Cd = 21 µg g^{-1}	20	Mostly undocumented DDT below detection limit	20
Environmental management issues	Conservation priority at national level	Very important Whole lagoon area protected National priority site n° 53	Important Whole lagoon area protected National priority site n° 50	11	Important Whole lagoon area protected National priority site n° 47	11	Very important Whole lagoon area protected National priority site n°44	11
	Conservation status	RAMSAR site Laguna de Términos ANP Sistema Nacional de Áreas Naturales Protegidas	RAMSAR site Sistema lagunar Alvarado ANP Sistema Nacional de Áreas Naturales Protegidas	12	RAMSAR site Laguna Tamiahua ANP Sistema Nacional de Áreas Naturales Protegidas	12	RAMSAR site Laguna Madre y Delta del Río Bravo ANP Sistema Nacional de Áreas Naturales Protegidas	12
	Global environmental status *OEC = Overall Eutrophic Condition* *ASSETS = Assessment of Estuarine Trophic Status*	Fair Locally poor around Ciudad del Carmen city	Poor Eutrophication due to agricultural runoff	11	Poor Massive decrease in catches and oyster beds Eutrophication due to agricultural runoff	11	Fair to poor Deforestation, watershed dams diverting freshwater inputs	11
	Harmful algal blooms	*Karenia brevis* blooms all along the coast of Mexico but no actual report of HABs blooms in the lagoon	*Karenia brevis* blooms all along the coast of Mexico but no actual report of HABs blooms in the lagoon	13	*Karenia brevis* blooms all along the coast of Mexico but no actual report of HABs blooms in the lagoon	13	*Karenia brevis* blooms all along the coast of Mexico but no actual report of HABs blooms in the lagoon	13
	Watershed land use and original vegetation loss	Severe Cattle ranching	Severe Cattle ranching and sugar cane cultivation occupy 65.5 % and 14.5 % of watershed, respectively	14	Severe Mangrove at risk	11	Very severe Agriculture activities have reduced original vegetation, drained fresh water, increasing eolic erosion and ground salinization	11
	Industrialization	Moderate Petrol extraction	Moderate Sugar cane industry, petrol extraction	11	Low (petrol extraction, mining)		Very low	
	Urbanization	Moderate approx. 200,000 residents	Low approx. 48,000 residents	15	Low approx. 30,000 residents	21	Very low approx. 9,600 residents	23
	Main challenges	Sea level rise (coastal erosion, storm surge) Watershed management (water supply, water quality) Fisheries management	Sea level rise (coastal erosion, storm surge) Watershed management (water supply, water quality) Fisheries management		Sea level rise (coastal erosion, storm surge) Climate change (desertification) Watershed management (water supply, water quality) Fisheries management		Sea level rise (coastal erosion, storm surge) Climate change (desertification) Watershed management Fisheries management	

		Lower Laguna Madre Texas	Ref	Corpus Christi Bay	Ref	Matagorda Bay	Ref	Galveston Bay	Ref
General setting	Lagoon morphology	Barrier island lagoon		Barrier island lagoon		Barrier island lagoon		Barrier island lagoon	
	Open water surface (km²)	1,308	26	571	26	1,115	26	1,456	26
	Mean depth (m)	0.76	26	2.7	26	1.41	26	1.5	26
	Volume (km³)	0.99		1.54		1.57		2.24	
	Connection to the GoM	Permanent narrow (0.6 km) + temporary (approx. 3 km)		Permanent narrow (0.4 km)		Permanent medium (1.1 km)		Permanent medium (2.9 km)	
	Köppen-Geiger Climate Classification	Humid Subtropical (Cfa)		Humid Subtropical (Cfa)		Humid Subtropical (Cfa)		Humid Subtropical (Cfa)	
	Yearly river discharge (km³ yr-1)	0.65	27	0.72	39	4.35	46	13.70	53
	Lagoon flushing time by river inputs (d) = (Volume : yearly river discharge)*365	558		782		132		60	
	ISI Web of science search (November 2014) Topic « key words » = nb of references	« Laguna Madre Texas » = 162 « Laguna Madre » = 235		« Corpus Christi Bay » = 101		« Matagorda Bay » = 54		« Galveston Bay » = 432	
	Hydrodynamics	Measurements and modeling (2D & 3D, currents, waves, storm surge, salinity, etc.)	28	Measurements and modeling (2D & 3D, currents, waves, storm surge, salinity, etc.)	40	Measurements and modeling (2D & 3D, currents, waves, storm surge, salinity, etc.)	28	Measurements and modeling (2D & 3D, currents, waves, storm surge, salinity, etc.)	28
	Coastal erosion vulnerability	High to very high seaward Moderate on the lagoon shores	29	High to very high seaward Moderate on the lagoon shores	29	High to very high seaward Moderate on the lagoon shores	29	High to very high seaward Moderate on the lagoon shores	29
Water mass	Salinity - Average (minimum to maximum)	35 (2 to 56)	30	30 (3 to 38)	41	25 (9 to 35) (Colorado River diversion channel opened in 1991)	47	15.4 (0.3 to 37.9)	54
	Temperature	24.7 °C (8 to 33)	30	24 °C (12 to 31)	41	24.3 °C (9 to 33)	30	22.3 °C (4.5 to 35.8)	54
	Turbidity - Average (minimum to maximum)	Secchi 0.7 m (0.1 to 2) Turbidity = 12 NTU (1 to 40)	30	Secchi 0.9 m (0.1 to 2) Turbidity 15 NTU (2 to 50)	41	Secchi = 0.4 m (0.1 to 1.2) Mean turbidity = 37±47 NTU	48	Secchi 0.7 m (0.15 to 2) Turbidity = 22 NTU (7 to 46)	54
	Dissolved oxygen - Average (minimum to maximum)	7.2 mg^{l-1} (1 to 13) 4 % hypoxia occurrence	30	7.5 mg l-1 (1 to 9) Decreasing trend and bottom hypoxia occurrence in summer	42	6.1 mg^{l-1} (1.8 to 9) Occasional bottom oxygen depletion in summer	49	8.3 mg^{l-1} (2.4 to 18.5)	54
	NH4 - Average (minimum to maximum)	0.7 µM (0 to 9.6)	31	0.67 µM (0 to 6.1)	30	0.08 µM (0 to 2.44)	30	0.08 µM (0 to 9)	54
	NO3+N02 - Average (minimum to maximum)	0.9 µM (0 to 6.2)	31	0.41 µM (0 to 7.8)	30	0.3 µM (0 to 4.0)	30	0.14 µM (0 to 1.3)	54
	PO4 - Average (minimum to maximum)	0.31 µM (0 to 3.8)	31	0.29 µM (0 to 1.5)	30	0.34 µM (0 to 0.98)	30	0.24 µM (0 to 4.7)	54
	N:P (molecular)	Mean = 5.2 (N limited)		Mean = 3.7 (N limited)		Mean = 1.1 (N limitation)		Mean = 0.9 (N)	
	Chrorophyll a - Average (minimum to maximum)	13.5 µg l-1 (0.1 to 87)	31	13.4 µg l^{-1}(2 to 94)	30	8.5 µg l^{-1}(3 to 28)	49	10.1 $µg^{l-1}$(0 to 469)	54
	Phytoplankton primary productivity	55 g C $m^{-2}yr^{-1}$	32	200 g C $m^{-2}yr^{-1}$	43	175 g C $m^{-2}yr^{-1}$	50	140 g C $m^{-2}yr^{-1}$	55
Fauna and Flora	Seagrass (most important, in decreasing order of abundance)	686 km² = 52 % *Halodule wrightii* (68 %) *Syringodium filiforme* (17 %) *Thalassia testudinum* (12 %)	33	25 km² = 4 % *Halodule wrightii* *Ruppia maritima* *Halophila* *Thalassia testudinum* *Syringodium filiforme*	44	11 km² = 1 % *Halodule wrightii* *Ruppia maritima,* *Halophila engelmannii*	51	Severely impacted, only 2.3 km² remaining = 0.2 % *Halodule wrightii* *Ruppia maritima* *Halophila engelmannii.* 4.6 km² of *H. Wrightii* lost in West Galveston Bay since 1956	56 51
	High commercial value species (artisanal, industrial and recreative resources)	Fishery : shrimp, blue crab, oyster, fishes (drum, flounder, sheepshead, sea bass). Aquaculture : non-significant		Fishery : shrimp, blue crab, oyster, fishes (redfish, drum, flounder, sheepshead, sea bass). Aquaculture : non-significant		Fishery : shrimp, blue crab, oyster, fishes (drum, croaker, flounder, Gulf menhaden, spotted sea trout, sheepshead). Aquaculture : very limited activity (shrimp)		Fisheries : Shrimp, blue crab, fish (southern flounder, black drum, striped mullet, sheepshead) Aquaculture : 1st oyster producer in the US	
	Invasive species	Pacific white shrimp (*Litopenaeus vannamei*)	34	5th US port: strongly exposed to invasive species settlement Brown Mussel (*Perna perna*) Green Mussel (*Perna viridis*)	34	Pacific white shrimp (*Litopenaeus vannamei*)	52	Pacific white shrimp (*Litopenaeus vannamei*) Sauerkraut grass, spaghetti Bryozoan (*Zoobotryon verticillatum*)	52
	Fishes (reported number of species)	48	22	126	45	201	45	278	45
	Annelids (reported number of species)	242	35	355	35	215	35	250	35
	Mollusks (reported number of species)	177	35	222	35	114	35	152	35
	Crustaceans (reported number of species)	115	35	179	35	64	35	118	35
	Contaminants concentrations in oyster *Crassostrea sp*. dry weight	Moderate PAH = 0.5 µg g^{-1}(0.06 to 1.98) ΣDDT = 7.8 ng g^{-1}(0.9 to 43) Pb = 0.8 µg g^{-1}(0.2 to 3.7)	36	Moderate to high PAH = 1.34 µg g^{-1}(0.3 to 6.7) ΣDDT = 20.2 ng g^{-1}(2 to 42) Pb = 1 µg g^{-1}(0.4 to 1.9)	36	Moderate PAH = 0.4 µg g^{-1}(0.03 to 2.5) ΣDDT = 33 ng g^{-1}(2.6 to 146) Pb = 0.7 µg g^{-1}(0.3 to 1.7) Past industrial mercury pollution in Lavaca Bay	36	Moderate to high PAH = 3.0 µg g^{-1}(0.1 to 96.2) ΣDDT = 48 ng g^{-1}(3.4 to 500) Pb = 0.77 µg g^{-1}(0 to 2)	36
Environmental management issues	Conservation priority at national level	High Large lagoon area protected and extension to the watershed	12	Very low	12	Very low	12	Low (only marsh and prairie are protected but no marine area is protected)	12
	Conservation status	Laguna Atascosa National Wildlife Refuge (Federal), Padre Island National Seashore protected areas (National)	12	Unprotected Distant contact with Mission- Aransas National Estuarine Research Reserve	12	Unprotected In remote contact with Aransas National Wildlife Refuge	12	Unprotected Anahuac National Wildlife Refuge (Federal) inland	12
	Global environmental status *OEC = Overall Eutrophic Condition* *ASSETS = Assessment of Estuarine Trophic Status*	OEC = Unknown ASSETS = Unknown Moderate to high eutrophication susceptibility (low ability for nutrients dilution and flushing)	26	OEC = Moderate ASSETS = Unknown	26	OEC = Moderate ASSETS = Poor	26	OEC = Moderate - low ASSETS = Moderate Severe ongoing deterioration	26
	Harmful algal blooms	Common *Aureoumbra lagunensis* brown tide lasted for 7 full years from 1990 to 1997*Karenia brevis*	37 38	*Karenia brevis* *Dynophysis spp*	37	*Karenia brevis* *Dynophysis sp.* (Recent bivalve harvesting closure due to *Dinophysis* blooms)	37	*Karenia brevis* *Dynophysis spp*	37
	Watershed land use and original vegetation loss	Extremely severe Only 6 % land occupied by forests and wetlands versus 94 % for agriculture, pasture and urban areas	26	Severe Only 16 % land occupied by forests and wetlands versus 84 % for agriculture, pasture and urban areas	26	Severe Only 18 % land occupied by forests and wetlands versus 82 % for agriculture, pasture and urban areas	26	Severe Only 29 % land occupied by forests and wetlands versus 71 % for agriculture, pasture and urban areas	26
	Industrialization	Low Manufacturing, agriculture- forestry-fisheries, construction, mining		High Oil and gas extraction, refinery, petrochemistry, alumina production, shipping		Moderate Oil and gas extraction, refinery, petrochemistry, alumina production, shipping		High Petrochemistry,aerospace and aeronautics, shipping	
	Urbanization	Low approx 20,000 direct residents	26	Moderate 0.4 M residents, 2 % land use	26	High 1.4 M residents, 4 % land use	26	Very high 7.6 M residents, 15 % land use	26
	Main challenges	Sea level rise (coastal erosion, storm surge) Climate change (desertification) Fisheries management Channel dredging		Water quality Sea level rise (coastal erosion, storm surge) Fisheries management Channel dredging		Water quality Sea level rise (coastal erosion, storm surge) Fisheries management		Water quality Sea level rise (coastal erosion, storm surge) Fisheries management Channel dredging	

