



Seasonal, spatial, and high-frequency monitoring of dissolved oxygen and net ecosystem metabolism in a shallow coastal lagoon, Ria Formosa – Portugal

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ABSTRACT

This study provides a detailed assessment of dissolved oxygen (DO) dynamics and net ecosystem metabolism (NEM) in the Ria Formosa coastal lagoon, highlighting how spatial and temporal variability shape mesotidal ecosystems. Complementary approaches were applied: short-term (24 h) diel oxygen open-water method at two stations (eastern and western boundaries) in comparison with the bottle incubation method, and a 2.5-year high-frequency dataset at an inner station lagoon. DO showed clear seasonal patterns, largely driven by photosynthesis and respiration, but strongly modulated by water circulation and hydrodynamics. Sporadic hypoxic events ($DO \leq 2 \text{ mg L}^{-1}$) were observed but do not represent a risk. The boundary stations are shallower and colonized by submerged vegetation, displayed stronger diel fluctuations than at the inner station, underscoring the role of biological processes in lagoon metabolism. NEM estimates revealed strong spatial contrasts: the western station was autotrophic, while the eastern station predominantly attributed to restricted water exchange. Long-term records from the inner station indicated a slightly heterotrophic status, reinforcing the value of sustained high-frequency monitoring for capturing ecosystem trends overlooked by short-term approaches. The results also highlight lagoon-coastal ocean connectivity, suggesting dual exchanges: local production may be exported offshore to sustain adjacent coastal areas, while coastal processes, such as upwelling, can also influence lagoon metabolism. Methodological comparisons confirmed that bottle incubation method underestimated NEM relative to diel oxygen open-water method, emphasizing the role of hydrodynamics in mesotidal system metabolism. Although sampling focused on western and eastern boundaries and inner lagoon, the strong tidal renewal in the main and secondary channels suggests Ria Formosa overall is close to metabolic balance, with spatial heterogeneity shaped by hydrodynamics, vegetation, and coastal forcing. By integrating short-term, high-frequency, and long-term observations, this study advances understanding of metabolism in coastal lagoons, offering key insights for predicting ecosystem responses to climate change and for guiding management of vulnerable coastal environments.

1. Introduction

Dissolved oxygen plays a crucial role in regulating life and the ecological and biogeochemical functioning of coastal aquatic ecosystems (Borges et al., 2022; Breitburg et al., 2018; Cole et al., 2020). The concentration of oxygen affects marine biogeochemical processes and has impact on the global carbon and nitrogen cycles (Stramma et al., 2008). Thus, it is one of the most important gases in aquatic ecosystems, quite relevant for understanding water quality. Because of its role, it is used in environmental legislation, such as the Water Framework Directive (WFD) and improving the understanding of the ecosystem

metabolism.

Quantifying metabolic rates in marine systems allows the understanding of exchanges of energy, nutrient cycling, trophic status, and food web dynamics (Bas-Silvestre et al., 2020; Dodds and Cole, 2007; Holtgrieve et al., 2010). The calculation of Net Ecosystem Metabolism (NEM) initially established in the 1950's by Odum (1956) indicate the trophic state of an environment and, therefore, its environmental health. It is useful as an indicator of the trophic conditions within estuaries, rivers, lakes and oceans, and to quantify the biogeochemical carbon and oxygen fluxes (Needoba et al., 2012; Staehr et al., 2012). This metric defines the difference between primary production (P) and aerobic

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respiration (R) in an ecosystem and indicates whether it is autotrophic or heterotrophic (Caffrey, 2003). Positive NEM values indicate that the ecosystem is autotrophic ($P > R$), absorbing more carbon and producing more dissolved oxygen through photosynthesis than it is used through respiration, while negative NEM values indicate that the ecosystem is heterotrophic ($P < R$) with a net release of carbon, meaning that the produced oxygen by photosynthesis is lower than that used in respiration.

Over the past years, several methods have been developed to quantify the NEM of an ecosystem (Bas-Silvestre et al., 2020; Staehr et al., 2012), either by measuring O_2 or ^{14}C based on the incubation method; or the open-water method (Bas-Silvestre et al., 2020; Caffrey, 2004; Gazeau et al., 2005; Kemp and Boynton, 1980; Odum, 1956; Staehr et al., 2012). These methods vary in precision and spatiotemporal scale, having limitations and strengths, with all of them showing advantages and disadvantages (Bas-Silvestre et al., 2020; Gazeau et al., 2005; Hull et al., 2016; Kemp and Testa, 2012; Murrell et al., 2018; Nidzieko et al., 2014; Staehr et al., 2012), adopting several assumption-based techniques. The NEM is widely determined by measuring DO using the bottle incubation method. However, this method may not necessarily be representative of the entire ecosystem, as it is not affected by the various physical processes that occur in the ecosystem during the incubation period (Staehr et al., 2012). The diel oxygen open-water method utilizes *in situ* and high-frequency DO measurements, accounting for the air-to-sea gas exchange (e.g., Caffrey, 2003; Coloso et al., 2008; Kemp and Boynton, 1980; Needoba et al., 2012; Staehr and Sand-Jensen, 2007).

Although no unique methodology has emerged as completely satisfactory, the diel oxygen open-water technique proposed originally by Odum (1956) provides a useful alternative to bottle and chamber incubations because it addresses aquatic metabolism directly at the ecosystem scale (Staehr et al., 2010, 2012). The development of reliable oxygen sensors has led to an increase in the use of aquatic metabolism measurements as an integrative indicator of ecosystem functioning worldwide (e.g. Hanson et al., 2008; Obrador and Pretus, 2013; Winslow et al., 2016), covering different spatial and temporal scales (Gazeau et al., 2005). Considering long time series, with high-frequency sampling intervals, it is possible to calculate NEM with high temporal resolution and accurately determine the rates of primary production and respiration, namely, to identify seasonal and interannual changes, as stated in literature (e.g. Cravo et al., 2020; Needoba et al., 2012). Long-term and high-frequency estimates of primary production and respiration are rare in coastal lagoons literature making the information about their main metabolic drivers still limited (Bas-Silvestre, 2021).

The dynamics of metabolism vary in response seasonal changes (e.g.: temperature, light and nutrients availability) or unpredictable disturbances (e.g.: floods and storms; Staehr et al., 2010). It is therefore essential to disentangle variations at different spatial and temporal scales, from daily to annual, and to distinguish shifts in physical-chemical-biological events in the water column from the internal processes occurring in the sediments that control biogeochemical fluxes (Kemp et al., 2009). Understanding the significance of biological processes is essential in highly productive transitional systems at the interface between land and sea, such as dynamic coastal lagoons, especially in the context of rapid environmental changes, including climate change.

Coastal lagoons occupy approximately 13 % of the world's coastline (Kennish and Paerl, 2010) and have a wide range of morphological, geological and hydrological characteristics, providing a wide range of ecosystems services, with high ecological and economic value (Pérez-Ruzafa et al., 2019). The proximity to land, shallowness and limited interaction with the ocean make coastal lagoons particularly vulnerable to local human-induced stressors (Kennish and Paerl, 2010; Newton et al., 2014, 2020), including eutrophication, deoxygenation and/or acidification (Rabalais et al., 2014; Breitbart et al., 2018). Each coastal lagoon has its own vulnerabilities depending on its peculiar characteristics and its responses to different changes over time.

The Ria Formosa is a productive multi-inlet coastal lagoon on the Portuguese south coast, characterized as a mesotidal system (Barbosa, 2010; Cravo et al., 2020; Domingues, 2022; Rosa et al., 2022). Many species of fish, crustaceans and bivalves use it for spawning and as a nursery (Cravo et al., 2015; Domingues, 2022; Falcão and Vale, 2003), making it of high ecological and socio-economic relevance. Ria Formosa is also exposed to various anthropogenic stressors (Newton et al., 2022), including discharge from wastewater treatment plants (Caetano et al., 2023; Cravo et al., 2015, 2022), and is vulnerable to climate change (Rodrigues et al., 2021; Rosa et al., 2022). In this context, given the importance of dissolved oxygen, assessing its concentration and estimating its metabolism (NEM) in Ria Formosa is of paramount importance. The present study aims to characterize dissolved oxygen (DO) concentrations in Ria Formosa, complementing previous research on the spatial variability of this gas, out of the main channels, where values could represent some concern, covering distinct anthropogenic pressures, environmental conditions and oceanic influence. The objectives of this work are:

- i) To examine the seasonal variability of DO in the western and eastern lagoon areas, where gradients are more pronounced, and to compare these patterns with an inner-station site under higher anthropogenic pressure.
- ii) To evaluate seasonal net ecosystem metabolism (NEM) at multiple temporal scales for the first time in Ria Formosa across these three locations.

