



Trophic status of a coastal lagoon - marine harbor system: Potential outwelling rates to the Mesoamerican Barrier Reef southern region

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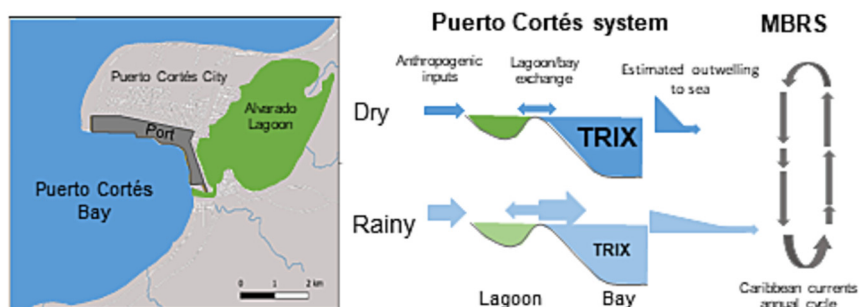
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HIGHLIGHTS

- The Puerto Cortés System is hyper eutrophic based on the TRIX index.
- Net community production and respiration was high like other tropical and subtropical systems
- Estimated outwelling nutrient and particulate matter concentrations offshore were high.
- Estimated fluxes of buoyant matter varied several-fold based on the approach used.
- Coastal organic and inorganic nutrients are expected to reach and impact the MBRS.

GRAPHICAL ABSTRACT



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ABSTRACT

Eutrophication is still a serious problem in many coastal areas, including the tropics, where river discharges of nutrients is usually high. The ecological stability and ecosystem services of the Mesoamerican Barrier Reef System (MBRS), the world's second-largest coral reef system, suffer a generalized impact by riverine discharge of sediment and organic and inorganic nutrients, which may lead to coastal eutrophication and a coral-macroalgal phase shift. However, few data exist on the MRBS coastal zone status, particularly in Honduras. Here, two in situ sampling campaigns were carried out (May 2017 and January 2018) in the Alvarado Lagoon and Puerto Cortés Bay (Honduras). Measurements included water column nutrients, chlorophyll-a (Chla), particulate organic and inorganic matter and net community metabolism, completed with satellite images analysis. The lagoon and bay environments are ecologically different systems and present different sensitivities to seasonal changes in precipitation as shown by the multivariate analysis. Nonetheless, net community production and respiration rates were neither different spatially, nor seasonally. In addition, both environments were highly eutrophic as shown by the TRIX index. Thus, the Puerto Cortés system represents an important source of dissolved nutrients and particulate matter to the coastal zone. Even though offshore, water quality, based on estimated outwelling rates from the Puerto Cortés system to the coastal waters of the southern MRBS region, improved considerably, concentrations of Chla and nutrients remained higher than those typically measured in non-polluted coral reefs in the Caribbean region and the suggested threshold values. In situ monitoring and assessment of these aspects are crucial to evaluate the ecological functioning of and threats on the MBRS, and elaborate and implement adequate policies for integrated management given its regional and global importance.

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1. Introduction

Eutrophication due to human activities is still a serious problem in many areas of the planet. In the tropics, the major causes of coastal eutrophication are uncontrolled organic matter and nutrient inputs from port activities, untreated municipal and industrial wastewater discharges, and runoff from agricultural land (Seitzinger et al., 2010; Peyman et al., 2017). Seaports and the adjacent coastal areas are particularly prone to eutrophication because ports are usually built in semi-enclosed bays or estuaries in close proximity to densely populated areas that are hot spots of additional commercial and industrial activities (Lee and Arega, 1999; Gómez et al., 2015; Jahan and Strezov, 2017). In addition, the environmental impact of ports in adjacent marine ecosystems also includes the release of ballast waters from ships and polluted waters from shipping, container and adjacent industrial activities (fecal, hazardous compounds and pathogens) and dredging (Byrnes and Dunn, 2020; Polrot et al., 2021) which can increase further the probability of eutrophication (Ng et al., 2015; Jahan and Strezov, 2017; Islam and Tanaka, 2004; Polrot et al., 2021; Yudhistira et al., 2022). Thus, point and diffuse pollution from these sources alter coastal biogeochemical cycles and ecosystem functioning in many ways producing habitat loss, decrease in biodiversity, low oxygen concentrations and massive mortality events during dystrophic crises, harmful micro- and macroalgae blooms, and even negative effects on human health (Diaz and Rosenberg, 2008; Levain et al., 2020; Ménesguen and Lacroix, 2018). This trend is expected to increase in developing countries, particularly in the tropics, where river discharges of total N, P and organic C is double that of northern temperate zones (Seitzinger et al., 2010).

The Mesoamerican Barrier Reef System (MBRS) extends over 1000 km, being the largest continuous coral reef of the western hemisphere and the second largest in the world (Paris and Chérubin, 2008). It sustains a high level of marine biodiversity providing ecosystem services and natural resources to local populations (Alastair et al., 2001; Heyman and Kjerfve, 2001). Coral reefs in the Gulf of Honduras are affected by various natural and anthropogenic disturbances and stresses (Kramer and Kramer, 2002). Among them, MBRS suffers a generalized impact by riverine discharge of sediment and organic and inorganic nutrients that is further aggravated during extreme weather events like tropical storms and hurricanes (Heyman and Kjerfve, 2001; Sheng et al., 2007; Paris and Chérubin,

2008; Lapointe et al., 2021; Berger et al., 2022). Export of organic matter and inorganic nutrients (outwelling) from highly productive tropical ecosystems along the coast, like mangroves and lagoons, via the local currents (cyclonic gyre close to North of Honduras coast) (Paris and Chérubin, 2008; Berger et al., 2022) can further affect negatively the ecology and net metabolism of coastal waters of the Gulf of Honduras and the MBRS. Thus, an increase in nutrients may enhance eutrophication and macroalgal growth leading potentially to a coral-macroalgae phase shift, with macroalgae covering and replacing corals, a phenomenon occurring worldwide, including in the Caribbean (Gardner et al., 2003; Littler et al., 2006; Arias-González et al., 2017).

Puerto Cortés is both one of the largest cities in the area (136,000 inhabitants in 2020) and one of the largest and busiest seaports in the Gulf of Honduras (Pérez, 2012; Caviedes et al., 2014) (Fig. 1). The port is closely connected to the mouth of the Alvarado coastal lagoon. The lagoon receives sediment, organic matter and inorganic nutrients from several sources: untreated wastewater from San Pedro Sula city together with surface runoff from the basins of the Chamelecón and Ulúa rivers and wastewater from the Puerto Cortés city. These make the Alvarado Lagoon - Puerto Cortés Bay system a potentially important source of high organic matter, inorganic nutrients and suspended solids contamination for the adjacent coastal zone, including the southern section of the MBRS. The impact of contamination likely changes during the dry and rainy seasons due to rain-dependent differences in land run-off. However, ecological and biogeochemical processes in tropical urbanized estuarine areas are considerably understudied compared with similar cases in temperate climates (Oczkowski et al., 2020), jeopardizing our ability to estimate their contribution to nutrient outwelling to the coastal zones.

The purpose of this study is to explore whether the outwelling of organic and inorganic nutrients, both of natural and anthropogenic origin, from the Alvarado Lagoon - Puerto Cortés Bay system are high and due to the marine water circulation can potentially affect the MBRS an area of high ecological value. First, we evaluated the water column concentrations of dissolved inorganic nutrients, particulate matter, rates of primary production and net metabolism, and estimated the trophic status of the Alvarado Lagoon - Puerto Cortés Bay system. Then, we estimated for the first time their potential contribution to the outwelling of inorganic nutrients and organic carbon in the adjacent MBRS region. Our results highlight

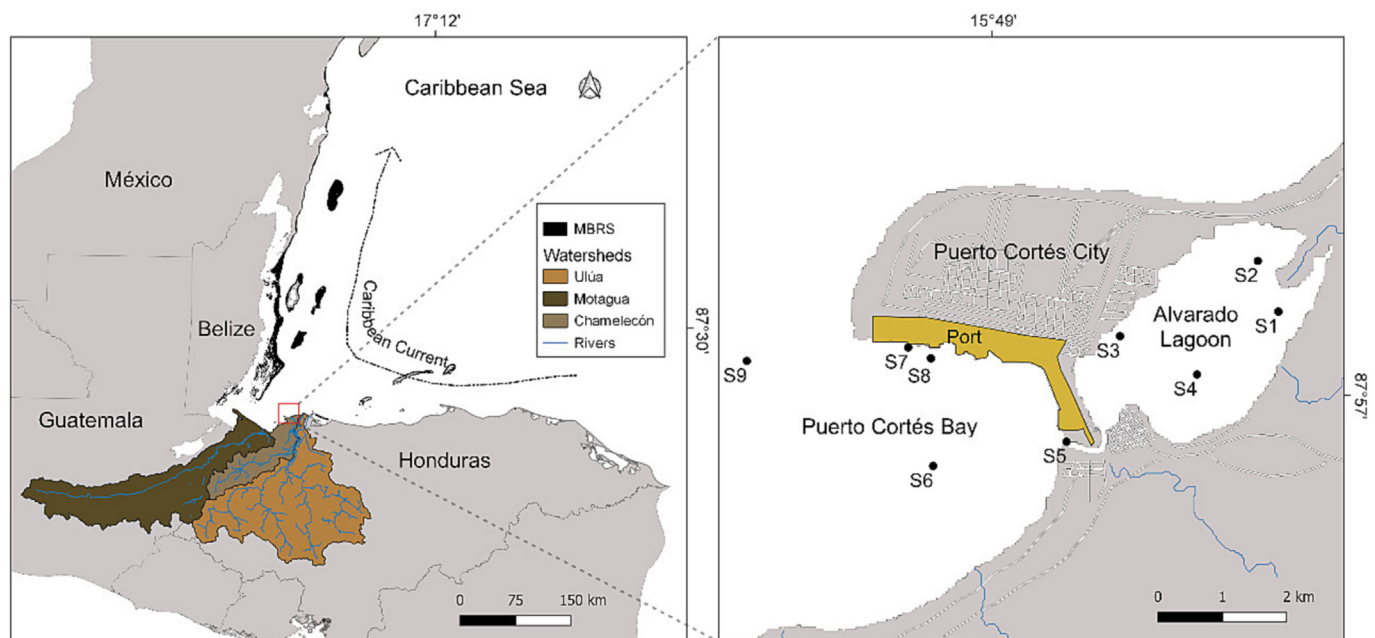


Fig. 1. Map of the Puerto Cortés system study area indicating the location of the sampling stations in the Alvarado Lagoon (S1-S5) and the Puerto Cortés Bay (S6-S9). Insert map shows the geographical area of the Mesoamerican Barrier Reef System. The principal river watersheds outwelling in the Gulf of Honduras are indicated on land and the reefs are shown in the sea.

the need to design regional cross border management strategies for the MBRS region, from the river basins to the coastal zones and coral reefs to sustain the important ecosystem services the latter provide.