		Lake Pontchartrain	Ref	Tampa Bay	Ref	Charlotte Harbor	Ref
General setting	Lagoon morphology	Marginal Deltaic Basin lagoon protected offshore by barrier islands (Chandeleur)		Buried shelf valley and karst system with external barrier island		Buried shelf valley and karst system with external barrier island lagoon	
	Open water surface (km²)	1,879	26	902	26	502	26
	Mean depth (m)	3.50	26	3.0	26	1.6	26
	Volume (km³)	6.58		2.71		0.82	
	Connection to the GoM	Permanent medium (1.2 km)		Permanent large (9 km)		Permanent large (5 km)	
	Köppen-Geiger Climate Classification	Humid Subtropical (Cfa)		Humid Subtropical (Cfa)		Humid Subtropical (Cfa)	
	Yearly river discharge (km³ yr-1)	5.71	57	1.25	62	4.14	69
	Lagoon flushing time by river inputs (d) = (Volume : yearly river discharge)*365	420		790		72	
	ISI Web of science search (November 2014) Topic « key words » = nb of references	« Lake Pontchartrain » = 170		« Tampa Bay » 705		« Charlotte Harbor » = 128	
	Hydrodynamics	Numerous measurements and modeling studies[(i)]	58	Measurements and modeling (2D & 3D, currents, waves, storm surge, sediment transport, etc.)	63	Measurements and modeling (2D & 3D)	70
	Coastal erosion vulnerability	Very high to high vulnerability to sea level rise and storm surge from the coastline to the inner lagoon and lowlands (compaction and subsidence)	29	Moderate to low Seaward barrier beach erosion, moderate lowland loss inside the bay	29	Moderate to low Seaward barrier beach erosion, moderate lowland loss inside the bay	29
Water mass	Salinity - Average (minimum to maximum)	4 (0.1 to 12)	30	27,8 (0 to 50)	30	24.7 (0 to 46.7)	30
	Temperature	25.2 °C (4 to 32)	30	25,1 °C (8 to 42)	30	25.2 °C (10 to 39.3)	30
	Turbidity - Average (minimum to maximum)	0.9 m (0.05 to 2.5) 8 NTU (5 to 29)	30 59	Secchi = 1.8 m (0.2 to 9) Turbidity = 3 NTU (0 to 94)	30 64	Secchi = 1.3 m (0.6 to 4.5) Turbidity = 3.5 NTU (0.1 to 120)	71
	Dissolved oxygen - Average (minimum to maximum)	6.3 mg l^{-1} (1 to 13) (oxic, very occasionally hypoxic close to the Mississippi diversion channel)	30	6.1 mg l^{-1} (0 to 16) summer bottom hypoxia in Hillsborough Bay)	30	6.3 mg l-1 (0.6 to 10) Summer bottom hypoxia	30
	NH4 - Average (minimum to maximum)	1.0 µM (0.7 to 1.3)	60	1.1 µM (0.17 to 5.2)	64	0.11 µM (0 to 0.8)	69
	NO3+N02 - Average (minimum to maximum)	2.5 µM (0 to 5.7)	60	0.85 µM (0.03 to 0.85)	64	0.16 µM (0 to 0.5)	69
	PO4 - Average (minimum to maximum)	0.6 µM (0.1 to 1.1)	60	0.74 µM (0.05 to 92.5)	64	0.16 µM (0 to 0.4)	69
	N:P (molecular)	Mean = 5.8 (N limited, occasional P limitation during freshwater diversion from Mississippi runoff)		2.6 (N limited)		Mean = 1.7 (N limited)	
	Chrorophyll a - Average (minimum to maximum)	5.5 µg l^{-1}(0.4 to 66) Average up to 29 µg l^{-1}during spillway opening	30 60	5.6 µg l^{-1}(1 to 44)	64	6 µg l-1 (0.01 to 114)	
	Phytoplankton primary productivity	Unavailable		385 g C m-2 yr-1	65	258 g C m-2 yr-1	72
Fauna and Flora	Seagrass (most important, in decreasing order of abundance)	Unavailable cover data (annual freshwater seagrass species) but alleged 50 % decrease since 1973, currently improving *Ruppia maritima* *Vallisneria americana*	57 61	120 km² = 13 % 37 % increase 1982 to 2008 *Halodule wrightii* *Thalassia testudinum* *Syringodium filiforme* *Ruppia maritima*	66	238 km² = 47 % 13 % increase 1999 to 2006 *Halodule wrightii* *Thalassia testudinum* *Syringodium filiforme*	73
	High commercial value species (artisanal, industrial and recreative resources)	Fishery: clam (*Rangia* sp.) shrimp, blue crab, oyster and fish (redfish, spotted seatrout, flounder, black drum) Aquaculture : non-significant		Fishery: shrimp, blue crab, stone crab, scallop and fish (tarpon, flounder, permit, snapper, seatrout, cobia, pompano) Aquaculture : hard clam		Fishery: shrimp, blue crab, stone crab, scallop, clam, oyster and fish (flounder, grouper, snapper, drum, pompano, etc.) Aquaculture : hard clam	
	Invasive species	*Myriophyllum spicatum*	61	Green mussel (*Perna viridis*), Lionfish (*Pterois volitans*)		Green mussel (*Perna viridis*), Lionfish (*Pterois volitans*)	
	Fishes (reported number of species)	171	35	173	35	198	35
	Annelids (reported number of species)	72	35	180	35	206	35
	Mollusks (reported number of species)	73	35	399	35	359	35
	Crustaceans (reported number of species)	63	35	115	35	205	35
	Contaminants concentrations in oyster *Crassostrea sp.* dry weight	High PAH = 10.2 µg g^{-1}(0.7 to 58) ΣDDT = 72 ng g^{-1}(26 to 226) Pb = 1.5 µg g^{-1}(0.3 to 4)	36	Moderate PAH = 0.9 µg g^{-1}(0.1 to 6.7) ΣDDT = 33 ng g^{-1}(1.2 to 175) Pb = 0.82 µg g^{-1}(0.15 to 2.5)	36	Low to moderate PAH = 0.4 µg g^{-1}(0.08 to 0.8) ΣDDT = 31 ng g^{-1}(1.3 to 230) Pb = 0.55 µg g^{-1}(0.1 to 1.1)	36
Environmental management issues	Conservation priority at national level	Low (76 km² of protected marshland, no open water reserve)	12	High 1/3 of total area protected	12	Maximum (whole area protected)	12
	Conservation status	Unprotected Big Branch Marsh National Wildlife Refuge (Federal) Clam dredging bans	12	Pinellas County Preserve (State) Terra Ceia Aquatic Preserve (State)	12	National Estuary Program (Federal) Aquatic preserves (State)	12
	Global environmental status *OEC = Overall Eutrophic Condition* *ASSETS = Assessment of Estuarine Trophic Status*	OEC = Moderate ASSETS = Poor	26	OEC = Moderate - high ASSETS = Poor But large seagrass recovery due to nitrogen load reductions	26	OEC = Moderate ASSETS = Poor	26
	Harmful algal blooms	Rare (Following diversion of Mississippi River water in 1996-1997)	60	*Karenia brevis* *Pyrodinium bahamense*	64 67	*Karenia brevis*	67
	Watershed land use and original vegetation loss	Severe 51 % forest and 12% wetland But critical marsh habitat loss	26	Severe Only 14 % land occupied by forests and wetlands versus 86 % for agriculture, pasture and urban areas	26 68	Severe Only 21 % land occupied by forests and wetlands versus 79 % for agriculture, pasture and urban areas	26
	Industrialization	High (petrol extraction, crude oil refineries, natural gas processing, petrochemistry)		High and diverse Cigar manufacturing, high-technology, aerospace, electronics, food processing		High and diverse phosphate ore processing, microelectronics, vehicle assembly, high-technology	
	Urbanization	Moderate 0.7 M residents, 10 % land use	26	High 1.3 M residents, 32 % land use	26	Moderate 0.4 M residents, 12 % land use	26
	Main challenges	Sea level rise Climate change impact on Mississippi hydrologic regime Wetland subsidence Living resources management		Sea level rise Fresh water supply Water quality improvement Habitat restoration (wetland, mangrove, seagrass)		Habitat protection (wetland, mangrove, seagrass) Freshwater management Waste management	