To achieve these objectives, two complementary approaches were applied. First, seasonal DO variability was assessed over the four seasons using the diel oxygen open-water method at the lagoon edges, in comparison with hourly measurements at the inner-station site. Second, NEM was estimated at the western and eastern stations using both the *in situ* bottle incubation method and the diel oxygen open-water approach of Needoba et al. (2012) for comparison.

2. Material and methods

To address the seasonal (summer, autumn, winter and spring) variability of dissolved oxygen at the western (CV) and eastern stations (PF) (Fig. 1), 24-h campaigns were conducted. Data acquired at the inner station (CC), from the real-time observation station (RTO), during periods of 24 h were also considered in equivalent seasons, as described below.

2.1. Study area

The study was conducted in the Ria Formosa coastal lagoon (Fig. 1), which is a 100 km² system extending about 55 km east-west and reaching a maximum width of 6 km near Cape Santa Maria. The lagoon is separated from the Atlantic Ocean by a barrier-island system with six inlets (Ancão, Faro-Olhão, Armona, Fuzeta, Tavira and Cacela). It has several main channels and extensive tidal flats areas which are intersected by a high density of shallow meandering tidal creeks (Barbosa, 2010; Cravo et al., 2022; de los Santos et al., 2022; Mudge et al., 2008). It is a shallow system with mean depth ~2 m that is exposed to a semi-diurnal mesotidal regime with mean tidal range of ca. 2 m, varying from 1.5 m to 3.5 m, in neap and spring tides, respectively (Jacob and Cravo, 2019). During a complete day a large fraction of the lagoon water volume (50–75 %) is exchanged with the ocean (Mudge et al., 1999). The water column remains well mixed and has no thermal or haline stratification (Cravo et al., 2019, 2020; Rosa et al., 2022) due to limited freshwater input, minor freshwater includes the Gilão River discharge (approximately 210 m³ day⁻¹) at Tavira (Falcão et al., 2003), and close to the effluents discharge points (total of four main wastewater treatment plants <30,000 m³ day⁻¹).

The Ria Formosa lagoon is classified as 'sheltered coastal waters'

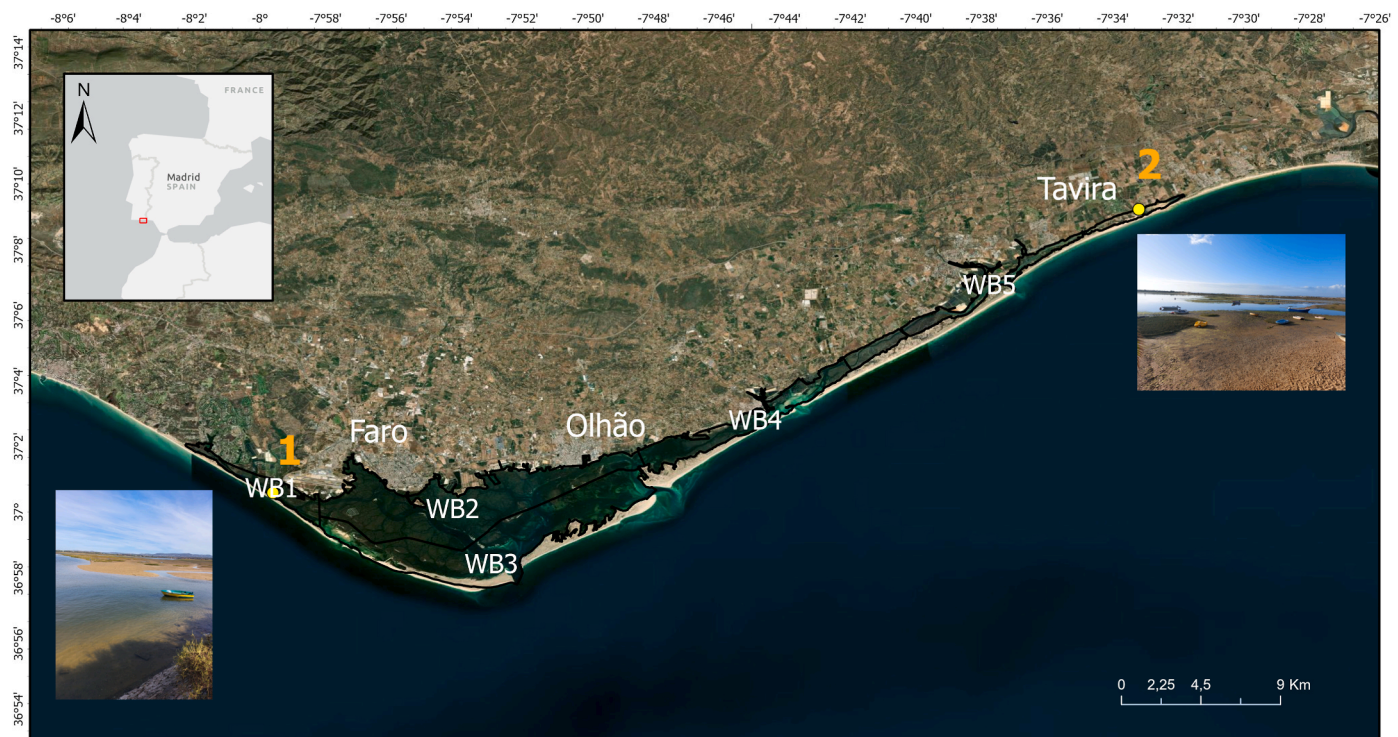


Fig. 1. Location of Ria Formosa, in the south coast of Portugal, with delimitation of the five water bodies (WB1 to WB5; delimited by the black polygons), and indication of the sampling stations 1 and 2, western and eastern edges, respectively and inner station (3), where the real time observation station (RTO) was deployed (also shown in the inset photographs). **Source:** Esri, Maxar, Earthstar Geographics, and the GIS User Community.

(Barbosa, 2010; Cravo et al., 2014; EC, 2000). It comprises five water bodies (WB) which are defined according to circulation patterns and human pressures. However, this subdivision is artificial within the WFD framework, as there are no physical barriers between them (Rosa et al., 2022). Based on a seasonal survey, Rosa et al. (2022) reported that, while water quality was generally homogeneous across the lagoon, greater variability occurred at western and eastern extremities (WB1 and WB5, respectively). WB5 also encompasses an area located about 10 km from the eastern edge which is only influenced by the permanent freshwater input of the Gilão River.

The adjacent coastal ocean, which is highly interconnected with the Ria Formosa lagoon, is frequently affected by upwelling events driven by westerly winds, which are more common during the spring and summer (Relvas and Barton, 2002). These events may ultimately affect the lagoon.

In the present work, three different water bodies in the Ria Formosa were selected. Two of these are located in shallow (<2 m) and relatively confined areas, at its western and eastern edges - Praia de Faro (PF) and Cacela (CV), both located near salt marshes (Fig. 1). Nevertheless, the eastern station is the shallowest and has no main channel in its vicinity. It is also more densely colonised by submerged vegetation and algal mats than the western station. The campaigns were conducted close to intertidal mudflats, predominantly occupied by meadows of seagrass species *Zostera noltei* and saltmarsh species *Sporobolus maritimus*. To better understand the seasonal behavior of NEM at an inner area in WB2, CC was selected, which is more exposed to human pressure than the other waterbodies. This station is close to Faro city, is deeper within the Ria Formosa (ca. 7 m) and closer to a main channel but also located near a salt marsh area (see Fig. 1). Between 2017 and 2020, a real-time observatory was deployed at this station for a period of two years and nine months.

2.2. Dissolved oxygen data for assessment of seasonal variability

To characterize the seasonal variability in DO, sampling campaigns in CV and PF were conducted in 2022 and 2023 (Table 1). DO data were acquired through *in-situ* measurements using a multiparametric probe, YSI EXO 2 (specifications described in Cravo et al., 2020), that also measures temperature, salinity and pH. To complement DO characterization, water samples for nutrients, chlorophyll-a and suspended solids determination were also taken every hour during ~25 h, covering two complete semi-diurnal tidal cycles during distinct phases of fortnightly tidal cycles (spring tides – SP, neap tides – NP, and intermediate tides – IT; see Table 1).