2. Material and methods

2.1. Description of the study site

The Alvarado Lagoon and Puerto Cortés Bay system is located in Honduras, in the MBRS region (Fig. 1). The lagoon has an area of 8.4 km² and an average depth of 4.5 m, being permanently connected to the bay through an estuarine mouth of 120 m wide and about 4 m deep (Carrasco Navas-Parejo and Flores, 2008). The lagoon is heavily impacted by human activities, mainly related to extended low density urban development. Natural habitats loss has been extensive although remnants of mangroves are still present on the southwest shoreline. The lagoon receives freshwater inputs through several small rivers and channels contaminated with untreated municipal wastewater (Carrasco Navas-Parejo and Caviedes, 2014). In addition, it receives water run-off from oil palm crops in the catchment area, an important source of inorganic nutrients due to uncontrolled fertilizer use.

The Puerto Cortés Bay has an area of 14 km² and an average depth of 11.5 m (Carrasco Navas-Parejo and Flores, 2008). Puerto Cortés is the main commercial port in the MBRS region and one of the main ports in the Caribbean region and Latin America (Pérez, 2012; Caviedes et al., 2014). The area adjacent to the Puerto Cortés Bay is densely populated (e.g. San Pedro Sula city) with waste ending up in various surrounding rivers due to deficient wastewater treatment systems (Burke and Sugg, 2006; Carrasco Navas-Parejo and Caviedes, 2014). The bay is strongly influenced by the discharges of Ulúa, Chamelecón, and Motagua rivers, whose basins exceed 49,000 km², extending over several countries, and are heavily affected by activities related agriculture and especially to oil palm monoculture (Berger et al., 2022).

2.2. Collection of samples

Nine sampling stations were established, five in the lagoon (S1- S5) and four in the bay (S6 - S9), in order to cover the environmental spatial heterogeneity of the study area (Fig. 1). One sampling campaign was carried out in each of the two predominant seasons, one at the end of the dry season (25–28 May 2017) and a second at the end of the rainy season (9–12 January 2018) to represent the two temporal extremes (Fig. S1). On each sampling campaign, vertical profiles of the water temperature, salinity, dissolved oxygen, and pH were recorded using a YSI-556 multiparameter probe by taking measurements every 25 cm from the surface to the bottom. Vertical profiles of Photosynthetically Active Radiation (PAR) were measured with a LiCor 250A radiometer equipped with a spherical sensor at the same resolution to estimate the light extinction coefficient with depth (k). Water column samples were collected during low tide using a 2.5 L Van Dorn bottle 0.5 m below the surface and 0.5 m above the sea bottom. In the bay, an additional sample was collected from the middle of the water column. The collected water samples were stored in carboys fully covered in ice until returning to the laboratory (within eight hours) for further processing.

2.3. Laboratory analyses

Once in the laboratory, 500 mL of water from each station and depth were filtered through pre-combusted and pre-weighed fiberglass filters (Whatman GF/F, 0.7 µm nominal pore size). The filters used for the determination of particulate organic carbon (POC) and particulate total nitrogen (PTN) were dried at 60 °C for 24 h and weighed. POC content was determined as the difference between total particulate carbon measured in a non-combusted filter and particulate inorganic carbon measured on the second replicate filter after combustion at 450 °C for 5 h. Both filters were analyzed on an elemental analyzer (LECO CHNS 932) (Analytical Central

Services, A Coruña University) (Kristensen and Andersen, 1987). Unfortunately, additional filters collected to measure total suspended solids (TSS) and chlorophyll-a (Chla) were lost during storage. Samples for inorganic nutrients were filtered through fiberglass filters (MF-300 Fisherbrand® 0.7 µm nominal pore size) and stored in a freezer at –20 °C until analyses. Inorganic nutrients were determined according to standards methods (Baird and Bridgewater, 2017): ammonium (4500-NH₃ F), nitrite (4500-NO₂⁻ B), nitrate (4500-NO₃⁻ B), phosphate (4500-P C) and dissolved silica (4500 - SiO₂) on a UV 1700 Pharmaspec Shimadzu spectrophotometer at the Analytical Services of Honduran Foundation of Agricultural Investigation.

2.4. Primary production and dark respiration rates

Primary production rates were measured by in situ incubations at each sampling site. Water was collected from the same depths as for the rest of the analyses, used to fill three transparent and three dark Winkler bottles (~ 300 mL), and incubated in situ at the corresponding depth for a maximum of 5 h, always between 8:00 and 13:00. Incubations were initiated during the day to achieve maximum irradiance for the light incubation. Incubations were kept as short as possible to minimize bottle effects or the formation of bubbles in these productive systems. Initial and final oxygen concentrations in the Winkler bottles were measured using an Oxygen Probe (YSI EcoSense OD 200).

Net primary production (NPP) and dark respiration hourly rates were estimated from the changes in O₂ concentrations in the transparent and dark bottles, respectively and transformed to daily depth-integrated water column net community production (NCP) and dark respiration (R) as described in Carrasco et al. (2020). Given that incubations were performed around midday and at maximum irradiance, rates should be considered maximum daily potential rates. The production to respiration ratio (P:R) was calculated as the ratio of daily depth-integrated water column gross community production (GCP = NCP + R) to respiration rates (R). Net primary production hourly rates (nNPP) for each station, only at the water column surface, were normalized by dividing with the corresponding Chla concentration estimated from satellite images (see below). A conservative estimate of a C: Chla ratio of 30 was used to estimate the carbon attributed to the phytoplankton (Chl—C) (Jakobsen and Markager, 2016; Putland and Iverson, 2007).

2.5. Sentinel-2A/B and Landsat-8 satellites

To explore in more detail the spatial and temporal variability of water variables in the area of study and to estimate TSS and Chla at the sampling sites on the days of sampling, satellite images were used as described below. Three Sentinel-2A/B cloud-free images (22/05/2017, 12/01/2018 and 22/01/2018) were downloaded as Level-1C (L1C) products from Onda-Dias (<https://catalogue.onda-dias.eu/catalogue/>). In addition, one Landsat-8 cloud-free image (23/05/2017) was downloaded from U.S. Geological Survey (USGS; <https://earthexplorer.usgs.gov/>). The open-access software Sentinel Application Platform (SNAP; <https://step.esa.int/main/download/snap-download/>) was used to process the multispectral images in two steps: (1) the Sentinel-2 bands at different resolutions (10-20-60 m) were resampled (bilinear resampling method) to 10 m spatial resolution (Landsat-8 bands are at 30 m spatial resolution), and (2) the Case 2 Regional Coast Color processor (C2RCC) was applied for generation of Chla and TSM concentration maps (Pereira-Sandoval et al., 2019; Caballero and Navarro, 2021). In brief, the C2RCC algorithm, trained using the Case-2 waters dataset based on a multi-sensor per-pixel artificial neural network method, incorporated an atmospheric and sunlight correction to create Level 2 Bottom-Of-Atmosphere (BOA) surface reflectance products from Level 1 Top-Of-Atmosphere data. The data provided by the algorithm include remote sensing reflectance in addition to a series of automatic products to evaluate water quality such as Chla and TSM concentrations. A square buffer analysis of 30 m was created in QGIS (<https://www.qgis.org>) for each sampling point and imported to SNAP to extract the values

of TSM and Chla from the acquired images nearest to sampling dates (23/05/2017 and 12/01/2018). Scenes were registered in WGS 84 / UTM zone 16 N coordinate system (EPSG: 32616) in QGIS.

2.6. Multivariate Trophic Status Index

To determine the trophic status of the surface of the water, we used the Multivariate Trophic Status Index (TRIX) proposed by Vollenweider et al. (1998) according to the following equation:

$$TRIX = \frac{\log (Chla \times |DO_2| \times DIN \times DIP) + 1.5}{1.2} \quad (1)$$

where, Chla is the concentration of chlorophyll-*a* (mg Chla m^{-3}), $|DO_2|$ is the absolute value of the deviation of the measured O_2 concentration in % saturation with respect to 100 % dissolved oxygen saturation ($100 - O_2$ measured), DIN is the dissolved inorganic nitrogen ($DIN = NO_3^- + NO_2^- + NH_4^+$) in ($\mu\text{g N L}^{-1}$) and DIP is the dissolved inorganic phosphorus determined as phosphate ($\mu\text{g PO}_4^{3-} \text{ L}^{-1}$). The constants 1.5 and 1.2 are scale values entered to adjust the lower limit value of the index and the related trophic scale from 0 to 10 TRIX units (Vollenweider et al., 1998).

2.7. Estimation of outwelling matter

In order to estimate the expected gradient of solutes, i.e. nutrients, as well as of particulate matter in the coastal waters and therefore their potential impact on the MBRS, we estimated two different fluxes, dispersive and advective, to a distance of 30 km from the coast. Both types of fluxes were estimated to facilitate comparison with published studies where only one of the fluxes is estimated. In addition, the total flux would be the sum of both, although it is always dominated by the latter. Most of the MBRS is characterized by a narrow continental shelf (< 10 km) and the reef area is aligned with the coast (Carrillo et al., 2015).

The first estimate used the rates of decrease in the concentration of buoyant matter from terrestrial runoff calculated previously for the waters of the MBRS region (Chérubin et al., 2008). Buoyant matter includes among other components, suspended inorganic particles (e.g., microplastics), particulate organic matter (e.g., phytoplankton and detritus), dissolved nutrients, dissolved organic matter, and dissolved major species (Chérubin et al., 2008; Druon et al., 2010; Galgani et al., 2019). Rates used here were obtained from a transect closest to our system (-0.31 km^{-1} January and 0.17 km^{-1} May 2008, Transect 2, Chérubin et al., 2008). This calculation assumes a conservative behavior for nutrients, similar to that of less reactive buoyant matter. Regardless, phytoplankton will consume quickly part of the nutrients, stimulating coastal primary production, the outwelled nutrients from land will likely reach the MBRS due to prevailing oceanic currents either as dissolved inorganic species or as nutrients assimilated in the phytoplanktonic biomass in the particulate form. The initial slope of the solute gradient was used to estimate the outwelling flux from the Alvarado Lagoon - Puerto Cortés Bay system using the equation:

$$J = D_h \cdot \Delta C / \Delta x \quad (2)$$

where *J* is the outwelling flux of the solute, D_h is the horizontal transport coefficient accounting for both diffusion and dispersion and $\Delta C / \Delta x$ is the initial slope of the offshore solute concentration change with distance (*x*). To the best of our knowledge, D_h coefficients have not been measured in the MRBS area. Lindo-Atichati et al. 2016 estimating D_h using a theoretical approach for a limited area of the Belize Reef area in the MRBS, highlighting the challenge of obtaining in situ values. Here, we use a constant value of $10 \text{ m}^2 \text{ s}^{-1}$ commonly used for passive tracers in the sea, and used previously in studies of the MBRS region (Paris and Chérubin, 2008; Chérubin et al., 2008), similar to that estimated by Lindo-Atichati et al. (2016) for low resolution estimations.