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ANNEXE C.

Global climate change and local watershed management as potential drivers of salinity variation in a tropical coastal lagoon (Laguna de Terminos, Mexico).

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Abstract

The wide range of ecological goods and services provided by tropical coastal lagoons and wetlands are under considerable pressure due to the synergistic effects of local anthropogenic impact and global climate change. In transitional waters, salinity is a key driver of ecological processes mostly depending on the balance between marine and river inputs, a balance that can be significantly modified by the conjunction of anthropogenic watershed alteration and climate change. Mesoamerica being considered as a climate change Hot-Spot and as an eco region strongly vulnerable to global change, our study aimed at analyzing the relationship between rainfall, river runoff, and salinity variability in a tropical coastal lagoon and to assess the respective influence of climate change and watershed management. The study focusing on the large and shallow coastal lagoon of Laguna de Terminos in south eastern Mexico established that: i) salinity variability in the lagoon was directly related to river discharge variability; ii) despite a projected future decrease in river discharge in the region, a sustained increase in river flow rates was observed during the past 60 years, indicating that salinity decreased rather than increased during this period; iii) because precipitation rates during the same past 60 years were constant, the simultaneous increase in flow rates was interpreted as resulting from unsustainable land use rather than climate change impact; iv) the occurrence of a positive salinity anomaly during the wet season of 2009 corresponded to an exceptional minimum river discharge, which was coincident to the 2009 El Niño Modoki event, and v) an historical study of river discharge versus ENSO index yielded too much variability to establish a solid enough general relationship. Those results should be of significant practical value to decision-makers who are often keen to point the finger at global climate change when local environmental management is also and sometime most significantly at stake.

1 Introduction

Alterations of the hydrological cycle has been related to the combined impacts of climate change and watershed anthropization, climate change generally having a direct impact on the global distribution of water resources when watershed alterations mainly control local, surface hydrological processes (Kundzewicz et al. 2007). On the global scale, Central America has been singled out as the most prominent tropical climate change Hot-Spot (Giorgi 2006) and, despite large modeling uncertainties about climate change impact, most studies converged to anticipate a general decrease in mean precipitation and an increase in drought and severe drought periods in Mesoamerica (southern Mexico and Central America) (Imbach et al. 2012; Chiabai 2015). Such climate change impacts on the hydrological cycle will be the source of significant environmental, economic and social impacts in a region where vulnerability to extreme climatic events is considered on the rise (Hidalgo et al. 2013; Vázquez-González et al. 2014). Changes in land use and watershed management is another significant source of hydrological cycle alteration as a doubling of overall freshwater runoff has been reported between humanly impacted and non-impacted watersheds in the Mesoamerican region (Burke and Sugg 2006).

Changes in freshwater regime and water quality are known to have direct impact on biodiversity, ecosystem functioning and living resources in coastal systems (Sale et al. 2014; Putland et al. 2014). Tropical coastal lagoons and wetlands, that stand as highly productive ecosystems providing numerous ecological goods and services essential to sustainable development (Moberg and Rönnbäck 2003), are highly sensitive to alterations in their hydrological cycle. In such systems, variations in river inputs and related variations in salinity evidently constrain the distribution of species as well as the reproductive and feeding behaviors of major ontogenetic species of economic value such as fishes or shrimps (Andrade et al. 2015, Palmer & Montagna 2015). In the gulf of Mexico, global change has often been held responsible for participating in the decline of fisheries (Martínez Arroyo et al. 2011) and land use intensity has been inversely correlated with lagoon fishing productivity (Vázquez-González et al. 2015), but little evidence of a straightforward relationship between rainfall, river runoff, and salinity and of its potential dependence with respect to climate change and watershed management have been provided. The overall objective of the present study was to analyze the hypothesis of such a relationship and to objectively assess how climate change and watershed management might impact salinity in tropical coastal lagoons of Mesoamerica.

Our focus on the large and shallow coastal lagoon of Laguna de Terminos, south eastern Mexico, was dictated by its high priority status in terms of environmental protection and its selection as a focus site in the frame of the Global Environment Facility (GEF) Gulf of Mexico Large Marine Ecosystem Program (GoM-LME). The diversity in environmental conditions and the presence of major habitats such as seagrass beds and mangroves all strongly contribute to the presence of highly complex communities in terms of biota diversity, distribution, abundance and trophic status (Yáñez-Arancibia et al. 1983; Grenz et al. 2015). As a consequence, Terminos Lagoon is considered to be a major site for breeding and for the juvenile development of commercial species encountered on the continental shelf of Campeche Sound. Catches in that area account for one-third of the Mexican fish market captured in the Gulf of Mexico and the Caribbean Sea, but have experienced a significant collapse since the early 1980s (Robadue et al. 2005; Fichez 2013). Shrimp for example, are one of the most valuable living resources in the Gulf and rely strongly on coastal lagoons to complete their reproductive cycle, yet this fishery has experienced drastic decline largely due to continually decreasing recruitment (Arreguin-Sanchez 2008). Based on the arising need for biodiversity conservation and economic resource protection, Terminos Lagoon was combined with its surrounding wetlands to form the largest RAMSAR protection site in Mexico (Mitsch and Hernandez 2013).

In such a critical ecosystem, recent concern has arisen that an increase in salinity related to climate change might be building up, detrimentally impacting juvenile developmental stages of exploited species (Ramos Miranda et al. 2005a; 2005b; Sosa Lopez et al. 2005; Villéger et al. 2010). Those authors observed a loss in functional diversity and a biotic homogenization in the fish community of Terminos Lagoon which they linked to a salinity increase between the years 1980-1981 and 1998-1999, and interpreted as a regular shift from hypohaline to euhaline/hyperhaline status due to climate change (Ramos Miranda et al. 2005a).