These samples were collected about 20 cm below the surface. PF typically had a water depth of <2.6 m, while CV depth was <1 m (except

Table 1

Sampling periods during the different seasons at stations 1 and 2, and at a specific date at station 3 using high frequency DO data acquired by the RTO considering the same season and the similar tidal height range. At Station 3 to evaluate seasonality of DO and NEM between June 2017 and March 2019, a period of 3 months was considered as representative of each season, indicated in brackets and asterisk. NT = Neap Tide, ST = Spring Tide, IT = Intermediate Tide.

	Praia de Faro – PF	Cacela Velha – CV	Cais Comercial – CC
Summer	6–7 September 2022 (NT)	6–7 July 2023 (IT)	10–11 September 2019 (NT) (15 June – 14 September) *
Autumn	24–25 November 2022 (ST)	21–22 November 2022 (ST)	26–27 November 2019 (ST) (15 September – 14 December) *
Winter	2– 3 March 2023 (NT)	16–17 March 2023 (NT)	3–4 March 2020 (NT) (15 December – 14 March) *
Spring	3–4 May 2023 (ST)	28–29 April 2023 (IT)	8–9 May 2019 (ST) (15 March – 14 June) *

in spring tide). However, during the flood when the water column was deep enough (>0.5 m), *in situ* measurements were also taken near the bottom. Differences in water temperature, salinity, pH and DO (concentration and % of saturation) greater than 5 % were never found between the surface and the bottom.

The dissolved oxygen is also expressed in percentage of saturation, based on the Weiss (1970) equation, to remove the effect of water temperature and salinity. To check the accuracy of the DO measurements by the optical sensor, the classical Winkler method (1888) was employed, as described in section 3.3.

This RTO was equipped with a YSI EXO 2 multiparameter probe, with coupled sensors for dissolved oxygen (given in concentration and percentage of saturation), water temperature, salinity, pH, turbidity and chlorophyll-a. The probe was deployed 2.8 m below the mean sea level and at a height of 4 m above the bottom, with specifications and maintenance procedures described in Cravo et al. (2020). Data was acquired at high frequency with a sampling interval of 15 min and made available almost in real time. At CV and PF the same model of multiparametric probe was used as that deployed at RTO.

2.3. Laboratory analysis

The Winkler (1888) method was employed to verify the accuracy of DO data from the RTO. An endpoint potentiometric titration conducted with the Metrohm 888 titrator was used, following the method described by Hansen and Grasshoff (1999). The difference between the DO values obtained with the multiparametric probe and the values obtained by the Winkler method throughout the campaigns was on average 0.2 mg L⁻¹, corresponding to an error of less than 5 %.

The water samples collected for nutrient, suspended solids and chlorophyll *a* determination were filtered using specific membrane filters (0.45 µm for suspended solids and GF/F glass fiber filter, 0.7 µm, for chlorophyll-a). Nutrient concentration was assessed using spectrophotometric methods based on calibrations curves, as described by Grasshoff et al., (1999). OSIL reference nutrients standards were employed to ensure concentration results accuracy. For chlorophyll *a* determination, the filters were frozen (-20 °C), ground and then analyzed using fluorescence, following method described in EPA 445.0 (Arar and Collins, 1997). Suspended solids were determined using a gravimetric method (APHA, 2017). To distinguish the organic fraction from the inorganic fraction, these filters were burnt at 450 °C, for 4 h and then cooled until reaching a constant weight.

2.4. Net ecosystem metabolism (NEM)

DO data from the western and eastern edges were also used to estimate NEM seasonally. At the inner station, the NEM was estimated to be over a three-month period using DO data from the RTO. This approach allowed each of the four seasons to be characterized more thoroughly than would have been possible using data from a single 24-h period. The periods covering the four seasons are shown in Table 1.

2.4.1. Filtering processes of DO data the inner station (CC)

The NEM was calculated using hourly measurements (diel oxygen open-water method) along 24-h cycles. This was achieved by summing the daily rates of organic matter production (photosynthesis) and aerobic respiration, employing the method described by Needoba et al. (2012) and the equations presented by Caffrey (2003, 2004).

DO data acquired by the RTO, were low-pass filtered (cut-off frequency: 1/18 h⁻¹) to reduce the influence of small-scale physical processes, and high-pass filtered (cut-off frequency: 1/33 h⁻¹) to isolate diel variability, as described in Cravo et al. (2020). This approach assumes, as noted by Caffrey (2004), that observed DO changes primarily reflect surrounding biological activity rather than physical advection.

2.4.2. Diel oxygen open-water method at the edges and inner stations

The DO flux caused by biological processes (BDO) was calculated for each time interval (see equation (1)), $dt = t(n) - t(n-1)$, between two consecutive measurements times $t(n-1)$ and $t(n)$, ($n = 1, \dots$ total number of samples) from the DO change multiplied by the water depth (h in meters) and subtracting the air-water diffusion flux (F_{O_2} , equation (2)) for the time interval.

$$BDO_{t(n)} = (DO_{t(n)} - DO_{t(n-1)}) \times h - F_{O_2} \quad (1)$$

DO is very sensitive to changes in air-sea fluxes (and ocean circulation and hydrodynamics), which makes those parameters also important, influencing NEM calculation (Caffrey, 2003, 2004; Needoba et al., 2012).

The air-water diffusion was calculated using the expression by Caffrey (2004, 2003) to describe the air-water exchange,

$$F_{O_2} = \left(1 - \frac{O_2 \%Sat.t(n) + O_2 \%Sat.t(n-1)}{200} \right) \times K \times dt \quad (2)$$

Where $O_2 \%Sat.t(n-1)$ and $O_2 \%Sat.t(n)$ are the oxygen percentage of saturation for the consecutive times $t(n-1)$ and $t(n)$, dt is the time interval between consecutive measurements in hours, and assuming a constant correction factor $K = 0.5$ (g O₂ m⁻² h⁻¹) as indicated by Needoba et al. (2012) since the winds at the study were mostly in the range 2–5 m s⁻¹. Parameter 200 is justified by the fact that units of the oxygen concentration $O_2 \%Sat.t(n-1)$ and $O_2 \%Sat.t(n)$ are in %. More details about the calculation of the DO flux and air-water diffusion are described in Cravo et al. (2020). Both positive and negative values were obtained, as the diffusion of oxygen across the air–water interface can either increase or decrease the concentrations in the water column. Diffusion occurs from air to water when the water is undersaturated, and in the opposite direction when it is supersaturated (Caffrey, 2003). The total daily NEM values were determined by summing the hourly BDO values obtained with equation (1) over 24 h periods, encompassing both the full photo period and the complete dark period. The day was divided into a photoperiod and a dark period segment (the sunrise and sunset hours were taken from the Lisbon Astronomical Observatory tables for the city of Faro for PF and for the city of Tavira for CV). Using these values, the total NEM can be split into a “Net Ecosystem Production” (NEP) during daylight hours and the “Night Respiration” (NR) during nighttime (Needoba et al., 2012).

2.4.3. Bottle incubation method at the edges

NEM estimation was also performed using the bottle incubation method during a 24-h at the edges. For this, 4 light and 4 dark bottles were incubated approximately 20 cm below the surface along a cable attached to buoys. Initially, at time 0 (t_0), four bottles were fixed by Winkler reagents at the same depth. Dissolved oxygen was determined using automated Winkler titration system, as described in section 3.3. Variability occurring in the light and dark bottles, incubated for 24 h, indicates the NEM (Eq. (3)), through the sum of the rates of production NEP (Eq. (4)) and respiration NR (Eq. (5)), calculated as indicated by the equations:

$$NEM = \sum BDO, \text{ over periods of } 24h \text{ (NEP + NR)} \quad (3)$$

$$NEP = O_2(24h)_{\text{light}} - O_2(t_0), \text{ complete light period (production)} \quad (4)$$

$$NR = O_2(24h)_{\text{dark}} - O_2(t_0), \text{ complete dark period (respiration)} \quad (5)$$

2.5. Environmental and oceanographic data settings

To understand the oceanographic conditions adjacent to Ria Formosa during the periods close to the sampling campaigns, composite images spanning 8 days of Sea Surface Temperature (SST) and chlorophyll-a concentration, were retrieved from the OceanColor Nasa

website (<https://oceancolor.gsfc.nasa.gov/>), with a spatial resolution 4 km (Fig. SM 1 and in Fig. SM 2, respectively). Information on the meteorological conditions (air temperature, precipitation), including wind direction and intensity (necessary for calculating the NEM) was provided by Weather Underground from the Faro Airport meteorological station (<https://www.wunderground.com/>) for PF and by SNIRH (Sistema Nacional de Informação de Recursos Hídricos) from the Picota meteorological station (<https://snirh.apambiente.pt/>) for CV. This information is shown in Table SM 1. IPMA (Portuguese Institute for sea and Atmosphere) also provided precipitation data for Faro Airport from the week before the campaigns during the winter period.