The second estimate of advective fluxes assumes again a conservative behavior, according to:

$$J = C \cdot v \quad (3)$$

by multiplying solute concentration *C* (mol m^{-3}) by water velocity *v* (m d^{-1}). The water velocity is highly variable spatially and seasonally in the MBRS region with reported velocities of almost zero near the reef in January 1999 and a strong northward velocity of 55 cm s^{-1} in April 1999 (Ezer et al., 2005). These two periods correspond to times when cyclonic and anticyclonic eddies were observed near the MBRS, respectively. Here, we used a more recently average estimated velocity, 6.94 cm s^{-1} (6 km d^{-1}), using remote sensing and plastic debris as tracers, off the northern coast of Honduras (range $2\text{--}14 \text{ cm s}^{-1}$; Kikaki et al., 2020). It should be noted that this approximation estimates advective fluxes and assumes that the currents act along the direction of the flow, perpendicular to the coast in this case. Thus, advective fluxes estimated here should be considered as values in the upper range, even though a moderate water velocity was used.

2.8. Statistical methods

To determine differences in the environmental conditions between May 2017 and January 2018 in the Alvarado Lagoon and the Puerto Cortés Bay, we compared each environmental variable using a one-way ANOVA test, followed by multiple comparison procedure (Tukey's pairwise comparison) when statistically clear differences were found. Additionally, in order to compare the overall variation in the environmental conditions across sites and seasons, we performed non-metric multidimensional scaling analysis (nMDS) using all the environmental variables measured. Averaged values for each station in each season included in the analysis were first graphically checked for extreme values or skewed distributions. Salinity, DO, NO_2^- , TSS, PTN, POC: PTN, Chla-C: POC, and *k* were $\log(x + 1)$ transformed prior to inclusion in the analysis. Temperature, pH, NO_3^- , NH_4^+ , PO_4^{3-} , DIN: DIP, Chla, POC, NCP, R, TRIX were also included untransformed. Next, all data were standardized by applying the z-score conversion, dissimilarities calculated based on the Euclidean distance metric, and samples' ordination visualized on a 2-D ordination plot. Differences between seasons and locations were tested applying a one-way PERMANOVA (permutations $n = 9999$). All results are interpreted through the "lens of statistical clarity" sensu Dushoff et al. (2019).

3. Results

3.1. Weather and water column physicochemical conditions

The weather conditions in the area followed the expected pattern of two seasons, a wet and a dry season (Fig. S1). Average rainfall in the period January 2017–June 2017 was 64.3 mm (dry) whereas July 2017–January 2018 was 159.4 mm (wet). Similarly, average maximum temperature was $32.4 \text{ }^\circ\text{C}$ in the dry season and $30.1 \text{ }^\circ\text{C}$ in the wet. No clear differences were recorded for the minimum temperature; on average, it was 22.5 in both seasons.

As a consequence of the meteorological conditions, the physicochemical properties between the lagoon and the bay were clearly different (Table 1). Temperature was lower during the rainy season than in the dry season in both systems (a difference of about $6 \text{ }^\circ\text{C}$), with the difference being higher in the lagoon (Fig. 2A). In contrast, temperature varied little spatially, just a couple of degrees. Salinity reflected clearly the brackish conditions in the lagoon compared to the marine conditions in the bay (Fig. 2B). Seasonal differences were more pronounced in the lagoon. There, during the rainy season, surface salinity was as low as 14 PSU at S1, leading to the formation of a halocline at two meters depth in the deepest zones (S4) (Figs. S2-S3). Oxygen saturation was generally close to 100 %, showing seasonal changes only in the lagoon (Fig. 2C), where, in the rainy season, O_2 saturation levels were extremely low (0.6 %) below 2 m at S3 and S4 (Fig. S2). The pH (6.8–8.0) did not show statistically clear variations, neither between environments, nor between seasons (Table 1). During the dry season, the irradiance

Table 1

Physicochemical and biological characteristics of the water column in Alvarado Lagoon and Puerto Cortés Bay in May 2017 (dry season) and January 2018 (rainy season). In the first two columns, the minimum and maximum values from all depths and seasons in each area are presented for each variable. The averages \pm standard deviation for each ecosystem in the two seasons are presented in the remaining four columns. * Only available at station S6. Superscript letters (a - d) indicate homogenous groups, i.e. groups that share the same superscript are not statistically clearly different ($p = 0.05$, Tukey's pairwise comparison).

Variables	Alvarado Lagoon	Puerto Cortés Bay	Alvarado Lagoon		Puerto Cortés Bay	
	Min - Max	Min - Max	Dry season	Rainy season	Dry season	Rainy season
Temperature (°C)	24.0–32.7	25.5–30.3	31.4 \pm 0.9 ^a	25.4 \pm 1.1 ^b	29.6 \pm 0.6 ^c	26.4 \pm 0.4 ^d
Salinity (UPS)	14.4–34.7	32.6–36.7	32.7 \pm 1.3 ^a	26.7 \pm 8.0 ^b	35.3 \pm 0.3 ^a	35.0 \pm 1.5 ^a
Diss. Oxygen (%)	0.2–106.5	86.4–100.6	89.9 \pm 21.1 ^a	52.1 \pm 36.2 ^b	95.7 \pm 4.6 ^a	92.9 \pm 4.8 ^a
pH	6.8–8.0	6.9–7.9	7.7 \pm 0.4	7.5 \pm 0.2	7.8 \pm 0.05	7.6 \pm 0.3
PO ₄ ³⁻ (μM)	15.9–48.4	14.6–35.5	37.7 \pm 8.5 ^a	23.8 \pm 6.0 ^b	30.7 \pm 4.4 ^c	18.0 \pm 2.3 ^b
NO ₃ ⁻ (μM)	28.4–204.0	56.8–273.2	162 \pm 20 ^a	52.2 \pm 21.8 ^b	185 \pm 42 ^a	71.4 \pm 11.9 ^b
NO ₂ ⁻ (μM)	0.3–4.6	0.3–1.1	0.7 \pm 0.2 ^a	1.7 \pm 1.8 ^b	0.6 \pm 0.2 ^a	0.5 \pm 0.1 ^a
NH ₄ ⁺ (μM)	155–930	313–823	685 \pm 125 ^a	290 \pm 90 ^b	633 \pm 108 ^a	448 \pm 106 ^c
DSi (μM)	19.1–141.5	15.0–102.4	49.0 \pm 16.1 ^a	70.2 \pm 41.2 ^a	22.2 [*]	38.5 \pm 27.7
DIN (μM)	190–1097	377–792	847 \pm 120 ^a	344 \pm 100 ^b	818 \pm 115 ^a	520 \pm 107 ^b
DIN: DIP	7.8–37.8	18.0–37.9	23.6 \pm 7.2 ^{a, b}	15.4 \pm 6.2 ^a	27.1 \pm 15.4 ^b	29.3 \pm 6.5 ^b
TSS (g m ⁻³)	1.8–16.1	1.0–3.9	3.1 \pm 1.6 ^a	7.9 \pm 4.7 ^b	1.6 \pm 0.6 ^c	2.7 \pm 1.1 ^a
Chla (mg m ⁻³)	1.9–20.9	0.15–1.2	12.9 \pm 5.9 ^a	5.5 \pm 3.3 ^b	1.1 \pm 0.13 ^b	0.4 \pm 0.29 ^b
k (m ⁻¹)	0.4–13.8	0.1–0.3	0.8 \pm 0.3 ^a	4.8 \pm 5.3 ^b	0.2 \pm 0.002 ^c	0.3 \pm 0.002 ^{a, c}
NCP (g C m ⁻² d ⁻¹)	0.08–4.03	0.62–3.07	2.18 \pm 0.87	1.17 \pm 1.65	1.74 \pm 1.04	1.52 \pm 0.57
R (g C m ⁻² d ⁻¹)	0.03–0.78	0.11–3.97	0.30 \pm 0.31	0.24 \pm 0.06	0.86 \pm 1.30	1.66 \pm 1.68
nNPP [†]	1.9–18.1	3.9–90.7	8.1 \pm 6.2 ^a	8.4 \pm 4.0 ^a	13.8 \pm 8.2 ^a	70.6 \pm 15.5 ^b
P:R ^{††}	1.20–60.02	1.97–6.30	33.8 \pm 24.9 ^a	14.7 \pm 13.9 ^a	5.25 \pm 1.32 ^a	2.9 \pm 1.71 ^b
POC (g m ⁻³)	0.004–1.29	0.02–0.29	0.45 \pm 0.25 ^{a, b}	0.85 \pm 0.45 ^a	0.07 \pm 0.05 ^b	0.17 \pm 0.05 ^b
PTN (g m ⁻³)	0.002–0.16	0.014–0.03	0.07 \pm 0.04 ^{a, b}	0.12 \pm 0.05 ^a	0.01 \pm 0.001 ^b	0.023 \pm 0.005 ^b
POC: PTN	2.3–9.3	1.7–10.5	6.5 \pm 2.4	8.2 \pm 1.1	5.7 \pm 3.6	8.3 \pm 1.5
Chla-C: POC	5.7–100.0	1.9–100.0	72.6 \pm 32.8 ^a	18.6 \pm 10.7 ^b	60.9 \pm 34.1 ^a	8.7 \pm 8.3 ^b
TRIX	8.3–9.7	6.4–8.4	9.2 \pm 0.4 ^a	9.0 \pm 0.5 ^a	7.9 \pm 0.4 ^b	7.4 \pm 0.7 ^b

[†] nNPP (mg C mg⁻¹ Chla h⁻¹).

^{††} P:R = (NCP + R)/R.

attenuation coefficient (k) was low and the photic layer reached the sediment surface in some stations in both the lagoon and the bay (Table 1, Fig. S2 - S3). In contrast, during the rainy season, the light extinction coefficient k increased considerably, reducing the depth of the photic layer and increasing the extent of the aphotic sediment surface in this coastal system.