Concurrent with this scenario, recent catastrophic flooding events occurred in the Tabasco and Chiapas Mexican states, resulting in economic - and more dramatically - human losses (Aparicio et al. 2009). Such events are commonly and hastily attributed to climate change, especially by political leaders for whom invoking the planetary dimension of global change is often a way to disclaim any direct responsibility. The truth is that most climate change studies predict periods of lower precipitation in Mesoamerica (Biasutti et al. 2012). No significant change in precipitation is anticipated during the first half of the 21st century but precipitation decline ranging fro 5 to 30 % is expected by the end of the 21st century, depending on the considered IPCC emission scenario (Barcena et al., 2010, Hidalgo et al. 201). Decreasing precipitation is also expected to be accompanied by an increase in hydrological variability, reinforcing extreme events of flooding and drought. Even though population exposure to water stress will increase substantially with climate change, climate prediction uncertainties at the regional to local scale are still considered as large (Met Office 2011), rendering the establishment of efficient long-term management policies difficult.

The present study used three distinct datasets: i) a 2 years survey of salinity profiles over a network of 34 stations; ii) long-term records of daily river flow rates; iii) and a long-term record of daily rainfall, in order to analyze the potential links between rainfall, river runoff, and salinity, and to assess their relationship with anthropogenic alteration of watershed, long term trends in climate change, and punctual occurrence of climate anomalies.

2 Material and methods

2.1 Study site

Terminos Lagoon is located on the southern coast of the Gulf of Mexico in the Mexican state of Campeche (Figure C.1a). It stretches over a surface of 1,936 km^2 (Figure. C.1b) with an average depth of only 2.4 m, corresponding to a total water volume of 4.65 km^3 (Contreras Ruiz Esparza et al. 2014). It is fringed by Carmen Island on its seaward side and connected to the Gulf of Mexico through Carmen Inlet Puerto Real Inlet on its westward and eastward sides, respectively. To the east stretches the Yucatan Peninsula, characterized by low rainfall and a porous calcareous basement resulting in the absence of proper river catchment, with rainfall penetrating directly through the carbonate basement, thus supplying the groundwater cap which discharges as diffusive non-point sources all along the Gulf of Mexico and Caribbean Sea coasts. To the west and south lie the lowlands of Tabasco and the highlands of Chiapas and Guatemala, the latter of which receives heavy tropical rainfall. Four rivers, of which two combine to form a single estuary, reach Terminos Lagoon (Robadue et al. 2004) delivering an average yearly volume of 11.96 10^9 m^3 yr^{-1} of freshwater, corresponding to roughly 2.6 times the lagoon volume. Yearly net rainfall of 293 mm yr^{-1} (1,805 mm yr^{-1} precipitation minus 1,512 mm yr^{-1} evaporation) (David and Kjerfve 1998; Espinal et al. 2007) accounted for a net fresh water input of 0.57 10^9 m^3 yr^{-1}, whereas groundwater contribution accounted for 4 10^6 m^3 yr^{-1} (David 1999). Total annual net freshwater input to Terminos Lagoon was thus estimated at 12.53 10^9 m^3 yr^{-1}, of which river discharge, net precipitation, and groundwater seepage accounted for 95.42 %, 4.55 % and 0.03 %, respectively, river discharge therefore being the most significant source of freshwater by far.

The rivers Chumpán, Candelaria-Mamantel and Palizada respectively deliver an average of 0.6, 2.26, and 9.1 10^9 m^3 yr^{-1} of freshwater to Terminos lagoon. Beyond its own small river catchment, the Palizada is a tributary of the Usumacinta River, which in turn relates to the intertwined Grijalva-Usumacinta basins that stretch over a total area of 112,550 km^2 (Hudson et al. 2005). Receiving an average annual rainfall of 1,709 mm yr^{-1}, the Usumacinta River discharges an average annual freshwater volume of 69 10^9 m^3 yr^{-1}, approximately one-tenth being diverted through the Palizada River into Terminos Lagoon, the remaining nine-tenths merging with the Grijalva River catchment and directly reaching the Gulf of Mexico open waters.

Climate varies between the tropical wet and dry category in the lowlands and the tropical rainforest category in the highlands. There are three distinct seasonal periods throughout the year: the relatively dry period from February to May and the rainy period from June to September are separated by a period of northern gales called “Nortes”.

2.2 Data collection and analysis

Daily rainfall at Bocca del Cerro station corresponding to river flow rate time series were obtained from the Servicio Meteorológico Nacional database, also managed by CONAGUA and accessible through the Centro de Investigación Científica y de Educación Superior de Ensenada (CICESE) website “Base de datos climatologica nacional – Sistema CLICOM” (http://clicom-mex.cicese.mx/ accessed 5-6 September 2014).

Daily river flow rates were obtained from the Mexican Comisión Nacional de Agua (CONAGUA) hydrological surveys database, available from the website (http://www.conagua.gob.mx/CONAGUA07/Contenido/Documentos/Portada%20BANDAS.htm, accessed 5-6 September 2014). Long-term records of daily river flow rates were available for the 1995-2011 period for the Mamantel River, for the 1992-2011 period for the Palizada River, for the 1953-2011 period for the Candelaria River, and for the 1948-2011 period for the Usumacinta River (Bocca del Cerro hydrological station, upstream Terminos Lagoon). Given the quality of each data series and the dominance of Palizada River inputs to Terminos Lagoon, the present paper focused on the data series from the Palizada and Bocca del Cerro stations from the Grijalva-Usumacinta watershed.

Salinity data with a precision of 0.001 were obtained from vertical profiles conducted with a SeaBird® SBE 19 CTD over a network of 34 stations (Figure C.1b) and a total of 13 sampling trips covering the 2-year period from October 2008 to November 2010, with a more intensive sampling effort during 2010 (7 sampling trips). Data acquisition frequency was 0.25 sec and only downward profiles at a velocity of circa 0.5 m sec^{-1} were retained for data analysis. The SBE 19 CTD was calibrated by the manufacturer on a yearly basis.

Average salinity between 0 and 75 cm depth was spatially interpolated using UNIRAS A/S® software to generate 2D distribution maps. However, the lagoon size imposed sampling over several days (4 to 6), potentially rendering such asynchronous sampling strategy sensitive to short term variability. Salinity variations in the lagoon are essentially driven by variations in i) tidal exchanges with the Gulf of Mexico, ii) internal lagoon hydrodynamics (tide accounting for 65 % of current variability (David and Kjerfve 1998), iii) precipitation versus evaporation budgets, and iv) river inputs. With limited exchange taking place through two shallow and narrow inlets and with average tidal amplitude of only 0.3 m, tidally driven salinity variations between two sampling points can be considered as negligible at the scale of a tidal cycle or even at the scale of a few days (Contreras Ruiz Esparza et al. 2014). River discharge, precipitation, wind regime and daily temperature cycles were constant over each sampling period as well as during the previous five days, so the results can be considered as being representative of a stable situation. Finally, it must be acknowledged that, all driving factors combined, water residence time in this 1,936 km^2 system ranges from one to five months (Robadue et al. 2004), which significantly limits daily variability in salinity at the sampling grid scale.

Linear regression and parametric Pearson (normal data, no outliers) or otherwise non parametric Spearman correlation tests were computed using Statistica® to assess relationships between data as well as trends in time series. In addition, the seasonal Mann-Kendall test (Hirsch and Slack 1984) was used as it constitutes a well-fitted nonparametric method to statistically assess the presence of monotonic trends in hydrological long-term time series that are generally asymmetrically distributed (Machiwal and Jha 2008).

3 Results

3.1 Salinity

Spatio-temporal variation in salinity was considered as most likely to respond to alleged joint impacts of climate and land-use changes in the region. Due to its nature as a semi-enclosed lagoon subject to significant freshwater inputs, salinity in Terminos Lagoon was strongly variable at the spatial as well as the temporal scale, as shown by the temporal survey of salinity distribution from October 2008 to November 2010 (Fig.ure C.2). Changes in salinity distribution during 2010 gave an overview of the general variability pattern of the system over a full yearly cycle. As a consequence of the dry season, salinity values averaged over the whole lagoon increased from (mean ± SD) 29.3 ± 4.3 in January to 33.0 ± 3.0 in May. At this time, salinity maximum values in the range of 33 to 37 over the whole lagoon approached open sea salinity values, which were in the range of 36 to 38 (Thacker 2007). This increase in salinity coincided with the progressive disappearance of brackish plumes from the Candelaria and Palizada Rivers in the eastern and western inshore parts of the lagoon. During the following rainy period, salinity values averaged over the whole lagoon decreased progressively to 16.41 ± 4.87 (mean ± SD) reaching one-digit values in the most inshore areas, while at the same time, values over 20 were only measured close to Puerto Real Inlet and leeward of Carmen Island. The observed progressive decrease in salinity corresponded to the progressive extension of Candelaria and Palizada brackish plumes within the lagoon.