For the analysis of the data obtained during the four seasonal campaigns, ancillary information on the variation of sea surface elevation (SSE) was also used. This information was obtained from the OTIS (Global Tidal Solution; Egbert and Erofeeva, 2002), at a fixed point near the Ria Formosa.

2.6. Data and statistical analysis

To assess significant differences between seasons, stations and tidal conditions the Mann-Whitney non-parametric test, equivalent to the two-way ANOVA parametric test, was used, since at least one of the variable distributions used in the comparisons was non-normal. A confidence level of 95 % was used. For a better interpretation of the results, both the medians and means of dissolved oxygen, temperature, salinity, pH, chlorophyll-a, total suspended solids, volatile suspended solids, percentage of organic matter and nutrients (ammonium, nitrate, phosphate and silicate) are presented, using the Prism program.

To illustrate the spatial and seasonal variability for the three studied stations, boxplots showing the mean, median, 1st and 3rd quartiles (25th and 75th percentiles, respectively) were created using the Prism program as well.

Principal Component Analysis (PCA) was performed in R using original data of water temperature, salinity, dissolved oxygen in percent of saturation, chlorophyll, suspended solids, fraction of organic matter, ammonium, nitrate, and NEM determined at stations 1 and 2 during the seasonal tidal cycles. This allows us to identify the main factors and processes that best explain the variability in the dataset, as well to explore the relationship among the variables for the different stations and seasons. To avoid redundancy of results, highly correlated parameters such as pH with dissolved oxygen and phosphate and silicate with ammonium were excluded from the PCA.

3. Results

3.1. Environmental context

Summer surveys were conducted at PF in September 2022, and at CV in July 2023. The air temperature in September 2022 (daily mean of $22.0\text{ }^{\circ}\text{C} \pm 1.9\text{ }^{\circ}\text{C}$) was lower than in July 2023 (daily mean of $27.4\text{ }^{\circ}\text{C} \pm 3.3\text{ }^{\circ}\text{C}$; Table SM 1), due to the influence of an upwelling event occurred along the southern coast of Portugal (Fig. SM 1A and 2A) under favorable westerly winds. This event caused a decrease in water temperature near the coast, of almost $3\text{ }^{\circ}\text{C}$ compared with offshore (Fig. SM 1A) and was accompanied by an increase in chlorophyll-a concentration ($3\text{--}4\text{ mg m}^{-3}$; Fig. SM 2A).

During the autumn surveys in November 2022, the mean air temperature at PF was $15.7\text{ }^{\circ}\text{C} (\pm 1.0\text{ }^{\circ}\text{C})$ and at CV $15.3\text{ }^{\circ}\text{C} (\pm 2.7\text{ }^{\circ}\text{C})$ and chlorophyll-a concentrations near the coast reached $1\text{--}2\text{ mg m}^{-3}$ near the coast (Fig. SM 2B and F).

Under winter conditions, as rainfall was very low during this period, the corresponding campaigns were delayed until March (2 March 2023 – PF, 17 March 2023 – CV), almost in the spring season. Ria Formosa has a Mediterranean climate, with mild winters and low rainfall in recent years ($<550\text{ mm year}^{-1}$ in the period of 2015–2023; <https://www.podata.pt/pt/documentos-indicadores?search=precipita%C3%A7%C3>

%A3o). The winter campaigns were conducted after a period during which $<15\text{ mm}$ of precipitation were recorded at the meteorological stations closest to CV (Castro Marim and Vila Real de Santo António), and approximately 18 mm at PF (Portuguese Institute for sea and Atmosphere, IPMA; <https://www.ipma.pt/pt/>; Table SM 1). For both winter campaigns, the air temperature was low, with an average daily temperature of $9.5\text{ }^{\circ}\text{C} (\pm 5.5\text{ }^{\circ}\text{C})$ at PF and $15.3\text{ }^{\circ}\text{C} (\pm 2.5\text{ }^{\circ}\text{C})$ at CV (Table SM 1). At the beginning of March, the concentration of chlorophyll-a along the south coast of Portugal was low, $<1\text{ mg m}^{-3}$ (Fig. SM 2C). However, in mid-March (Fig. SM 2G), due to upwelling event along the south coast of Portugal and/or a possible initiation of the typical spring bloom, chlorophyll-a values were high ($>5\text{ mg m}^{-3}$).

During the spring field surveys (end of April to beginning of May 2023), air temperature was $19.7\text{ }^{\circ}\text{C} (\pm 1.8\text{ }^{\circ}\text{C})$ in PF and $24.7\text{ }^{\circ}\text{C} (\pm 2.7\text{ }^{\circ}\text{C})$ at CV. The chlorophyll-a concentrations near the coast were the lowest ($1\text{--}2\text{ mg m}^{-3}$), and $<0.5\text{ mg m}^{-3}$ offshore (Fig. SM 2D and H).

3.2. Seasonal and spatial variability and tidal influence on dissolved oxygen at the edges of Ria Formosa

The DO concentration was highest with concentration and greater variability during the summer campaigns (

Table 2). Within each season, the highest and lowest values were found at PF in summer ($3.0\text{--}12.6\text{ mg L}^{-1}$) and at CV in winter ($3.9\text{--}14.1\text{ mg L}^{-1}$), respectively. The minimum range of variation ($3.6\text{--}4.0\text{ mg L}^{-1}$) was found in autumn for both stations. CV exhibited extreme concentration values, ranging from 1.2 mg L^{-1} in spring to 14.1 mg L^{-1} in winter. During the four seasons the mean/median concentrations were not significantly different between the two stations ($p > 0.05$), except for summer campaigns, when it was significantly higher at PF than at CV ($p < 0.05$).

To eliminate the influence of temperature and salinity on DO concentration, and to enable a comparison between different seasons and stations, DO is also expressed in percentage of saturation (Fig. 2). During the day, the highest concentrations were recorded in the afternoon, when photosynthetic activity is typically higher. Minimum values were observed in the early morning, due to the maximum respiratory rate during the night period (Odum, 1956). Daily data were almost in anti-phase with the tidal height, except during the autumn campaigns. Minimum values are affected by low tide, when the water column is shallower and biological processes occurring in the water column and/or in the sediments are more intense, particularly during neap tides.

At PF, the maximum range of DO in percentage saturation values were found during the summer survey, varying between 41 % at 7 a.m. and 197 % at 4 p.m. Regarding tidal influence, statistically significant differences were found ($p < 0.05$) in this station. Both DO concentration and DO percentage of saturation were significantly higher during neap tides than during spring tides.

At CV the maximum value of DO in percentage saturation was recorded during the winter campaign (194 % at 4 p.m.), while the minimum was observed in spring (16 % between 6 and 7 a.m.). This last value is critical as it corresponds to $<2\text{ mg L}^{-1}$, which is indicative of hypoxia. As with the DO concentration, there are no significant differences between stations ($p > 0.05$), except in summer, when particularly high values were observed at PF during the afternoon, matching low tide (Fig. 2 A and E). At this station, the tidal influence of DO concentration followed the pattern Neap tide (NP) > Spring tide (SP) > Intermediate tide (IT), while for DO in percentage saturation, values were also significantly higher during neap tides compared to spring tides (NT > ST and NT > IT), but no significant difference was found between intermediate and spring tides ($p > 0.05$).

3.3. Long-term temporal variability of dissolved oxygen at an inner area of Ria Formosa (CC)

To assess the seasonal variability of DO at CC, located at an inner

Table 2

Maximum, minimum, mean and median of dissolved oxygen (mg L⁻¹) concentrations at the edges of the Ria Formosa (PF - Praia de Faro and CV – Cacela Velha) along different seasons.