3.2. Dissolved inorganic nutrients

In our study area, concentrations of NO₃⁻, NH₄⁺ and PO₄³⁻ were higher during the dry season, whereas no clear differences could be established for dissolved silica (DSi) (Fig. 3, Table 1). Mean NH₄⁺ concentration during the rainy season was 290 \pm 90 and 448 \pm 105 μM in the lagoon and bay, respectively, being about 2.4 and 1.4 times higher during the dry season. NO₃⁻ concentrations were lower than those of NH₄⁺ but still remarkably high (28.4–273.2 μM). In addition, NO₃⁻ and NH₄⁺ showed higher sensitivity to seasonal changes, increasing 3 and 2.6 times during the dry season in the lagoon and bay, respectively. NO₂⁻ concentrations in both environments were orders of magnitude lower than NO₃⁻ (0.3–4.6 μM) and did not show a consistent seasonal pattern. Dissolved inorganic nitrogen (DIN = NO₃⁻ + NO₂⁻ + NH₄⁺) was dominated by the contribution of NH₄⁺ (~ 81 %) followed by NO₃⁻. Therefore, DIN showed a spatial and seasonal pattern similar to that of NH₄⁺ and NO₃⁻ with higher values during the dry season. PO₄³⁻ concentrations (14.6–48.4 μM) were 1.6 and 1.7 times higher in the lagoon and bay during the rainy season, respectively. In contrast, DSi showed 1.4 and 1.7 times higher concentrations during the rainy season, for the lagoon and bay, respectively (Fig. 3F, Table 1). The mean ratio between DIN and dissolved inorganic phosphate concentrations (DIN: DIP), where DIP = PO₄³⁻, did not vary statistically clearly between the lagoon and the bay during the dry season, whereas in the rainy season, mean DIN: DIP ratio in the latter was almost double that in the lagoon, (29.3 and 15.4, respectively).

3.3. Particulate material and photosynthetic pigments

TSS and Chla spatial distributions in the Alvarado Lagoon-Puerto Cortés Bay system determined by remote sensing during the dry and rainy seasons

showed a clear seasonal variability and a considerable degree of spatial heterogeneity even within each subsystem (Fig. 4, Fig. 5). A large short term variability was also recorded over just a few days. TSS concentrations, estimated from satellite images, were statistically higher in the lagoon during the rainy season (Fig. 4, Fig. 6, Table 1), with the maximum concentration recorded closer to the river mouth (S2: 16.1 g TSS m⁻³). The highest Chla value was also observed in the lagoon during the dry season near the river mouth (S2: 21 mg Chla m⁻³). Mean Chla was about one order of magnitude higher in the lagoon than in the bay and about 2.5 times higher during the dry season in both subsystems (Fig. 6, Table 1).

Mean POC and PTN were 5–6 times lower in the bay than in the lagoon and 2–2.3 times higher during the rainy season in both subsystems. However, only in the bay, were seasonal variations clear statistically (Fig. 6, Table 1). The POC: PTN ratio was similar in both areas, being lower in the dry season (~ 6.5 vs ~ 8.3) (Fig. 6, Table 1). The Chla-C: POC ratio was higher during the dry season, about 73 and 61 % for the lagoon and bay respectively, compared to 19 and 9 % during the rainy season, being always slightly higher in the lagoon (Fig. 6, Table 1).

3.4. Primary production, respiration and TRIX index

Water column depth-integrated net community primary production (NCP) ranged between 0.08 and 4.0 g C m⁻² d⁻¹ (Table 1). In general, NCP tended to be higher during the dry season in both the lagoon and the bay, but values were not clearly different. No clear differences in NCP were found between the two environments either (Fig. 7). Both the highest and lowest average values were observed in the lagoon during the dry (2.18 g C m⁻² d⁻¹) and rainy season (1.17 g C m⁻² d⁻¹), respectively. In the bay, seasonal changes in NCP were less evident (Fig. 7, Table 1).

No clear differences in the daily depth-integrated community respiration rate (R) were found between the bay and the lagoon (Table 1, Fig. 7). High R was observed in S7 and S8, located in front of the port in the bay, during both seasons. The mean P: R ratio was always >1, suggesting that the planktonic community was net autotrophic in both systems and seasons. The P: R was highest in the lagoon during the dry season (33.8 \pm 24.9) and lowest in the bay during the rainy season (2.9 \pm 1.7) (Table 1).

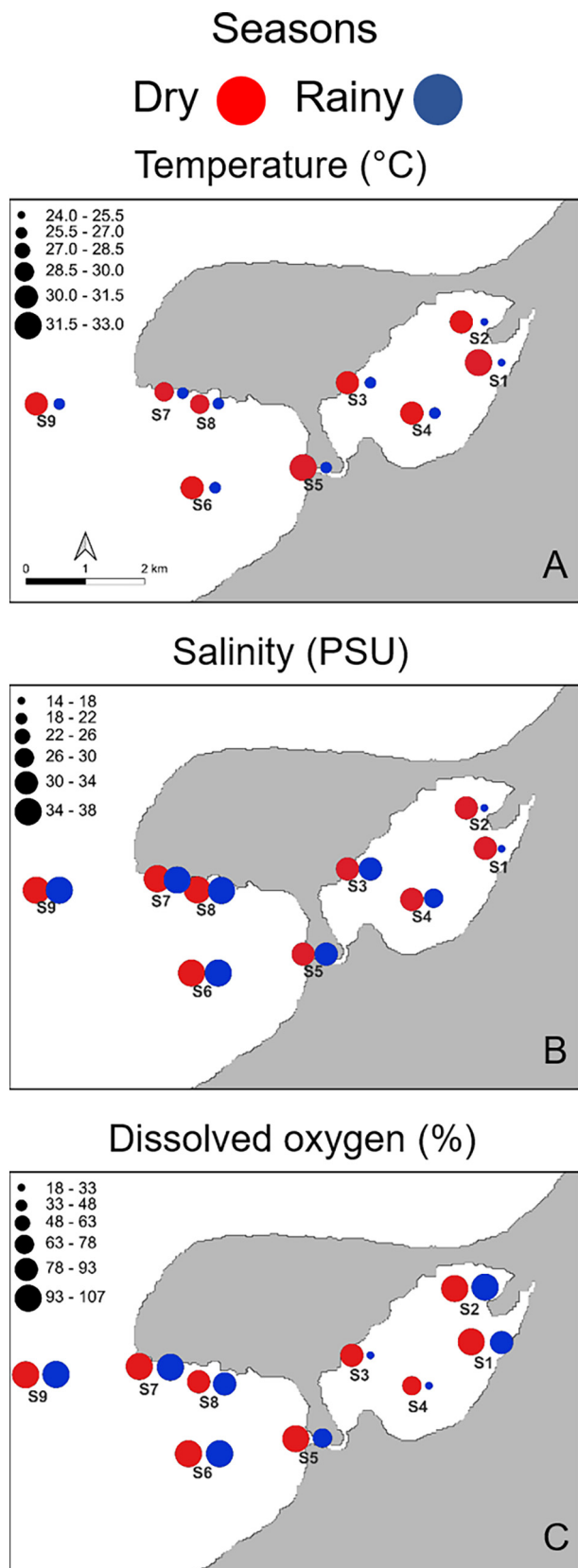


Fig. 2. Seasonal and spatial variation of (A) temperature (°C), (B) salinity (PSU) and (C) dissolved oxygen (%) in the water column of the Alvarado Lagoon (S1-S5) and Puerto Cortés Bay (S6-S9) in May 2017 (dry season, in red) and January 2018 (rainy season, in blue). Values represent averages of values recorded at the different layers depending on station ($n = 1-3$).

Hourly rates of net primary production normalized to Chla (nNPP) presented evident seasonal variations in the bay but not in the lagoon (Table 1, Fig. 7). The highest mean nNPP values were observed during the rainy season (8.40 and 70.6 mg C mg⁻¹ Chla d⁻¹ in the lagoon and bay, respectively). nNPP during the rainy season in the bay was clearly higher to that measured during the dry season or in the lagoon at any season.

TRIX ranged between 6.4 and 9.7 for the area of study, indicating a water quality status ranging between eutrophic and hypertrophic (Table 1, Fig. 7). Average TRIX was higher in the lagoon (~ 9.0) compared to the bay (~ 7.6) and increased slightly during the dry season in both environments.

3.5. Multivariate analysis of the lagoon and bay systems

The integrated analysis of all variables by one-way PERMANOVA analysis of the Euclidean dissimilarity distance in the different stations and seasons showed that the differences were statistically clear (Fig. 8, Table S1). The MDS analysis showed a higher degree of environmental variability in the lagoon during the rainy season, particularly for S1 and S2, the most inner and shallower stations of the lagoon during the rainy season. Therefore, the lagoon and the bay can be considered two different ecological systems based on the variables analyzed that are severely affected by season. The variables that correlated more (>0.8) with the first axis were temperature and NH₄⁺, whereas with the second axis were Chla and TRIX.

3.6. Outwelling rates to the MRBS

Although the initial nutrient concentrations at the Puerto Cortés system were always lower during the rainy season, likely due to a higher dilution because of higher fresh water runoff. Thus, although the gradient intensity was lower due to the higher runoff, as indicated by the transport coefficients, the intrusion of the buoyant matter plume into the ocean - which includes dissolved inorganic nutrients - would be larger. Thus, their concentrations at 10–30 km offshore would be higher during the rainy season despite the lower concentrations close to shore compared to the dry season (Table 2).

The calculated outwelling flux of DIN from the Puerto Cortés system was 6.35 and 22.01 mol m⁻² d⁻¹ during rainy and dry seasons, respectively. Similar calculations applied to PO₄³⁻ produced fluxes of 0.31 and 0.90 mol m⁻² d⁻¹ during the rainy and dry seasons, respectively. Using the mean water velocity approach, fluxes of DIN and PO₄³⁻ during the dry and the rainy seasons were two to three orders of magnitude higher than the dispersive ones (Table 3). For the particulate matter, the Puerto Cortés system could be source of 0.06 to 31.8 kg TSS m⁻² d⁻¹, 6.7–2700 g POC m⁻² d⁻¹, 1.1–240 g PTN m⁻² d⁻¹ and 0.04–42 g Chla m⁻² d⁻¹, depending on season and the type of flux estimated (Table 3).

Using the nutrient and Chla offshore gradients, we can also estimate the decrease of TRIX offshore from the Puerto Cortés system assuming a conservative behavior for nutrients and Chla and 100 % oxygen saturation for surface water offshore. TRIX decreases to 4.1 and 4.3 for dry and rainy season respectively at 10 km offshore the AL-PCB system, which represents a good seawater quality and medium eutrophication levels.