Comparison of salinity distribution for corresponding periods of 2008, 2009 and 2010 revealed that a strong positive anomaly occurred during the wet season of 2009. Salinity distributions in March 2009 and March 2010 were strongly similar, with average values (mean ± SD) of 32.41 ± 3.35 and 31.29 ± 3.36, respectively. In 2009, salinity remained high in September and October, at 34.45 ± 1.96 and 32.64 ± 4.34, respectively, and decreased only slightly in December to 28.12 ± 3.62. In comparison, lagoon-wide average salinity in October 2008, September 2010 and November 2010 was significantly lower at 13.70 ± 5.65, 17.00 ± 5.40 and 16.41 ± 4.87, respectively. Whereas salinity distributions in October 2008 and in September and November 2010 can be considered as representative of the peak of the wet season with minimum values of salinity in most parts of the lagoon, the situation observed in 2009 during the same period stands out as a strong positive anomaly to the usual seasonal cycle. Data from October 2008 to November 2010 were plotted along with what we considered as a reference yearly salinity cycle derived from a previous survey conducted in 1980 (Yañez-Arancibia et al.

1983) (Figure C.3). Despite the strong variability generated by the spatial heterogeneity, we observed that, even though salinity roughly followed the reference pattern at the beginning and the end of the 2008-2010 survey, the suspected positive salinity anomaly during the so called wet season of 2009 could be statistically evidenced.

3.2 River flow rate anomaly

Given the previously established predominance of river discharge over other sources of fresh water input to the lagoon, it was necessary to analyze historical records of river flow rates in order to assess the potential relationship with salinity. In September 2009, monthly discharge in the Palizada River reached a maximum of 224 $m^3 s^{-1}$, by far the lowest value for the post wet season yearly maximum derived for the 1992-2011 period (average 458 $m^3 s^{-1}$). The salinity anomaly observed during 2009 in Terminos Lagoon can thus be related to a historical minimum discharge from Palizada River. Analysis of the relationship between salinity averaged over the whole lagoon and Palizada River inputs averaged over the previous month during the 2008-2010 survey (Figure C.4) established a statistically significant linear relationship (Spearman R = -0.69, $p<0.05$) yielding an y-intercept value of 35.61 consistent with average seawater salinity in the southern Gulf of Mexico.

Confirmation of the direct impact of river discharge on salinity raised the issue of a possible long-term relationship between climate change, river flow rates, and salinity in Terminos Lagoon, with potential consequences in terms of environmental status alteration. However, the Palizada database only covered a 19 year period, insufficient to support climatic trend analysis (Hanson et al. 2004), and alternatively reasoning on the long term time series available for upstream Usumacinta watershed required a preliminary check on the relationship with its Palizada tributary. Monthly averaged Palizada River discharge was very strongly correlated (Spearman R=0.93, $p<<0.05$) with Usumacinta River discharge at Boca del Cerro hydrological station and amounted 9 to 11% of the latter depending on the calculation method (average ratio, linear regression, linear regression with through-origin intercept). The 1948 to 2011 long term series available for Usumacinta River (Fig. 5a) followed a yearly pattern identical to that from Palizada River, showing minimum and maximum discharges during the April to June and September to November period, respectively, and recording the 2009 wet season discharge as the lowest of the whole time series. The seasonal Mann Kendall nonparametric test yielded a score of 4,242 and a p-value of 1.3 10^{-12}, confirming the occurrence of a statistically significant positive trend. From the linear regression equation it was possible to estimate the increase in annually averaged flow rate at 25 % from 1948 (1,768 $m^3 s^{-1}$) to 2011 (2,214 $m^3 s^{-1}$).

Such a long term increase in river discharge could most likely originate from an increase in precipitation, so available synchronous long-term series of rainfall at Boca del Cerro were used to test that hypothesis. Long-term records of precipitation over the same 1948-2011 period at Boca del Cerro station (Figure C.5b) yielded an average monthly precipitation rate of 190 mm with a wide range of variation, from no rainfall at all to a maximum monthly precipitation of 661 mm in September 1966. The Man-Kendall test did not **allowe**d for the rejection of the “no trend” null hypothesis, and, together with the slope-less linear regression, demonstrated the absence of a long-term change in precipitation rates. That stable trend in precipitation over the 64-year period thus strongly contrasted with the observed increase in river discharge over the same period of time at the Bocca del Cerro station on the Usumacinta River.

3.3 ENSO relationship

The local anomaly in salinity and river discharge also could be related to an ENSO anomaly. The Oceanic Niño Index (ONI) rose to the 0.5 threshold value in the June-August period of 2009 and up to a maximum of 1.6 in the November-January and December-February 2009-2010 periods, before decreasing below the 0.5 threshold value during the April-June period of 2010 and rapidly entering a 10- month La Niña event beginning in the June-August period. Even though 2009 appeared as the most drastic year in terms of low river discharge, it was far from the most severe El Niño event of the past 60 years, so the long-term relationship between the El Niño index and Usumacinta River discharge needed further analysis to assess the general pertinence of a potential cause and effect relationship.

In order to test this hypothesis, we crossed the NOAA Oceanic Niño Index (ONI) against river flow rates at Boca del Cerro station. For monthly averaged river flow rates, a best fit was obtained for a two-month lag with ONI central month (Figure C.6), only yielding a weak correlation (Spearman R = -0.044, p = 0.23). Slightly stronger but still non-significant correlation was obtained between yearly averaged ONI and river flow rates (Spearman R = -0.133, p = 0.31). Even extreme El Niño or La Niña events could not systemically be related to decreases or increases in river discharge, respectively.

4 Discussion

Data analysis permitted to establish a relationship between salinity variations and river runoff and to show that long term increase of the latter was not linked to a change in precipitation. Additionally, a strong positive salinity anomaly during the wet season of 2009 was concomitant with a positive ENSO anomaly. Cross interpretation of those results was called for to reach a better understanding on how Terminos Lagoon salinity respectively responded to climate and land-use drivers.

Salinity variation in time and space was high, ranging from one digit values (estuarine) to 36 (marine), with spatial gradients shifting strongly as a function of the balance between marine and freshwater inputs. A low salinity plume generally spread north of Palizada Estuary toward Carmen Inlet along the western part of the lagoon. Considering their respective freshwater discharges, the Candelaria-Panlau system and the Chumpan River clearly had a much lower impact on salinity distribution in the lagoon. Salinities of up to 33-36, thus fairly close to salinities of the Gulf of Mexico marine waters (Thacker 2007), were always measured close to the Puerto Real Inlet and leeward of Carmen Island, confirming that marine waters enter through Puerto Real Inlet during tidal flooding and are transported westward along the coast of Carmen Island (Graham et al. 1981; Kjerfve 1988; David and Kjerfve 1998; Contreras Ruiz Esparza et al. 2014).

Inter-annual comparison based on our data for years 2009 and 2010 and on the few existing studies yielding salinity temporal surveys (Yañez Arancibia et al. 1983; Ramos Miranda et al. 2005a) revealed the presence of a strong positive salinity anomaly during the wet season of 2009. The environmental drivers leading to such an exceptional situation had to be identified, logically starting with the analysis of river inputs.

To access long term data on river flow rates to Terminos Lagoon it was first established that the river discharge from the Palizada River tributary was 8.7 times lower than the one from Usumacinta River. The long term analysis of Usumacinta River discharge revealed a long-term increase trend instead of the climate change-related decrease trend anticipated from previous studies (Ramos Miranda et al. 2005a; Sosa Lopez et al. 2005). A key issue, both in terms of scientific inquiry and of environmental management, was to understand the reasons for such a long-term change and, in particular, to assess whether it is related to changes in climatic conditions and/or to poor practices in local watershed management. No significant historical change in precipitation rates was observed at Boca del Cerro hydrological station, a trend consistent with climate modeling approaches which generally predicted undetectable changes at the beginning of the 21st century, followed by a decrease in precipitation (Barcena et al. 2010, Sáenz-Romero et al. 2010, Met Office 2011, Biasutti et al. 2012, Hidalgo et al. 2013). Despite that long term rainfall stability, Usumacinta River discharge regularly increased during the past 60 years therefore excluding climate change as a driver of that long-term historical change in hydrological regime and, instead, lending support to the hypothesis of a local impact related to watershed management. Deforestation to expand agricultural and ranching lands has been consistently linked to increased rainwater runoff resulting in higher river discharges and such a relationship was locally supported by previous work on satellite image analysis. Soto-Galera et al. (2010) evidenced changes from original land cover in more than half of the Terminos Lagoon area during the period from 1974 to 2001, and revealed that 31% of the area occupied by mature vegetation in 1974 had been degraded by 2001: tropical forest and mangroves presented the most extensive coverage losses, while urban areas and grassland for livestock farming increased considerably. Net mangrove surface loss was 17,426 ha in Campeche between 1970 and 2005, corresponding to an 8 % loss from the initial mangrove surface area (Valderrama et al. 2014). At a larger scale, during the 1976 to 2009 period, the watersheds surrounding Terminos Lagoon were the most affected by deforestation of all the watersheds of Mexico: the Grijalva-Usumacinta, Mamantel and Candelaria basins lost 20-30 %, 30-50 % and <10 % of their primary vegetation, respectively. Furthermore, all three basins lost 30-50 % of their secondary vegetation (Cotler Ávalos, 2010). Additionally, a comparable increase in river discharge unrelated to precipitation and linked to deforestation and expansion of the agricultural and ranching land was reported from the Candelaria watershed (Benitez et al. 2005). In such a context, and considering the tight relationship between the Usumacinta River and the Palizada River, the ongoing long-term trend in Terminos Lagoon is more likely to be one of salinity decrease rather than increase.