	PF				CV			
	Max.	Min.	Mean	Median	Max.	Min.	Mean	Median
Summer	12.6	3.0	7.5	7.4	7.4	2.2	5.3	6.2
Autumn	8.5	4.9	6.9	7.1	9.1	5.1	6.9	6.7
Winter	11.7	5.4	9.0	8.9	14.1	3.9	8.8	8.6
Spring	9.2	5.3	7.2	7.3	9.3	1.2	6.0	6.8

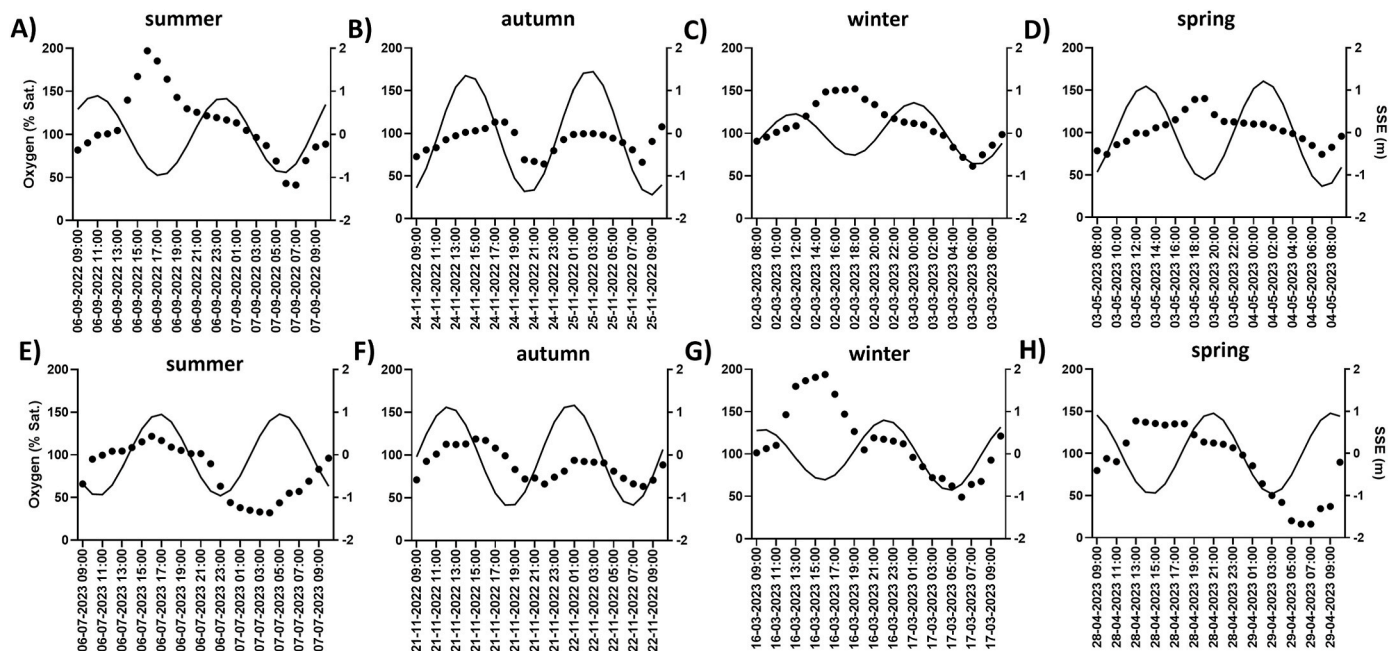


Fig. 2. Variability of dissolved oxygen in percentage of saturation (black dots), along the diurnal tidal sea surface elevation (black line) at PF (western station) during: (A) autumn (B), winter (C) and spring (D) seasons, and at CV (eastern station) during: summer (E), autumn (F), winter (G) and spring (H) seasons; Sea Surface Elevation data (SSE) from the OTIS global tidal solution (Egbert and Erofeeva, 2002), close to coastal lagoon, on the right-hand axis.

area of Ria Formosa, a more robust temporal assessment was employed using high-frequency DO saturation percentages records, acquired every 15 min by the RTO in WB2, over a period of 2 years and 9 months, from June 2017 to March 2020 (global period; n = 83781 records). For this, specific periods three months periods representative of each were considered (approximately 8491–8820 records per season), except autumn 2018, for which there were fewer measurements (approximately 5710 records) due to temporary sensor malfunction. These data are summarised in Table 3 and illustrated in Fig. 3. Between seasons, the variability of oxygen in percentage of saturation was greatest during summer and minimum during winter (Table 3; Fig. 3), with minimum values during the summer campaigns and maximum values during the spring campaigns. The lowest values during the summer (June to September), sometimes fall below 60 %, the minimum acceptable value (MAV) for shellfish waters by Portuguese legislation (Decree-Law 236/98), leading to the lowest median of 2018 (87 %, Table 3). During the

winter, values were closer to saturation (100 %). For the global period, values varied within the range 28 %–137 %, which is smaller than at stations 1 and 2, with the median values for each season slightly undersaturated, lowest for summer (90 %; Table 3) and maximum for winter (94 %; Table 3). The dissolved oxygen concentrations trend was significantly different between years ($p < 0.05$), with 2017 > 2018 > 2019. Seasonal differences in oxygen levels were significant ($p < 0.05$), except between winter and spring that are similar ($p > 0.05$). There is a clear difference between seasons, with significantly higher values observed in winter than in summer ($p < 0.05$).

Temporal DO variability also reflects the tidal signal with greater variability and highest values found during neap tide cycles.

Table 3

Statistical parameters: minima, maxima and median for dissolved oxygen in percentage of saturation for data acquired by RTO (inner station - CC) for different seasons, during the period of June 2017 to March 2020. N = number of observations at 15 min interval.

	Summer				Autumn				Winter				Spring			
	N	Min.	Max.	Median	N	Min.	Max.	Median	N	Min.	Max.	Median	N	Min.	Max.	Median
2017	8770	45	123	94	8720	57	117	95	8625	78	111	94	–	–	–	–
2018	8814	28	137	87	5710	46	116	89	8551	56	118	97	8824	49	121	93
2019	8817	29	125	89	8729	36	116	89	8491	56	116	92	8820	49	117	108

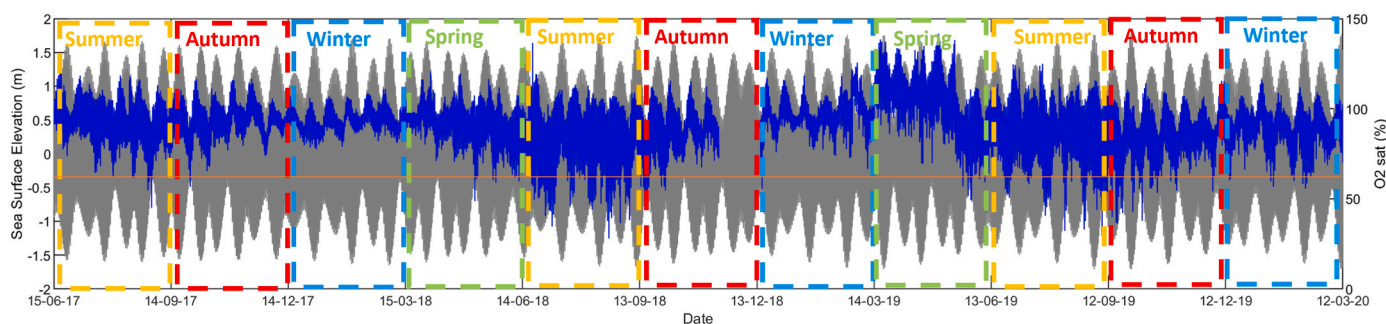


Fig. 3. Time series of dissolved oxygen in percentage of saturation (blue points on the right-hand axis), data acquired by RTO, in inner station (CC), for 2 years and 9 months (from June 2017 to March 2020) during the following seasons: summer (orange boxes), autumn (red boxes), winter (blue boxes) and spring (green boxes) seasons. In late autumn 2018 there was a failure in data transmission from all sensors. The orange line represents 60 % of saturation, the imposed benchmark as individual minimum acceptable value for shellfish waters for Portuguese Legislation (Decree-Law 236/98). Sea Surface Elevation data (SSE) from the OTIS global tidal solution (Egbert and Erofeeva, 2002), close to coastal lagoon, on the left-hand axis (grey shadow). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

3.4. Comparison of the seasonal variability of dissolved oxygen at the three sampling stations of Ria Formosa

The comparison of the seasonal variability of DO at both stations 1 and 2 with station 3 for a day in each season with similar tidal height range, is shown in Fig. 4.