4. Discussion

The Alvarado Lagoon and Puerto Cortés Bay (Puerto Cortés system henceforth) are ecologically different systems, as evidenced by the differences in physicochemical and biological properties and the analysis by nMDS (Table 1, Fig. 8). However, they can both contribute to coastal contamination and eutrophication. This system is a clear example of how different types of anthropogenic activities, i.e. a large and active seaport, fertilizer drainage and untreated wastewater discharge, affect the ecological quality of coastal waters. Among these, the most important one for the adjacent watershed areas is that of agricultural production accounting for 92 % of all terrestrial N pollution (Berger et al., 2022). The increased precipitation and more extreme events, like tropical storms and hurricanes,

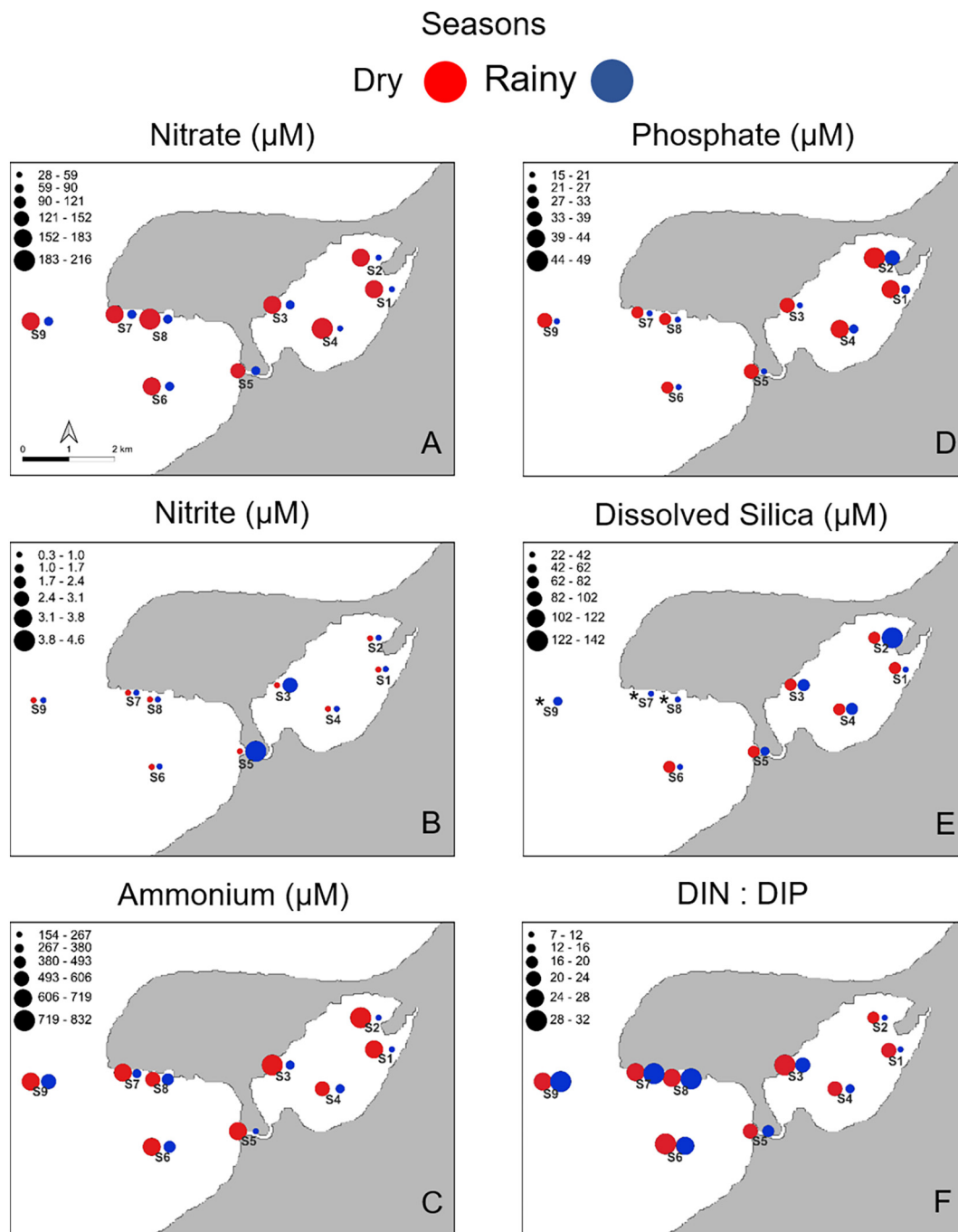


Fig. 3. Seasonal and spatial variation of inorganic nutrients (nitrate, nitrite, ammonium, phosphate and dissolved silica; panels A-E) concentrations in the water column, expressed as μM , and dissolved inorganic nitrogen to dissolved inorganic phosphorus ratio (DIN: DIP; panel F) in the Alvarado Lagoon (S1-S5) and Puerto Cortés Bay (S6-S9) in May 2017 (dry season, in red) and January 2018 (rainy season, in blue). Values represent averages of values recorded at the different layers depending on station ($n = 1-3$). Asterisks in DSI indicate missing values.

during the rainy season compared to the dry one have a higher impact on the connectivity between the watershed and the MBRS coastal ecosystem and the water quality of the latter (Sheng et al., 2007; Paris and Chérubin, 2008). Seasonal precipitations alter the water residence time and outflow rates to coastal waters in the area, not only of sediment and buoyant matter as shown previously (Chérubin et al., 2008), but also of organic and inorganic nutrients as shown here. Therefore, the impact of these pressures depends on the season in this tropical system and requires to be considered for the management of anthropogenic impacts to the coastal system.

4.1. Environmental conditions in the Alvarado lagoon and Puerto Cortés bay

The Alvarado lagoon is a shallow and semi-enclosed water body receiving runoff water through several small rivers running through urbanized areas, channels from agricultural areas and the Ulúa river, the major contaminant of the area (Burke and Sugg, 2006; Berger et al., 2022). As a result, the lagoon is thus more prone to seasonal changes than the Puerto Cortés Bay as suggested by the changes in most physicochemical variables between seasons (Figs. 2-3, Table 1). The lagoon's spatial heterogeneity was also higher, particularly in the rainy season, as shown by the lower

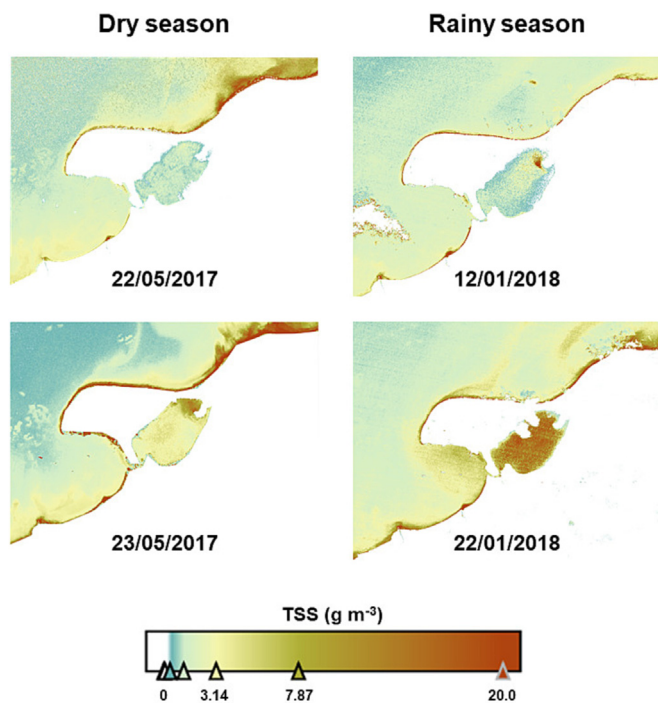


Fig. 4. Concentration of total suspended matter (TSS) in the water, expressed as g m^{-3} , of the Alvarado Lagoon and Puerto Cortés Bay in the dry season (22 and 23/May/2017) and rainy season (12 and 22/January/2018), estimated from satellite images using the Case 2 Regional Coast Color processor (C2RCC).

similarity of the lagoon stations in the nMDS (Fig. 8). The higher input of nutrient-rich freshwater runoff leads to the formation of a halocline in the deeper areas of the lagoon, a more intense stratification that affects mixing, and generates hypoxic - anoxic conditions in the water column below the halocline (S4, Fig. S2). However, at present, the hypoxic-anoxic conditions seem to be restricted in a small area of the lagoon. Due to its relatively shallow depth and freshwater inflow year-round, the water column was for the

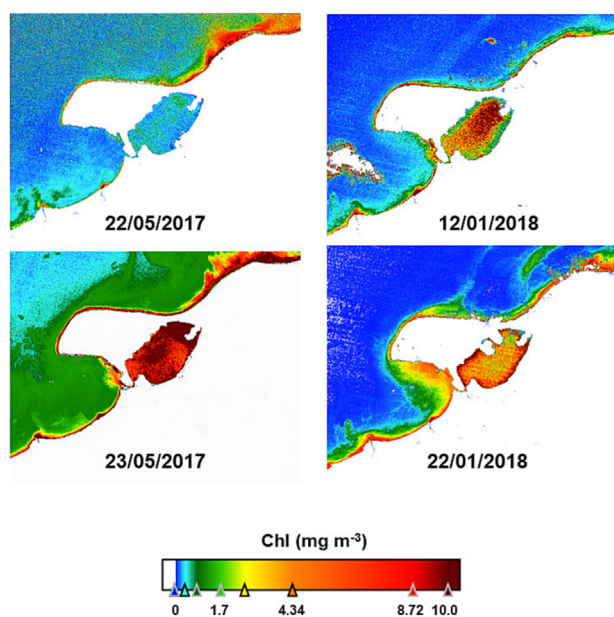


Fig. 5. Concentration of chlorophyll-a (Chla) in the water, expressed mg m^{-3} , of the Alvarado Lagoon and Puerto Cortés Bay in the dry season (22 and 23/May/2017) and rainy season (12 and 22/January/2018), estimated from satellite images using the Case 2 Regional Coast Color processor (C2RCC).

most part well-mixed and oxygenated, even during the dry season, when the higher temperatures could stimulate microbial metabolism and increase O_2 consumption. In contrast, the bay is a more open, clearly marine, environment with lower spatial and seasonal variability than the lagoon. Despite being much deeper, the water column in the bay was vertically homogeneous, as evident from the T, S and O_2 saturation vertical profiles, particularly during the dry season. Moreover, horizontal mixing due to coastal currents was high as expected (Ezer et al., 2005; Chérubin et al., 2008) resulting in small, if any, horizontal differences for most variables studied (Table 1, Fig. 2). Overall, the two subsystems are more similar during the dry season and diverge during the rainy season under the pressure of shifting environmental conditions.