We also observed the coincidental occurrence of (i) a low yearly maximum river discharge, (ii) a positive salinity anomaly in Terminos Lagoon and (iii) a moderately severe El Niño event during the period from July 2009 to April 2010 which was immediately followed by a La Niña event from July 2010 to April 2011. However, our study on the relationship between Usumacinta River flow rates and ENSO ONI index during the past 60 years yielded inconclusive results. Other studies relating ENSO with rainfall in Mexico similarly reported noticeable but very weak correlation (Pavia et al. 2006; Bravo Cabrera et al. 2010), with precipitation decreasing southward and increasing northward under “El Niño” conditions and globally increasing under “La Niña” conditions. The same studies also predicted future stronger precipitation deficit during the wet season, leading to severe drought events such as the one observed in 2009. However, a recent study also evidenced river discharge in the Usumacinta-Grijalva basin to be higher during both El Niño and La Niña than during normal periods of ENSO (Muñoz-Salinas & Castillo, 2015), a conclusion in reasonable agreement with the distribution pattern of river discharge versus ONI index observed herein.

Additionally, it must be commented that the 2009 ENSO anomaly was classified as an ENSO Modoki (Ashok et al. 2007). Traditional Eastern-Pacific El Niño events are characterized by strong anomalous warming in the eastern equatorial Pacific, whereas Modoki El Niño, pertaining to the Central Pacific El Niño category, is associated with strong anomalous warming in the central tropical Pacific and cooling in the eastern and western tropical Pacific (Kang et al., 2013). El Niño Modoki has different effects than Eastern-Pacific El Niño (Kang et al., 2013), and its relationship with American river discharge has been reported to range from insignificant in the US Georgian Altamaha River (Sheldon & Burd, 2014) to generating extreme low discharge events in the Brazilian Paranaiba River (Sahu et al. 2014). However, in the absence of studies specifically dealing with the impact of El Niño Modoki on the Gulf of Mexico region, more data gathering, historical analysis, and modeling, are needed before considering a potential relationship with drought events in the south-eastern part of Mexico.

As related to the two available sets of historical salinity data in Terminos Lagoon, it must be stressed that year 1980 (data from Yañez-Arancibia et al. 1983) corresponded to a several years period of above average river discharge and normal ENSO conditions, whereas the October 1997 to September 1998 period (data from Ramos Miranda et al. 2005a) corresponded to a period of around average river discharge following a strong deficit year in 1995 and strong El Niño conditions from May 1997 to April 1998 (maximum ONI value of 2.4 in November 1997). The difference in salinity observed by Ramos Miranda et al. (2005a) between 1980 and 1997-1998 in Terminos Lagoon hence would be due to cyclic variability rather than climate change long-term shift in river discharge, and despite weak evidence of a general relationship, could be partly related to the 1997-1998 El Niño event.

5 Conclusion

The present study established that salinity in Terminos Lagoon depended on river inputs and that the occurrence of an exceptional river discharge minimum during the wet season of 2009 was responsible for a positive salinity anomaly. Over the long term, and in the context of a potential future regional decrease in river discharge, we observed a sustained increase in river flow rates in the Usumacinta River watershed during the past 60 years, implying that salinity in Terminos Lagoon decreased rather than increased during this same period. Stable precipitation rates during that 60 years period proved that the recorded past increase in river discharge resulted from unsustainable land use rather than climate change impact. Finally, despite the coincidence between the 2009 ENSO event, the observed decrease in river flow rate, and the positive salinity anomaly in Terminos Lagoon, no clear general relationship could be established between river flow rates and the ONI ENSO index. These results should be of significant value to decision-makers who are often keen to hastily point the finger at global climate change when, in fact, local environmental management is also and most likely involved. In the context of ongoing global change it is essential to precisely account for the respective contribution of watershed alteration and climate change in order to more sustainably manage their synergistic effects on river runoff and mitigate their impacts in terms of the economy and, more importantly, of population safety (Brody et al. 2012).

Environmental management has to be planned on a long-term scale and the context of predicted future changes urgently calls for gathering long-term information on key environmental variables, starting with basic drivers such as temperature and salinity. If a shift in rainfall is likely to occur as predicted by converging climate models, salinity in Terminos Lagoon will be directly impacted. For this reason, assessing future trends and their potential impacts on biodiversity and living resources within - as well as beyond - the limits of this critical ecosystem is essential. A major environmental protection site such as Terminos Lagoon should, at the least, have its own observation network surveying key environmental variables such as salinity on a long-term basis. Such a monitoring objective should even be extended to the Gulf of Mexico scale - if not to the national and regional scales - since environmental protection in the Mesoamerican region is not confined within the boundaries of national frontiers. The current lack of long-term information is detrimental both to the understanding of ecosystem equilibrium as well as to sustainable development in the context of the ongoing global change and its potential critical impact on the Gulf of Mexico and Caribbean region.

Acknowledgment

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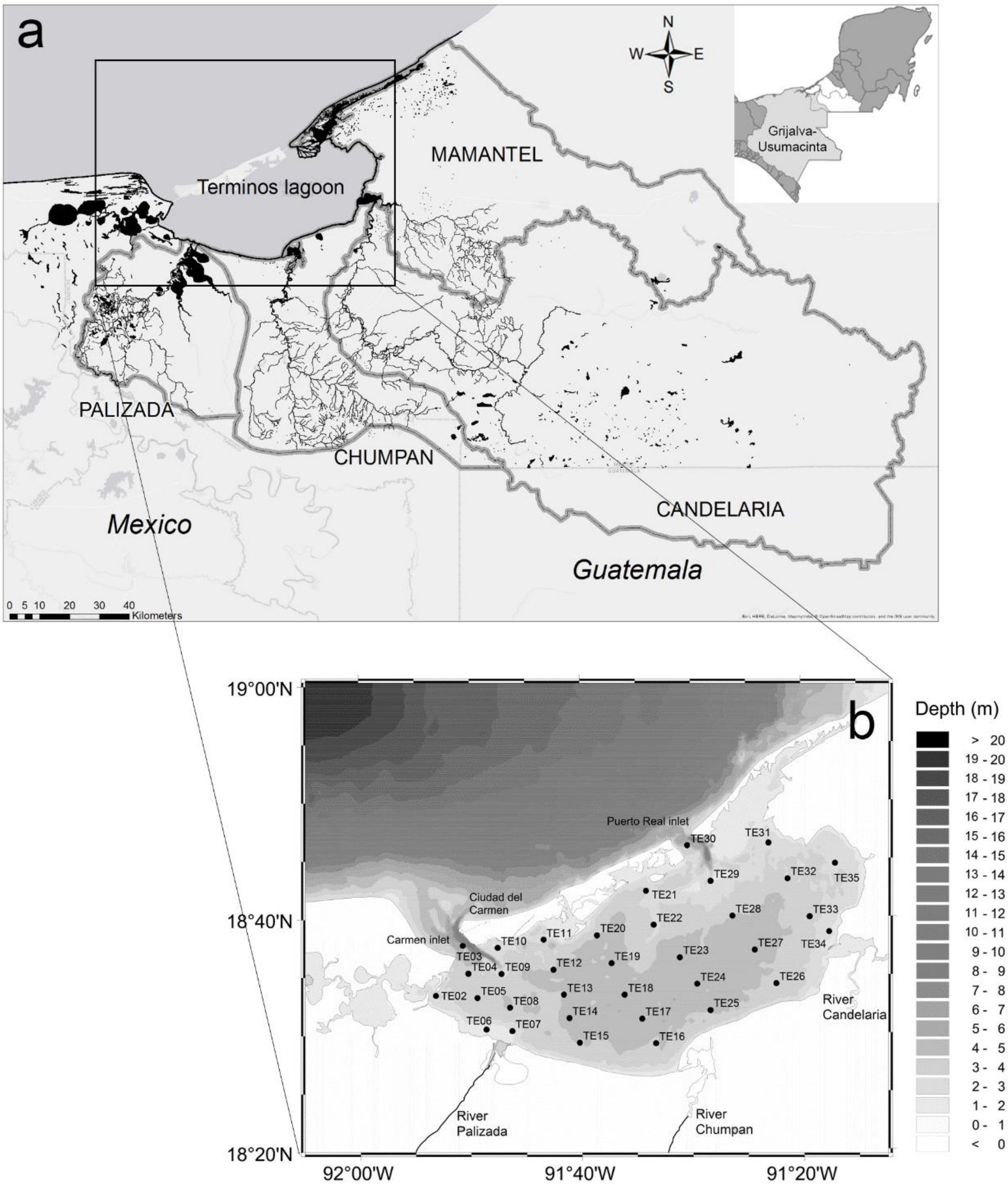

Figure C.1 (a) Main and detailed watersheds contributing to freshwater inputs to the Terminos Lagoon and (b) bathymetry of Terminos Lagoon with location of sampling stations.