The data show that the daily seasonal DO variations at both edge stations was higher than at the inner station. In summer and winter, DO percentage of saturation values were significantly higher ($p < 0.0001$) at PF than at CC that was like CV ($p > 0.05$). In the autumn, DO percentage of saturation values were similar between the three stations ($p > 0.05$). In spring, CC had DO significantly higher than in CV ($p < 0.05$).

3.5. Seasonal NEM estimates using a spatial approach combining two methodological analysis – diel oxygen open-water vs. bottles incubation methods

In this study, NEM was estimated using the daily variability of dissolved oxygen concentration to infer primary production during the day and aerobic respiration at night. The NEM was calculated using the open method described by Needoba et al. (2012), obtained by summing the BDO values over 24 h. NEP results from the sum of BDO during the hours of sunlight while NR is accounting for the night hours.

BDO (see section 3.2) and the values of the air-water diffusion flux, F_{O_2} , are shown in Fig. 5 for the four seasons, at PF (Fig. 5A–D) and CV (Fig. 5E–H). The air-water diffusion flux of DO is much smaller than the BDO, accounting for less than 10 % for NEM, but this proportion increased when water flow and especially wind intensity higher than 5 ms^{-1} were considered (Table SM 1). F_{O_2} values were slightly higher in summer and spring than in autumn and winter, which can be attributed

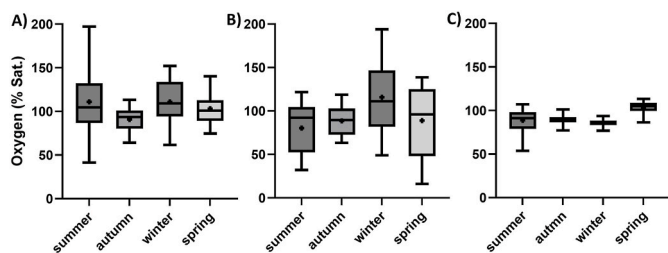


Fig. 4. Box plot of seasonal variability of dissolved oxygen in percentage of saturation at PF (western; A), CV (eastern; B), and inner station (CC; C) representative for each season. In the boxplots, the solid line represents the median, the black dots represent the mean, the lower and upper hinges are the 25 % and 75 % percentiles and whiskers represent minimum and maximum values.

to a greater air-water temperature gradient as well as increase in wind intensity (Table SM 1). Positive fluxes indicate that oxygen was predominantly transferred from the atmosphere to the water, while negative fluxes represent the reverse.

During the day most of the BDO values were positive while during the night most of the values were negative. BDO values were significantly lower at CV than at PF ($p > 0.05$), reaching a minimum during the winter campaigns.

The daily NEM values were positive at PF, indicating autotrophic behaviour in this area of Ria Formosa for all four seasonal campaigns, with values ranging from 57 to $215 \text{ mmol m}^{-2} \text{ day}^{-1}$ (Table 4). In contrast, the NEM values at the western station varied from -48 to $-35 \text{ mmol m}^{-2} \text{ day}^{-1}$ (Table 4) indicated a net heterotrophic metabolism in spring, summer and autumn, and thus except winter when this site behaved as autotrophic ($49 \text{ mmol m}^{-2} \text{ day}^{-1}$; Table 4).

The bottle incubation method was also employed to evaluate the seasonal variations in daily NEM at both stations, comparing the bottle incubation and diel oxygen open-water method provided in Table 4.

The NEM based on the incubation method were lower than those estimated with the diel oxygen open water method by $2\text{--}345 \text{ mmol m}^{-2} \text{ day}^{-1}$ (Table 4). PF, using the incubation method, was autotrophic in the summer and winter seasons while heterotrophic (with highest absolute value) in autumn and spring. CV, using this method was shown to be autotrophic in summer but reverted to heterotrophic behaviour in winter and spring.

3.6. Principal component analysis applied to overall seasonal data recorded at edges (PF and CV)

PCA was applied to discriminate the factors that best describe the seasonal variability of data for each of the sampled stations (Fig. 6) using the most relevant parameters water temperature, salinity, dissolved oxygen percentage of saturation, chlorophyll-a, suspended solids, fraction of organic matter, ammonium, nitrate and NEM. In this analysis, the three main components explain ca. 59 % of the variance of the results. PC1 accounts for 24 % of the variance, while PC2 and PC3 account for 17 %.

PC1 is explained by seasonality of biological processes with increased temperature and chlorophyll-a in the summer campaigns against increased organic matter fraction and suspended solids in the winter campaigns, at both edges (PF and CV) and autumn at CV. PC2, with a secondary role, showed a clear spatial separation between edges for the four seasons, justified by the highest NEM and organic matter and lower nitrate at PF, in opposition to CV. PC3 is explained by the tidal height variability, mostly explained by the highest values of DO in PF in summer and in CV in winter during neap tidal cycles in opposition to the highest ammonium and suspended solids values during intermediate

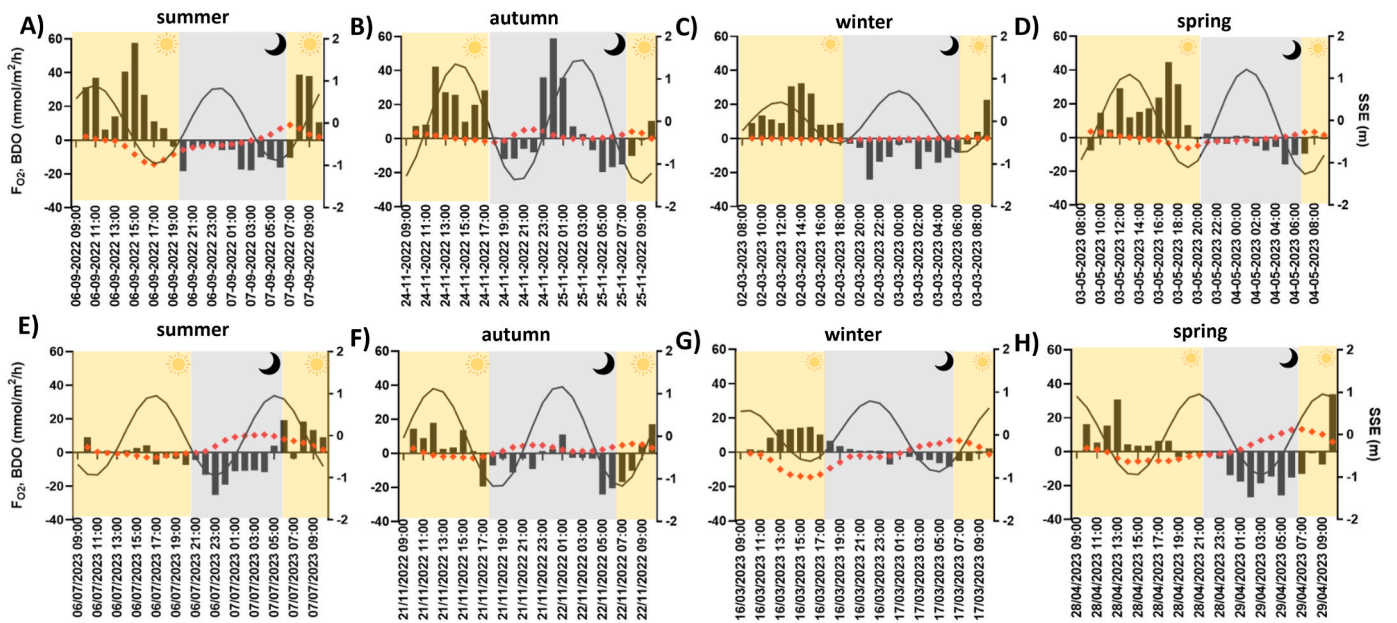


Fig. 5. Hourly biological dissolved oxygen flux (BDO, black bars) and Air-water diffusion flux (F_{O_2} , red dots), at PF (western station) during: summer (A), autumn (B), winter (C) and spring (D) and at CV (eastern station) during: summer (E), autumn (F), winter (G) and spring (H) seasons, along the 24 h diurnal tidal cycle; Sea Surface Elevation data (SSE) from the OTIS global tidal solution (Egbert and Erofeeva, 2002), close to coastal lagoon, on the right-hand axis. The yellow shading represents the sampling hours of sunlight; the grey shading represents the night period. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

Table 4

Seasonal estimates for NEM (Net Ecosystem Metabolism, in Bold), NEP (Net Ecosystem Production) and NR (Night Respiration) in $\text{mmol m}^{-2} \text{day}^{-1}$ at the Ria Formosa lagoon margins (PF – western region and CV – eastern region). Values represent integrated period estimates from single diel cycles (oxygen diel open-water method) and mean values from the bottle incubations, the coefficient of variation between replicate measurements was generally below 5%.