The Puerto Cortés system represents an important source of dissolved inorganic nutrients to the coastal waters of Honduras Gulf and likely contributes to increase the eutrophication levels in the MBRS. Very high concentrations of NH_4^+ (155–930 μM), NO_3^- (28–273 μM) and PO_4^{3-} (15–48 μM) were observed in the water column of the lagoon-bay system. Despite the differences in basic hydrographic properties and in residence time between the two subsystems, the range of concentrations and mean values for the different nutrients were similar in both environments. Overall, seasonal differences were more important than spatial ones (Table 1, Fig. 3). Concentrations during the dry season were 1.4 to 3 times higher, depending on the nutrient, than in the rainy season. Given that riverine discharge in the Gulf of Honduras during the rainy season is about six times higher than during the dry season (Burke and Sugg, 2006; Chérubin et al., 2008), the decrease in nutrients during the rainy season is likely due to a dilution effect as observed in other estuarine systems (Seguro et al., 2015). This is supported further by the inverse trend observed for DSI, reaching up to 70 μM in the rainy season, 1.4 times higher than in the dry season in the lagoon. High concentrations of DSI are common in tropical estuarine shallow coastal areas and generally increase during the rainy season due to higher runoff (Herrera-Silveira, 1994; Sosa-Avalos et al., 2013; Seguro et al., 2015).

Despite their importance for proper monitoring of coastal systems, data on nutrients in the area are scarce. Concentrations of N measured in the vicinity of San Pedro Sula city in 2008 ($>2.8 \text{ mM N}$) (Consortium International MarConsult Inc and CSI Ingenieros, 2010) were orders of magnitude higher than those measured previously in 2003 at several sampling points in the Chamelecón river (Merida et al., 2007) ($57 \pm 42 \mu\text{M NH}_4^+$ and $27 \pm 16 \mu\text{M}$). This increase is most likely an indication of the impact primarily of the fertilizers used increasingly and the livestock in agricultural lands of the Chamelecón and Ulúa watersheds as well as the release of untreated sewage in the rivers (Merida et al., 2007; Carrasco Navas-Parejo and Caviedes, 2014; Berger et al., 2022). Published data clearly show that for the period 1990–2020 the use of fertilizers has increased 2000 % (from 10 to 200 kg/ha) whereas the agricultural land just 4 % (from 33,700 to 35,100 km^2) (The World Bank, 2022). This observation agrees with similar observations for other systems in the wider Caribbean area (Lapointe et al., 2021). The only previous available measurements of inorganic nutrients in the Puerto Cortés bay system date from August 2008. NH_4^+ was around 10 μM , being slightly higher in Puerto Cortés than in the Alvarado Lagoon, NO_3^- below 3 μM in both systems and PO_4^{3-} below the detection limit in the bay and about 2 μM in the lagoon (Consortium International MarConsult Inc and CSI Ingenieros, 2010). Although neither the sampling points nor the sampling month were the same as here, these concentrations were very low compared with those measured in our study 10 years later (Table 1), suggesting a considerable increase in the concentrations in the area and the outwelling of inorganic nutrients to coastal waters of the northern Honduras coast in the last decade (Berger et al., 2022).

The range of NH_4^+ , NO_3^- and PO_4^{3-} concentrations in our study were also much higher than those in other tropical estuarine environment; for instance, the Tempisque estuary in the Pacific coast of Costa Rica (Seguro et al., 2015), Mexican coastal lagoons (Contreras et al., 1996) or the temporarily open-closed estuarine lagoon Los Micos, located in the Gulf of Honduras (Carrasco et al., 2020). The comparison with Los Micos lagoon

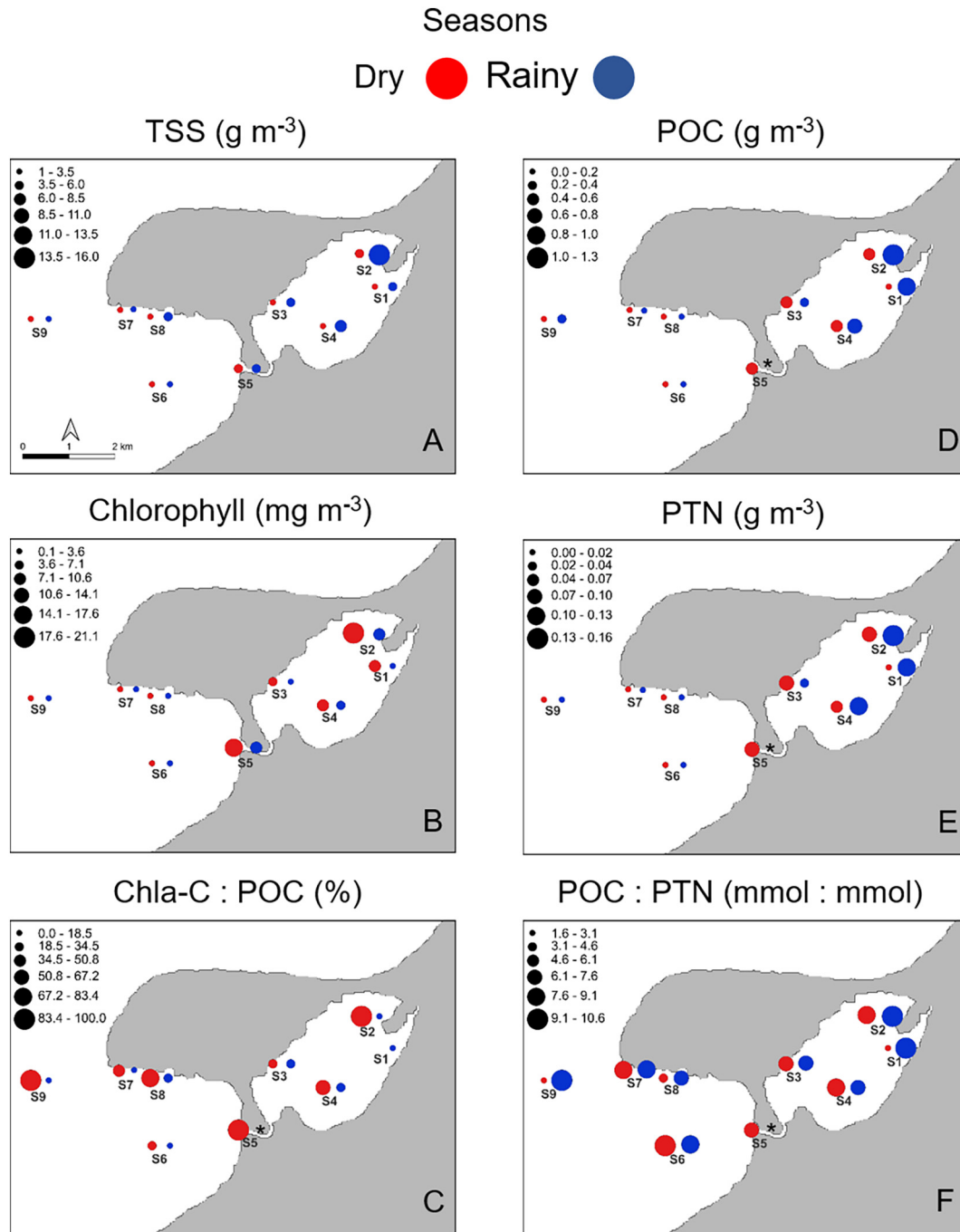


Fig. 6. Seasonal and spatial variation of total suspended solid (TSS), Chlorophyll (Chla), particulate organic carbon (POC), and particulate total nitrogen (PTN) concentrations, POC:PTN ratio and Chla-C: POC (%) in the water column of the Alvarado Lagoon (S1-S5) and Puerto Cortés Bay (S5-S9) in May 2017 (dry season) and January 2018 (rainy season). Values represent averages of values recorded only at the surface layer. TSS and Chla values were extracted from satellite images on the 23/5/2017 and 12/1/2018.

is particularly relevant to analyze the potential impact of two coastal systems with a very different level and types of anthropogenic impact on the coastal waters of the wider MBRS region. Mean annual nutrient concentrations in Los Micos lagoon during the estuarine open mouth phase were up to three orders of magnitude lower than those measured in this study (NH_4^+ : 0.6 μM ; NO_3^- : 8 μM ; and PO_4^{3-} : 12.6 μM , Carrasco et al., 2020). In addition, the annual mean DIN: DIP ratio was about 4.4 ± 5.6 in Los Micos, while in the Puerto Cortés system it was 3–5 times higher showing excessive amounts of N. Another difference is that the dominant form of DIN in Los Micos was NO_3^- . These differences are likely due to the fact that the main anthropogenic impact in Los Micos is drainage of fertilizers from

palm oil crop fields explaining the prevalence of NO_3^- and PO_4^{3-} (Carrasco et al., 2020). In contrast, contamination by untreated domestic wastewater and seaport activities are probably the primary source in the Puerto Cortés system, producing extremely high relative discharges of NH_4^+ , suggesting recent decomposition of organic matter, with respect to NO_3^- and PO_4^{3-} and a high DIN: DIP ratio.

Organic and inorganic particulate matter, similarly to nutrients, was generally higher in the lagoon than in the bay with higher seasonal and spatial variability, resulting also in higher values of the attenuation coefficient in the former (Table 1, Fig. 6). The relatively small size of the lagoon, lower water turnover time, and the direct discharge of several small rivers and