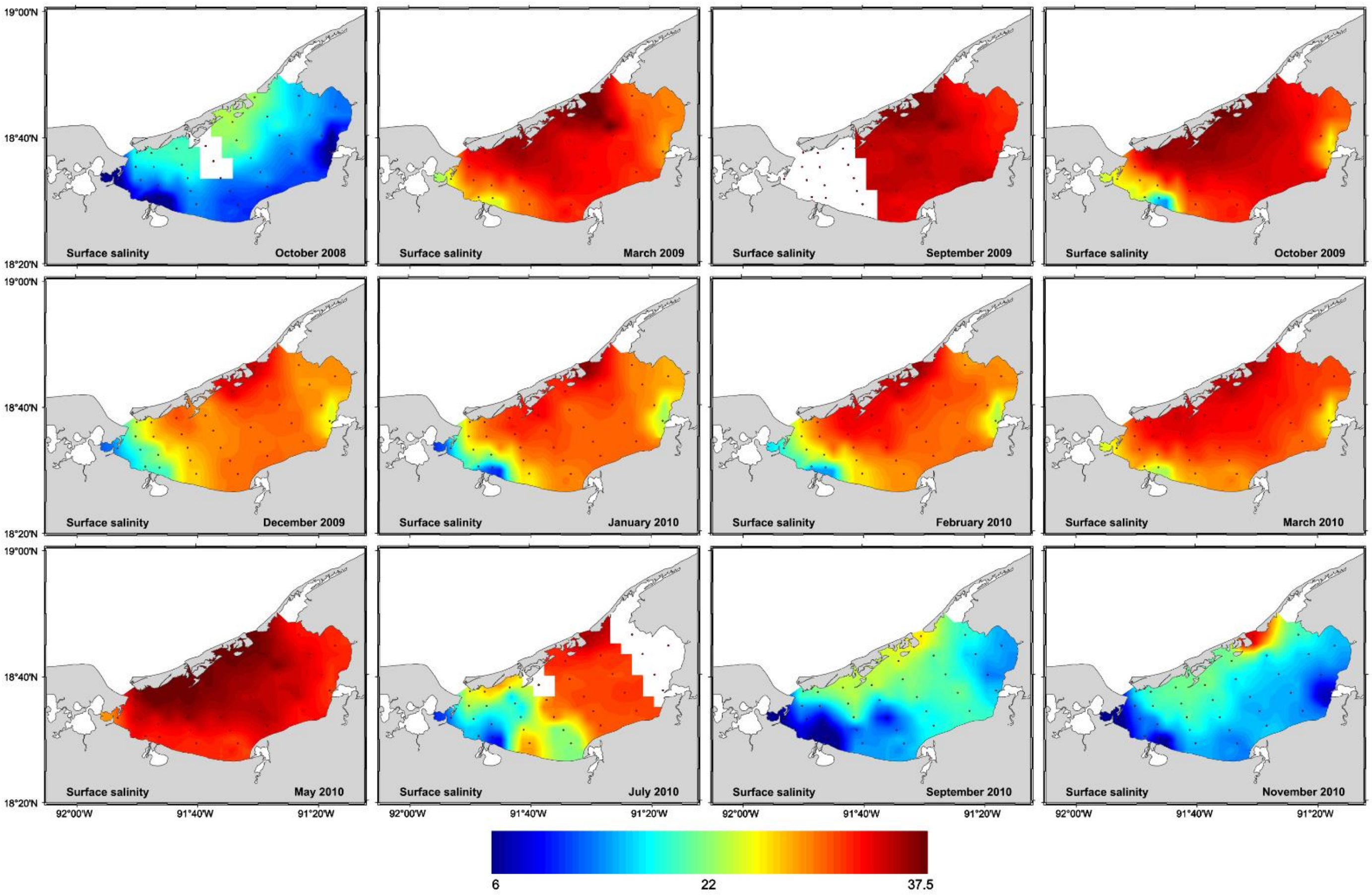

Figure C.2 Distribution of salinity (0 to 75 cm surface layer average) in Terminos Lagoon from October 2008 to November 2010. The November 2008 salinity distribution has not been reported for practical editing format reason and because it was very similar to the October 2008 distribution.

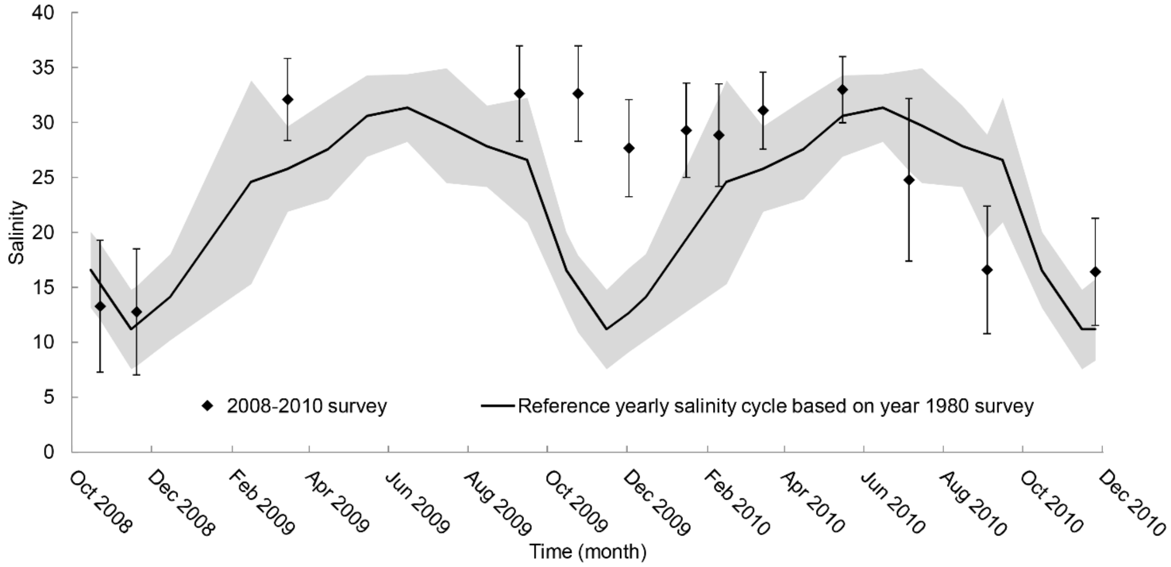

Figure C.3 Monthly evolution of salinity averaged over the whole Terminos Lagoon during the 2009-2010 survey (black dots ± standard deviation as vertical bars) and comparison with a reference yearly cycle dating from 1980 (Yanez-Arancibia et al., 1983) (continuous black line ± standard deviation as gray shade).

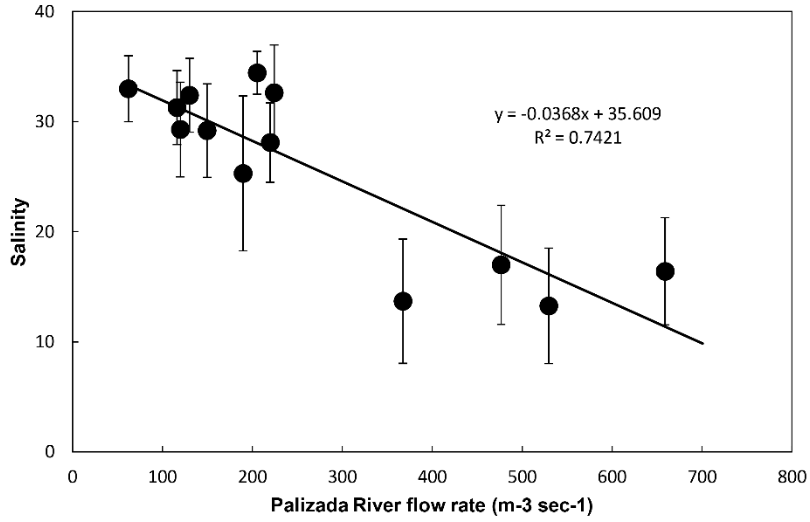

Figure C.4 Relationship between average salinity in Terminos Lagoon (black dots ± standard deviation) and monthly averaged Palizada River discharge from October 2008 to November 2010. Linear regression line (black straight line) has been plotted together with equation and determination coefficient (R^2).