	PF						CV					
	Diel oxygen open-water method ($\text{mmol m}^{-2} \text{day}^{-1}$)			Bottle incubation method ($\text{mmol m}^{-2} \text{day}^{-1}$)			Diel oxygen open-water method ($\text{mmol m}^{-2} \text{day}^{-1}$)			Bottle incubation method ($\text{mmol m}^{-2} \text{day}^{-1}$)		
	NEM	NEP	NR	NEM	NEP	NR	NEM	NEP	NR	NEM	NEP	NR
Summer	191	304	-114	25	51	-26	-48	36	-83	37	43	-6
Autumn	215	169	45	-130	-63	-67	-35	37	-73	-	-	-
Winter	57	180	-123	8	6	2	49	70	-21	-8	8	-16
Spring	147	195	-48	-38	-18	-21	-40	99	-139	-38	-34	-4

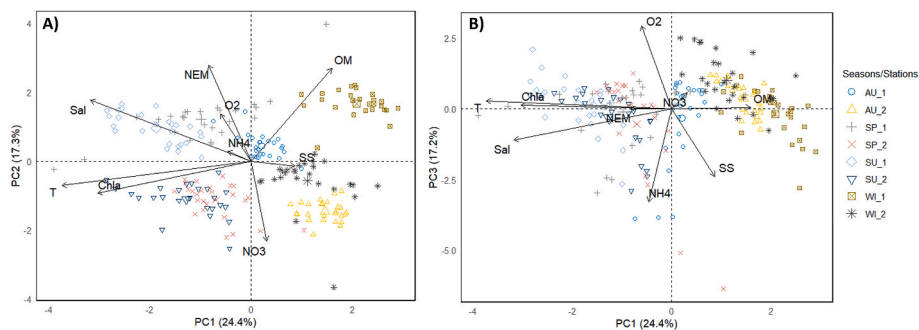


Fig. 6. Principal component analysis. A) PC1 vs PC2 and B) PC1 vs PC3 applied to water temperature -T ($^{\circ}\text{C}$), salinity - Sal, dissolved oxygen percentage of saturation - O2, chlorophyll-a - Chla ($\mu\text{g L}^{-1}$), suspended solids - SS (mg L^{-1}), fraction of organic matter - OM (%), ammonium - NH_4^+ (μM), nitrate - NO_3^- (μM), and NEM ($\text{mmol m}^{-2} \text{day}^{-1}$) for each season and station (AU – autumn, SP – spring, SU – summer, WI – winter for PF (1) and CV (2)).

and spring tidal cycles, at the edges.

3.7. Seasonal NEM estimates using a high-frequency approach at inner station (CC)

Air-water diffusion flux (FO_2), BDO, NEP and ER are shown in Fig. 7.

The air-water diffusion flux was mostly positive during the period of almost three years (Fig. 7A). This indicates that the ocean is gaining DO by atmospheric aeration due to influence from wind, as previously reported by Cravo et al. (2020).

Biologically dissolved oxygen flux shows a well-defined seasonal cycle, with higher values in spring and summer seasons and lower values

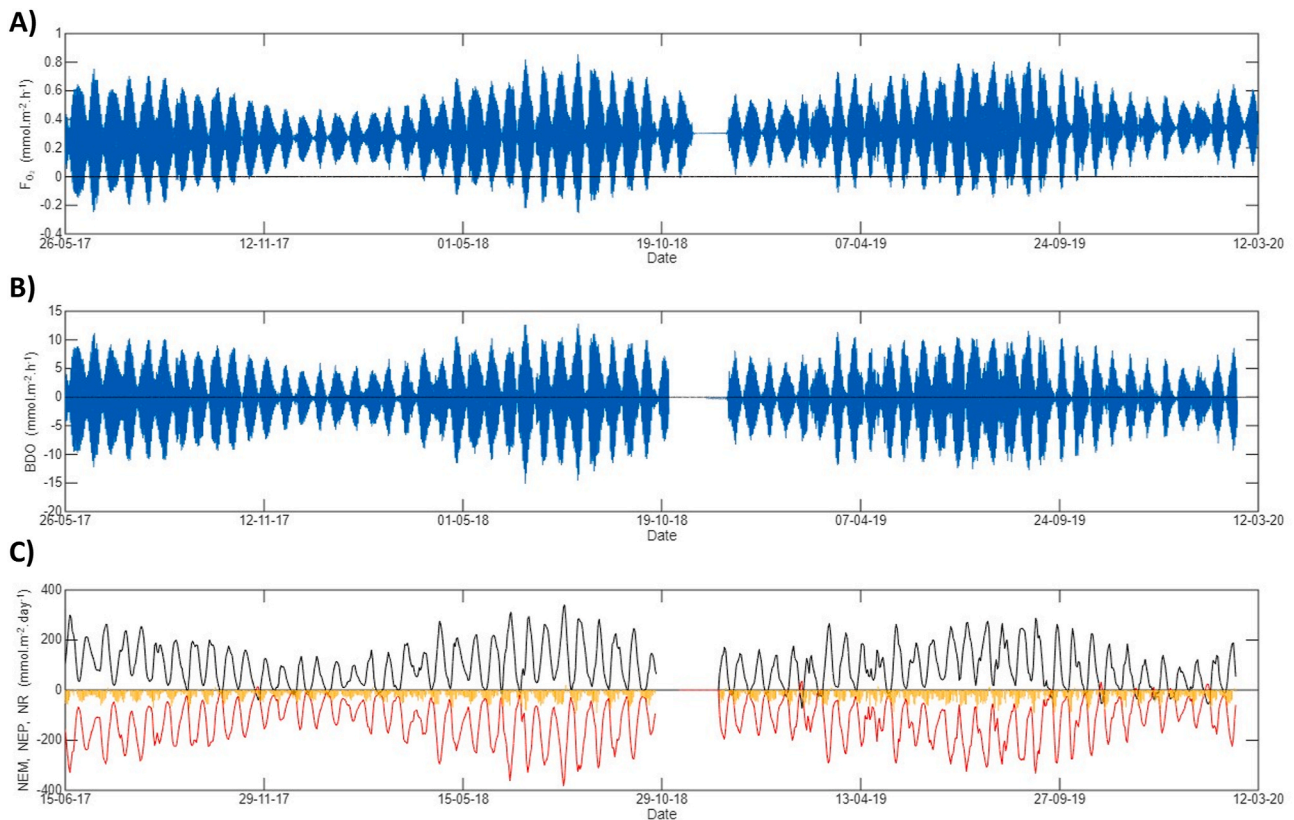


Fig. 7. (A) Hourly air-water diffusion flux, F_{O_2} , using constant correction factor, (B) Biological dissolved oxygen flux (BDO) and (C) daily calculated Net Ecosystem Production (NEP, black line), Night Respiration (NR, red line) and Net Ecosystem Metabolism (NEM, yellow bars), at station 3, referred to the RTO installed in Cais Comercial (WB2). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

Table 5

Seasonal and daily NEM (Net Ecosystem Metabolism) calculations during autumn, winter, spring and summer for the RTO installed in station 3, using the open water method described by Needoba et al. (2012).

	year	Number of days	NEM per season ($\text{mmol m}^{-2} \text{ season}^{-1}$)	NEM per day ($\text{mmol m}^{-2} \text{ day}^{-1}$)
Summer	2017	91	-62	-0.7
	2018	91	-153	-1.7
	2019	91	-117	-1.3
Autumn	2017	90	-57	-0.6
	2018	59	-66	-1.1
	2019	90	-118	-1.3
Winter	2017–2018	89	-64	-0.7
	2018–2019	56	-28	-0.5
	2019–2020	89	-99	-1.1
Spring	2018	91	-91	-1.0
	2019	30	-34	-1.2

in autumn and winter, reflecting the intensification of the biological activity (i.e. primary production vs. respiration) in spring and summer (Fig. 7B). However, these values as well as F_{O_2} estimated at this station are lower than those at the edges (Fig. 5). Interestingly, the highest NEP and NR values at inner station (Fig. 7C) were similar in magnitude to the highest values found at PF (Table 4; Fig. 5).