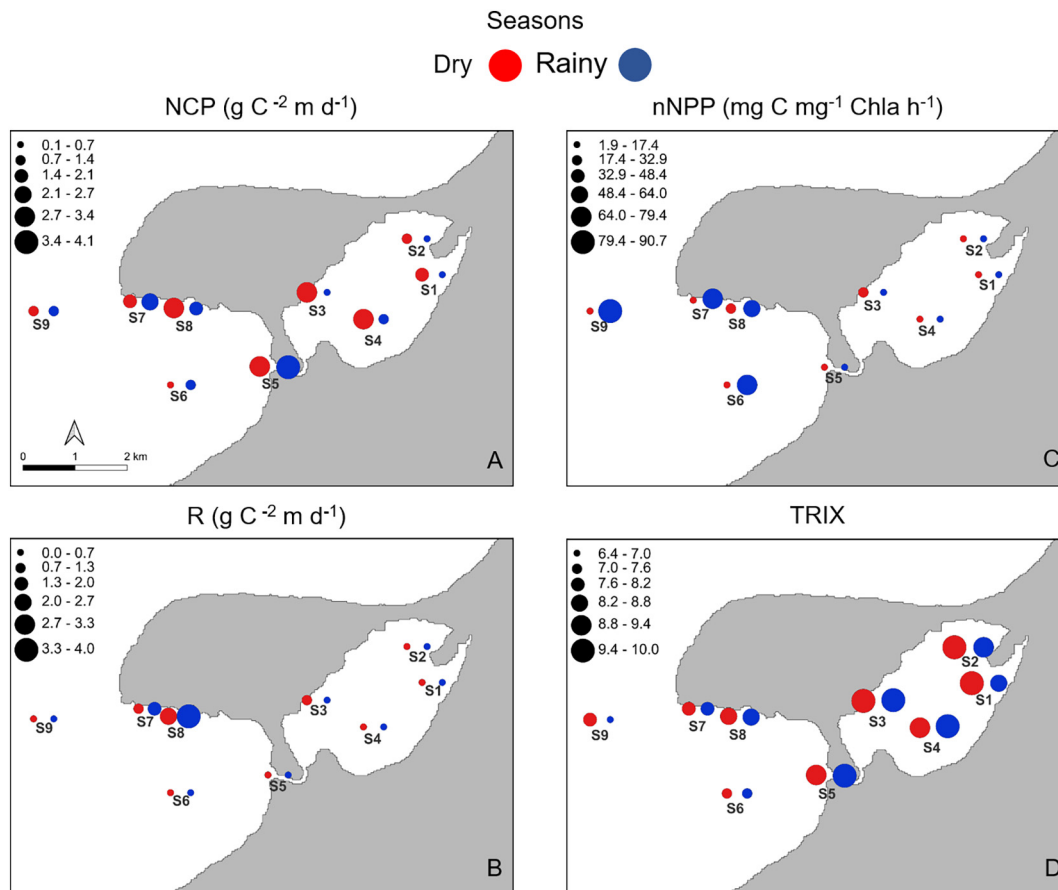


Fig. 7. Seasonal and spatial changes in net community production (NCP), respiration rate (R), net primary production normalized to Chla (nNPP) and the trophic state index (TRIX) in the Alvarado Lagoon (S1-S5) and Puerto Cortés Bay (S5-S9) in May 2017 (dry season) and January 2018 (rainy season). Values for NCP and R represent integrated values for the entire water column based on recorded values at different layers depending on station ($n = 1-3$). nNPP and TRIX were calculated only for the surface layer.

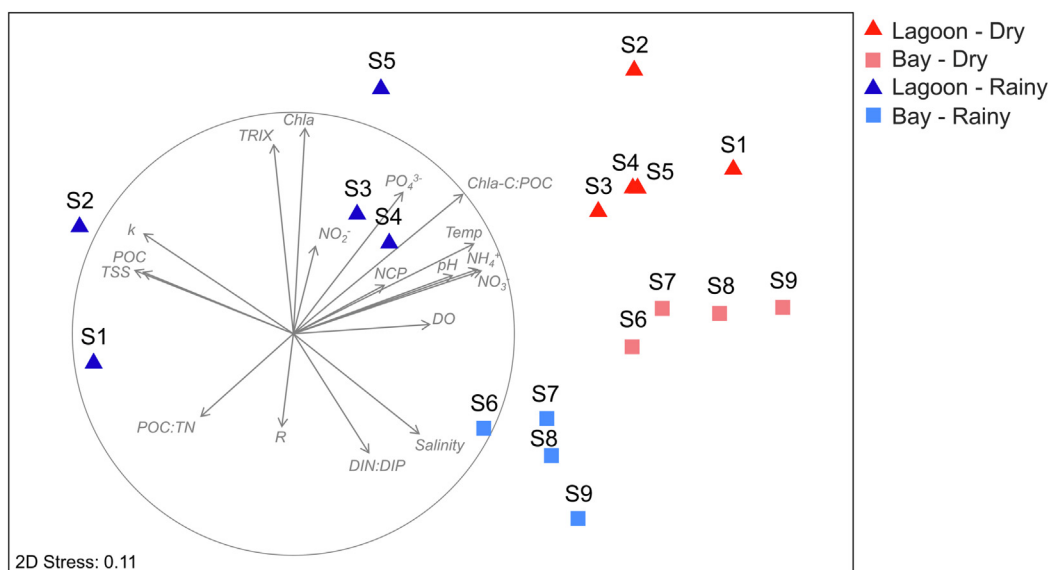


Fig. 8. Non metric multidimensional scaling analysis (nMDS) of sampling stations across seasons in the Alvarado Lagoon (triangles) and Puerto Cortés Bay (squares) in May 2017 (dry season, in red) and January 2018 (rainy season, in blue). Resemblance matrix was calculated from the Euclidean distances based on the environmental and biological properties. The four groups were significantly different based on PERMANOVA (Pseudo-F = 7.342, $p = 0.0001$). The Spearman correlations of the base variables used for the MDS with the ordination plot are overlaid. Chla: chlorophyll α ; TRIX: Trophic Status Index; Temp: Temperature; NCP: net community production; DO: Dissolved oxygen; TSS: total suspended solids; POC: Particulate organic carbon; K: light extinction coefficient.

Table 2

Calculated concentration of inorganic nutrients assuming a similar conservative behavior in the sea as buoyant matter. Calculations are based in the mean nutrient concentration for the Alvarado Lagoon- Puerto Cortés Bay system in the dry and rainy seasons (0 km) and the gradient intensity determined by fitting the buoyant matter data of Transect 2 (Fig. 10c in Chérubin et al., 2008) to a negative exponential with distance (K_m). The slopes of the respective exponential equations were -0.31 and -0.17 km^{-1} in January (dry) and May (rainy), respectively.

Distance (km)	DIN (μM)		NH_4^+ (μM)		NO_3^- (μM)		PO_4^{3-} (μM)	
	Dry	Rainy	Dry	Rainy	Dry	Rainy	Dry	Rainy
0	832.45	432.10	658.85	369.20	173.00	61.80	34.20	20.90
10	39.03	78.94	30.89	67.45	8.11	11.29	1.60	3.82
20	1.83	14.42	1.45	12.32	0.38	2.06	0.08	0.70
30	0.09	2.63	0.07	2.25	0.02	0.38	0.00	0.13

channels makes this system very sensitive to seasonal and random precipitations in its watershed. This is evident in the dramatic changes in TSS and Chla in just two consecutive days (May 22nd and 23rd, Figs. 4 and 5) and shows how random rainy events, occurring even during the dry season, can dramatically affect concentrations. Interestingly, TSS as well as POC and PTN concentrations in the Puerto Cortés system are about 1–2 orders of magnitude lower than in Los Micos Lagoon (Carrasco et al., 2020) and other tropical coastal lagoons in Brazil and India (Costa et al., 2011; Nayar, 2006; Patra et al., 2016). This suggests that contrary to dissolved inorganic nutrients, the overall contribution of the Puerto Cortés system to the particulate load that might affect negatively the coastal environment and the MBRS is low compared with the contribution of big rivers like Motagua, Chamelecón and Ulúa (Thattai et al., 2003; Chérubin et al., 2006). POC: PTN ratio values in the dry season were close to that typical of phytoplankton (Redfield ratio: 6.6) in the dry season (5.7–6.5) and slightly higher in the rainy season (8.2–8.3) with no clear differences between subsystems. The slight increase of POC: PTN in the rainy season is probably due to an increase of the allochthonous particulate organic matter inputs from the watershed, with a lower N content due to either and increased contribution of higher plant material or older and more degraded organic matter (Middelburg and Herman, 2007).

Chla in the Puerto Cortés system ranged between 0.15 and 20.9 mg m^{-3} , being generally higher in the lagoon and in the dry season (Table 1, Fig. 6B). The values of Chla in our system are within the range reported for the Sarstoon-Temash system (Belize) and a little higher than those recorded in Amatique Bay (Guatemala), both considered the most polluted areas in the MBRS area (Yáñez-Arancibia et al., 1995; Consortium International MarConsult Inc and CSI Ingenieros, 2010). However, they are within the low range or below the values observed in Los Micos Lagoon (1.1 – $125.6 \text{ mg Chla m}^{-3}$, Carrasco et al., 2020) and in the low range of those found in other tropical lagoons and lagoon-estuarine systems in Brazil and India (22.7 to 134.1 mg m^{-3} , Costa et al., 2011; 0.87 to 23.11 mg m^{-3} , Nayar, 2006; 5.67 to 37.47 mg m^{-3} , Patra et al., 2016). Comparison of our Chla values with those of other studies should be made with caution because here Chla was estimated by remote sensing. Regardless, the low levels of Chla in the Puerto Cortés system are surprising given the high concentrations of dissolved inorganic nutrients compared with other coastal lagoons and suggest the existence of other potential bottom-up or top-down factors (e.g., DIN:DIP, metal and other contaminant, grazing), limiting the Chla standing stocks in this system.

Table 3

Outwelling fluxes of different dissolved and particulate fractions from the Alvarado Lagoon- Puerto Cortés Bay system during the dry and rainy seasons calculated according to eqs. 2 (dispersive) and 3 (advective) (see text for further explanations). DIN and PO_4^{3-} are in $\text{mol m}^{-2} \text{ d}^{-1}$, TSS, POC, PTN and Chla are in $\text{g m}^{-2} \text{ d}^{-1}$.

Fluxes	Season	DIN	PO_4^{3-}	TSS	POC	PTN	Chla
Dispersive	Dry	22	0.9	62.13	8.19	1.06	0.18
	Rainy	6.35	0.3	77.85	6.76	1.06	0.04
Advective	Dry	4994.4	205.2	14,100	1860	240	42
	Rainy	2592.6	125.4	31,800	2760	429	18

4.2. Water column metabolism and trophic status of the Puerto Cortés system

The range of NCP and R rates in the Puerto Cortés system were slightly lower than those observed during an annual cycle in Los Micos (Carrasco et al., 2020) but comparable with other tropical and subtropical coastal lagoon systems (Anandraj et al., 2008; Hernández and Gocke, 1990) or even higher than those measured in the Gulf of Nicoya (Soria-Pérez et al., 2017), which include some of the most productive coastal environments worldwide (Cloern et al., 2014). Between subsystems and seasons, NCP and R tended to be higher during the dry season and in the lagoon compared to the bay although differences were not statistically clear (Table 1, Fig. 7). A lack of evident seasonality in the NCP and R rates has been observed in other tropical coastal lagoons as well (Contreras et al., 1996; Carrasco et al., 2020). The pelagic community net metabolism in these highly productive environments is likely not limited by ecological drivers such as nutrient availability, temperature or light that are constant year round. Here, neither NCP nor R correlated in a statistically clear way with any of the environmental variables measured. Other drivers such as water residence time, the pelagic autotrophic and heterotrophic biomass ratio and grazing may play a role. The relative weights of these bottom-up and top-down mechanisms are likely to change, compensating each other over the annual cycle even under different environmental conditions, such as different levels of fresh water runoff.