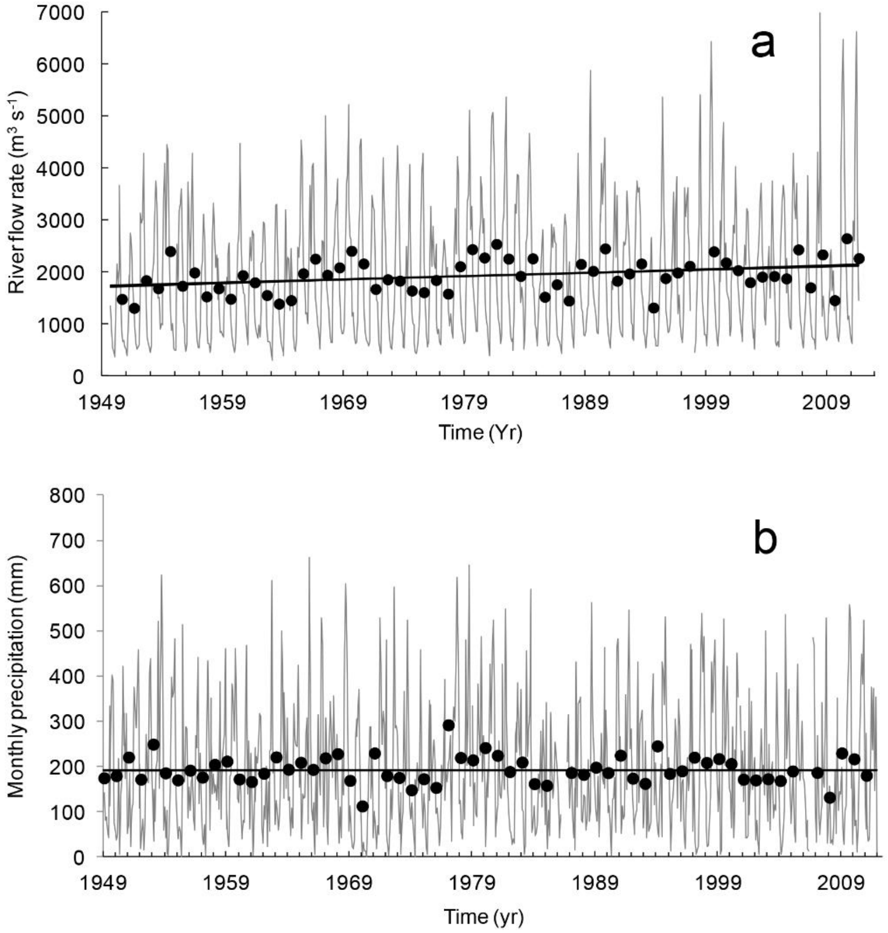

Figure C.5 (a) River discharge in $m^3\ s^{-1}$ averaged on a monthly (gray line) and yearly (black dots) basis, and (b) monthly precipitation rates in mm (gray line) and averaged on a yearly basis (black dots), at Boca del Cerro station during the 1948-2011 period. Added linear regression lines (black line) are from yearly averaged values (black dots).

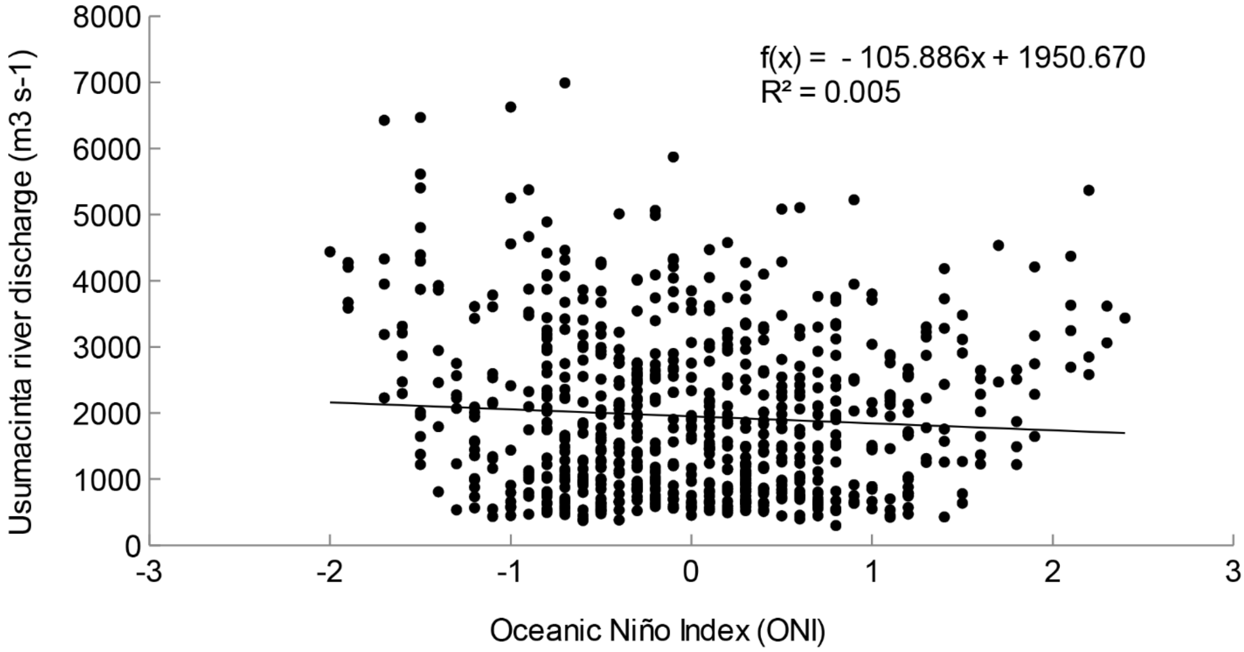

Figure C.6 Relationship between NOAA Oceanic Niño Index (ONI) and monthly averaged river flow rates at Bocca del Cerro station using a positive time shift of 2 months. Linear regression line (black straight line) has been plotted together with equation and determination coefficient (R^2).

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Variabilité spatiale et temporelle des cycles biogéochimiques à l'interface eau-sédiment dans la lagune lagune de Terminos, Mexique

L'objectif de cette thèse concerne la quantification des flux benthos-pélagiques dans une lagune soumise à un régime climatique tropical rythmé de périodes humides et périodes sèches. La lagune de Terminos, située au sud du golfe du Mexique, le long du plateau de Campeche, est le plus vaste écosystème laguno-estuarien du Mexique (2000 km^2). Du fait de sa faible profondeur (3.5 m en moyenne), les processus benthiques sont sensés participer activement à l'ensemble du cycle biogéochimique de cet Ecosystème. Les mesures de flux benthiques ont eu lieu au cours de campagnes de terrains sur un réseau de 13 stations pendant une saison sèche (mars 2009 et 2010) et une saison humide (octobre 2009 et novembre 2010). Quatre stations de ce réseau ont fait l'objet de mesures plus fréquentes entre 2008 et 2010. Des incubations *ex-situ* de carottes de sédiment prélevées au moyen d'un carottier monotube ont permis de mesurer la variabilité spatio-temporelle des taux de respiration benthique (SOD) et des flux de sels nutritifs. Les SOD sont significativement différents entre les périodes sèches et humides (1327±161 et 2248±359 µmol m^{-2} h^{-1} respectivement). Les flux de silicates sont significativement plus importants pendant la saison des pluies (89.4±15.9 µmol m^{-2} h^{-1}) que pendant la saison sèche (46.5±11.4 µmol m^{-2} h^{-1}). Les flux de phosphates, faibles tout au long des périodes étudiées, n'ont pas montré de différence significative. Les flux d'azote dissous (DIN) sont de même intensité mais de sens opposé (2.9±18.8 µmol m^{-2} h^{-1} et 24.3±7.3 µmol m^{-2} h^{-1}). Ces flux caractérisés par un fort signal saisonnier sont fortement corrélés avec les caractéristiques biogéochimiques des sédiments (Corg, N et chloropigments) et contribuent significativement au bilan du carbone et des éléments associés.

Mots Clefs : Cycles biogéochimiques, écosystème estuarien, matière organique, respiration benthique, changement climatique, mineralisation.

Spatial and temporal variability of biogeochemical cycles at the sediment-water in Terminos lagoon, Mexico

The goal of this study concerns the quantification of sediment-water fluxes in a tropical lagoon under climatic forcing regulated by successive dry and wet periods. Terminos lagoon on the South coast of Gulf of Mexico (Campeche sound) is a shallow (3.5 m) but vast estuarine system (2000 km^2) where the sediments are supposed to contribute largely to the overall biogeochemical cycling. Benthic flux measurements were performed twice over a network of 13 stations during dry (March 2009 and 2010) and wet periods (October 2009 and November 2010). A selection of 4 stations from this network were visited more frequently between 2008 and 2010. Sediment Oxygen Demand (SOD) and nutrient fluxes were measured through *ex-situ* incubations of sediment cores sampled manually. SOD were significantly different between both dry and wet seasons (1327±161 and 2248±359 µmol m^{-2} h^{-1} respectively). Silicates fluxes were significantly more intense during the wet season (89.4±15.9 µmol m^{-2} h^{-1}) than during the dry one (46.5±11.4 µmol m^{-2} h^{-1}). Phosphate fluxes, low during all periods did not show a temporal trend. Finally DIN fluxes showed a net uptake during the wet season (2.9±18.8 µmol m^{-2} h^{-1}) and conversely an efflux during the dry season (24.3±7.3 µmol m^{-2} h^{-1}). These fluxes depicted a pronounced seasonal signal, showed a significant correlation to sediment characteristics (Corg, N and chloropigments) and finally contributed to the overall carbon and nutrient budget of the lagoon.

Key words: Biogeochemical cycles, estuarine ecosystems, organic matter, benthic respiration, climate change, mineralization.