Overall, the pelagic environment of the Puerto Cortés system was net autotrophic, with a P:R ratio always >1 . Therefore, the pelagic community exported C to the sediments and the adjacent coastal waters. Further studies are needed to determine the fraction being stored locally in the sediments and the one outwelled seaward over the course of a year. The P:R ratio was higher during the dry season and in the lagoon in particular, when the seasonal precipitation is lower and therefore the water residence time higher. When net primary production in light was normalized to Chla (nNPP), to take into account the differences in phytoplankton biomass, the highest values were found in the bay, particularly during the rainy season (Table 1), suggesting the presence of a very active phytoplankton community. However, most of this production was consumed in the water column since the R rate was high resulting in the lowest observed mean P:R during the study (Table 1). In fact, the high values of R in S7 and S8, located close to the port, are a worth-mentioning exception and suggest that the port must be a focal point of dissolved organic carbon contamination, probably of wastewater from the Puerto Cortés city, since we did not detect higher values of POC.

TRIX is a helpful tool in management and monitoring facilitating the comparison of the trophic status between different water bodies and between different seasonal periods or years by using simple environmental variables like Chla, O_2 and DIN and DIP (Vollenweider et al., 1998; Tugrul et al., 2019). The Puerto Cortés system scores very high in the trophic scale (7.6–9.08) for both subsystems and seasons (Table 1), indicating a poor water quality status and very high levels of eutrophication, particularly in the lagoon. These values were similar to those measured in the river mouth of three Indonesian bays classified as hypereutrophic (Damar, 2003), but higher than some tropical estuaries in Brazil, which reached a maximum TRIX of ~ 6.5 in their most degraded areas (Alves et al., 2013; Flores-Montes et al., 2011). The slightly higher trophic status in the lagoon is due to its shallow depth and reduced exchange with the bay via the channel, resulting in higher residence time compared to the bay and consequently high nutrient and chla concentrations. In the latter, nutrients and phytoplanktonic biomass are diluted quickly and exported offshore, improving water quality locally, as is often observed in estuaries and in front of river mouths (Damar, 2003; Alves et al., 2013; Flores-Montes et al., 2011; Tugrul et al., 2019).

4.3. Outwelling of nutrients and particulate and potential impact to the MRBS system

The MBRS is highly affected by riverine discharges of dissolved and particulate organic matter, inorganic nutrients, suspended solids and even

plastic debris, which can reach even the most offshore parts of the reef due to the ocean circulation in the region (Chérubin et al., 2008; Carrillo et al., 2015; Kikaki et al., 2020). Model estimations based on the watersheds' contribution in the area suggest that about three-quarters of all nutrients that the MBRS region receives originate from the river discharge in the Guatemala and Honduras coastlines in standard weather conditions and with a higher contribution during tropical storms (Burke and Sugg, 2006; Anderson et al., 2002). However, despite the well-known effects of eutrophication caused by high nutrients concentrations on coral reefs (Wooldridge, 2009; Vega-Thurber et al., 2014; Lapointe, 1997), there are very few data available for the coastal waters of the MBRS region.

Estimated nutrient concentrations even 30 km offshore, particularly during the rainy season (Table 2), were higher than those typically measured in non-polluted coastal reef waters (combined $\text{NO}_3^- + \text{NO}_2^- < 1 \mu\text{M}$ and $\text{PO}_4^{3-} < 0.01 \mu\text{M}$) in the greater Caribbean area (Bellairs Research Institute, 1989, cited in Rawlins et al., 1998; Lapointe, 1997; Lapointe et al., 2019) and the Great Barrier Reef (Bell, 1992; Furnas et al., 2005; Bell et al., 2014). They were also higher than the Eutrophication or Nutrient Threshold Concentrations suggested for both the Caribbean and Great Barrier Reef ($\sim 1 \mu\text{M}$ for DIN and $\sim 0.1 \mu\text{M}$ for DIP) (Bell, 1992; Lapointe, 1997). In addition, the estimated DIN:DIP ratio, assuming always a conservative behavior for both nutrients, was around 20, much higher than the values considered healthy for corals (Furnas et al., 1995). The excess of dissolved inorganic nitrogen from rivers and untreated wastewater, particularly NH_4^+ , outwelled from heavily impacted environments like the Puerto Cortés system can be especially deleterious for organisms in the MBRS (e.g., seagrasses, fish). The average total ammonium levels measured here ($\sim 680 \mu\text{M}$) are above the limits established as toxic for prolonged exposure for many marine species (ANZECC, 2000; Ip et al., 2001; Moreno-Marín et al., 2016) - at a pH of 7.6 and temperature of 30°C the total NH_4^+ measured here produces levels of 0.37 mg L^{-1} unionised ammonia (Emerson et al., 1975). In addition, nutrients can directly stimulate macroalgal growth, favoring the coral-macroalgal phase shifts observed in many reefs worldwide, including the greater Caribbean area, where macroalgae outcompete corals, reduce coral recruitment, and inhibit coral growth (Gardner et al., 2003; Littler et al., 2006; Arias-González et al., 2017; Bell et al., 2014). An increase in nutrients in general and DIN specifically, as well as the high ratio DIN:DIP, can have direct negative effects on coral health (Bell et al., 2014; Lapointe et al., 2021), their resistance to diseases like the black band (Voss and Richardson, 2006) and to bleaching by lowering coral thermal tolerance (Wooldridge, 2009; Carilli et al., 2010; Wang et al., 2018). Therefore, the sensitivity of corals to climate change in the MBRS also increases (Mcfield et al., 2020).

Our data highlight considerable potential impact of nutrient outflowing from coastal environments being subjected to high anthropogenic impacts, such as the Puerto Cortés system, on the MRBS. The calculations of the advective fluxes, i.e. using an estimate using the mean water velocity for the area of study and the mean concentrations measured in the Puerto Cortés system, produced fluxes two to three orders of magnitude higher than the dispersive (turbulent) flux estimations based on the dispersion gradient of buoyant matter (Chérubin et al., 2008); therefore the total flux in the zone is dominated by the former. The seasonal effect on both D_h and v in these estimations is likely to be very important since river runoff increases between 6 and 9 times during the rainy season (Burke and Sugg, 2006; Chérubin et al., 2008, Carrillo 2008, Berger et al., 2022). The accurate evaluation of the impact of organic and inorganic nutrient and other pollutants outflowing from the continent to the coastal waters of the Gulf of Honduras and the MBRS depends on the collection of physical oceanographic information for the area with sufficient spatiotemporal resolution. Even more urgent, already pointed out years ago (Rawlins et al., 1998), is to increase the monitoring of nutrients, potential causes of coastal eutrophication which can have an impact on organisms in the MBRS region.

The composition and characteristics of the particulate matter changed seasonally, as observed from the changes in the slope of the regressions between Chla and TSS, POC and PTN (Fig. S4). During the dry season, the particulate fraction was enriched in Chla, most likely of autochthonous origin,

whereas during the rainy season, the opposite occurred probably due to a higher importance of allochthonous detritic inorganic and organic matter passing through the Puerto Cortés watershed system as well as to the increase in turbidity limiting light availability. Using the same estimation approaches discussed for nutrients and bearing in mind the same limitations, the Puerto Cortés system could be source of 0.06 to $31.8 \text{ kg TSS m}^{-2} \text{ d}^{-1}$, 6.7 – $2700 \text{ g POC m}^{-2} \text{ d}^{-1}$, 1.1 – $240 \text{ g PTN m}^{-2} \text{ d}^{-1}$ and 0.04 – $42 \text{ g Chla m}^{-2} \text{ d}^{-1}$, depending on season and the approach used in the calculations (Table 3). Random precipitations in the watershed, during either the dry season or the rainy season would increase the estimations made here (Figs. 4, 5) (Fig. S1). Comparison of these data is difficult due to the scarcity of previous studies and the differences in the calculation approaches used as most authors normalize riverine export by the watershed area. Burke and Sugg (2006) estimated an export of between 1×10^4 and $5 \times 10^5 \text{ Mt. sediment y}^{-1}$ and up to $5 \times 10^2 \text{ Mt. N y}^{-1}$ for the Puerto Cortés watershed. This calculation is probably an underestimation as they did not take into account the connection between the extremely productive Ulúa river watershed and Chamelecón River with the Puerto Cortés system through the existing channel (Fig. 1). Overall, Burke and Sugg (2006) concluded that 80 % of the sediment and >50 % of the N arriving in the MRBS system derives from the Honduran watersheds. The more recent study of Berger et al. (2022) also found that Rio Ulua and Rio Motagua contribute just over 50 % of the N pollution in the MPRBS.

The estimations from both studies, however, did not consider the predominant coastal circulation that might bring nutrients and sediment discharged by the Ulúa River to the system. Paris and Chérubin (2008) reported that the suspended material that outwells from the eastern coast of Honduras during the rainy season returns to the southwest MBRS during the dry one due to the coastal currents. This results in the MBRS being affected twice from the same suspended matter from different directions, first directly from land runoff and second from sediments of mixed origin and degradation stage returning from the ocean. Thus, in addition to the qualitative changes in the characteristics of outwelled materials, quantitative changes in the outwelling rate dependent on the precipitation pattern and residence time of the transported material at sea may also determine the impact on and survival of corals.

Estimated TRIX decreased at 10 km offshore, to values corresponding to good seawater quality and medium eutrophication levels (Alves et al., 2013; Vollenweider et al., 1998). The increase in water quality offshore is due to the dilution and dispersion of the excess dissolved inorganic nutrient and Chla produced in the Puerto Cortés system and represents a rough first estimate, which should be improved by direct measurements. Given the effects high nutrients and Chla levels, as well as nutrient ratios, have on reef systems, the goal of management practices is their reduction; thus, corals will be able to tolerate better the increased temperatures in the future due to climate change (Wooldridge, 2009; Wang et al., 2018). México, Belize, Guatemala, and Honduras share the MBRS and the benefits of the ecosystem services it provides, but also the environmental and socio-economic problems associated with its deterioration. Regional stakeholders and particularly governments should jointly lead the design and implementation of integrated management strategies for the MBRS region with the reduction of contamination by agrochemicals, untreated municipal discharges, and ports activities being the first priority. In this process, the scientific evaluation of the contribution of different coastal environments submitted to variable degrees and types of anthropogenic impacts is essential to achieve the sustainable development of the region.

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CRediT authorship contribution statement

Juan Carlos Carrasco Navas-Parejo: Conceptualization, Investigation, Formal analysis, Visualization, Funding acquisition, Project administration, Writing - original draft, Writing - review & editing. **Sokratis Papispyrou:** Conceptualization, Formal analysis, Resources, Visualization, Supervision, Funding acquisition, Writing - original draft, Writing - review

& editing. **Sara Haro:** Formal analysis, Writing - review & editing. **Isabel Caballero de Frutos:** Formal analysis, Writing - review & editing. **Alfonso Corzo:** Conceptualization, Formal analysis, Resources, Funding acquisition, Supervision, Writing - original draft, Writing - review & editing.

Data availability

Data will be made available on request.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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