Daily NEM values (Fig. 7 C), ranged from -14 to $0.7 \text{ mmol m}^{-2} \text{ day}^{-1}$, were predominantly heterotrophic, with an average for the 2.5 years of the probe deployment of $-0.9 \text{ mmol m}^{-2} \text{ day}^{-1}$. So, this station showed slight heterotrophy during the overall study period, indicating almost an equilibrium between both rates. This range was narrower, and the values were lower than at the other two stations. However, it is important to note that the depth at this station is much greater, bearing

in mind that the height of the water column is multiplied in BDO calculation (see Section 3.2, Equation (1)). NEM data at CC were analyzed by season over the global period of 2.5 years (2017–2020; Table 5). In general, greater daily negative values (i.e., more heterotrophic) were recorded in 2018 and 2019 compared to 2017, particularly in summer and spring.

3.8. Temporal evolution of DO in Ria Formosa in the last 40 years

To evaluate the temporal evolution of DO in Ria Formosa, data of DO in percentage of saturation data from the present study were compared with historical data of long-term records for Ria Formosa using data available from 1980s to 2020: Alcântara et al. (2012); APA - Agência

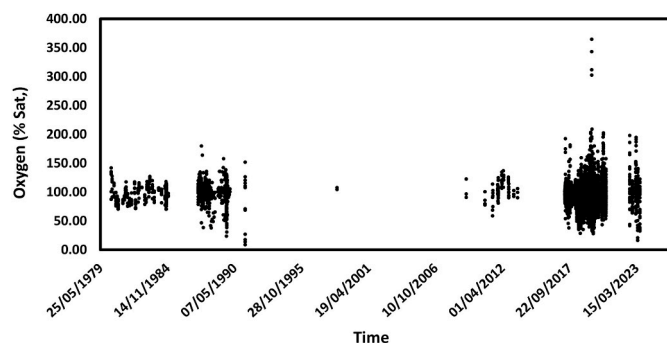


Fig. 8. Historical data of dissolved oxygen concentrations in the five water bodies of Ria Formosa from the 80's until 2020.

Portuguesa do ambiente, 2010; Barbosa (2010); Benoliel (1989), 1985, 1984; Cravo et al. (2022), 2020; Falcão (1997); Newton (1995); Rosa et al. (2022) and unpublished data from research projects: e.g. COALA (ref: PTDC/MAR/114217/2009), UBEST (ref: PTDC/AAG-MAA/6899/2014) and CONPRAR (ref: MAR-01.04.02-FEAMP-0003). These results are present in Fig. 8 and reveal no significant downward trend in DO saturation in Ria Formosa in the last 40 years.

4. Discussion

The threshold concentration of DO necessary to avoid adverse effects on marine life is reported to be approximately 5 mg L^{-1} by the United States of America Environmental Protection Agency (USA EPA, 2000) and 6 mg L^{-1} by the Environmental European Agency (European Environmental Agency EEA, 2025). Low oxygen conditions, typical of hypoxia ($<2 \text{ mg L}^{-1}$; Best et al., 2007; EPA, 2000), can have severe consequences for ecosystems, including reduced ocean productivity, decreased biodiversity, impacts on fisheries (Yin et al., 2024), and disruptions to biogeochemical cycles (Borges et al., 2022; Breitburg et al., 2018; Limburg et al., 2020; Sampaio et al., 2021). Given the critical role of oxygen levels in determining the severity of impacts on marine organisms (Best et al., 2007) and considering the metabolic status of this ecosystem, a spatial and temporal assessment of DO variability was conducted in the water bodies located at the lagoon's extremes, which are subject to various pressures.

This study shows that most DO values recorded at the three sampling stations across different water bodies in Ria Formosa remain above these critical concentrations, suggesting no persistent risk. However, hypoxic events were observed three times during the dawn period of the spring campaign at CV, corresponding to DO saturation $\leq 20\%$ (Fig. 2 H). At inner station, hypoxia was also recorded only episodical three times out of more than 83,000 measurements under specific conditions such as upwelling events or summer night periods, consistent with previous observations in Ria Formosa (Cravo et al., 2020; Mudge et al., 2007; Newton et al., 2010; Rosa et al., 2022). In a coastal lagoon like Ria Formosa, where fishing and aquaculture are major economic activities and the region represents the Portugal's main bivalve production center ($>90\%$; Cravo et al., 2015; Serpa et al., 2005), frequent hypoxic events could have substantial consequences for both local and national economies.

4.1. Key factors and processes explaining the seasonal, spatial and tidal variability of dissolved oxygen in the three waterbodies surveyed in Ria Formosa

In Ria Formosa, tidal forcing plays a central role in shaping dissolved oxygen variability, given that lagoon hydrodynamics is predominantly tide-driven (Cravo et al., 2020; Rosa et al., 2019, 2022). This strong tidal influence contrasts with microtidal lagoons, as those on the Mediterranean region, where water renewal is weaker (Cravo et al., 2014; Newton

and Mudge, 2003). Although hydrodynamics is important for explaining the variability of DO data, biogeochemical processes are the dominant driver of diurnal variations and reported elsewhere (e.g. Tian et al., 2022).

PCA results from the edge stations (Fig. 6) indicated that biological factors, photosynthesis matching summer peaks in chlorophyll-a and respiration in winter with increases in organic matter and suspended solids, were the primary drivers to explain the seasonal water quality variability at both stations. Spatial differences emerged as a secondary role in PCA, with NEM distinguishing the two sites, along with a similar influence of tides on DO (also affected probably by upwelling) and ammonium (PC3). Upwelling occurred at both stations under neap tides, either in summer at PF or in winter at CV, as shown in Fig. SM 1A, 2A, 1G and 2G. These figures showed elevated chlorophyll-a near both stations and measured at CV during the winter campaign (Fig. SM 3G). Upwelling events are common along the south coast of Portugal between March and October (García-Lafuente et al., 2006; Relvas and Barton, 2002). Higher winter DO may also be explained by cooler temperatures enhancing oxygen solubility (Cravo et al., 2020; Ghandourah et al., 2023; Rosa et al., 2022) and by reduced organic matter inputs.

Edges showed greater DO variability than inner station, reflecting differences in biological processes, affected by aquatic vegetation and human pressure, depth, hydrodynamics and water renewal. The shallow edge stations ($\leq 20 \text{ cm}$ depth at low tide) enhance benthic-pelagic coupling, as found by other authors in Ria Formosa (Brito et al., 2010, 2011; Falcão and Vale, 2003), with low current velocities (usually in these regions $<0.3 \text{ m s}^{-1}$; Duarte et al., 2008; Soares et al., 2001) favoring organic matter accumulation and low energy dissipation (Dias and Sousa, 2009). Conditions at CV are further constrained by reduced flushing due to the declining efficiency of Cacela inlet (Ferreira, 2024), which can leave the station periodically almost dry at low tide. The tidal effect is delayed at this inlet, with a lower tidal prism than at the inlets close to PF and CC (Kombiadou et al., 2019; Pacheco et al., 2010). In this area, the increased water residence time promotes macroalgal mat development, organic matter decomposition, and large diel DO variability, often leading to night minimum, not only by respiration but also maybe by increased bacterial decomposition of organic matter (Seco, 2025) consistent with findings by Rosa et al. (2022) in the same area (in 2017 and 2019), and a heterotrophic behaviour, expressed by the key role of NEM in PC2, with negative values at CV (Fig. 6). At CC, located in a deeper inner area near Faro Channel, DO variability was less pronounced but long-term records confirmed the tidal imprint, at different scales, either semidiurnal, diurnal or fortnightly, as also shown by spectral analysis (Tufoni, 2020). Seasonal comparisons (Fig. 4) revealed lower median DO saturation at this station, slightly undersaturated for the period 2017–2020 (90–94%; Table 3) although still near equilibrium, with maxima (supersaturated) in spring and summer (Fig. 3) confirming the role of biological processes, driven by primary production, maximum during these periods (Barbosa, 2006; Falcão et al., 1991). Nighttime DO minima during neap tides in summer highlighted the effect of enhanced respiration under long residence times, a pattern also noted by Mudge et al. (2007). In addition to reduced oxygen solubility under high temperature and salinity (Breitburg et al., 2018; Calliari et al., 2005; Cravo et al., 2020; Ghandourah et al., 2023; Mudge et al., 2007; Needoba et al., 2012; Rosa et al., 2022), elevated summer temperatures likely further increased community respiration, as metabolic oxygen demand is strongly temperature-dependent in coastal systems.

Winter conditions contrasted with higher DO saturation at edges than at the inner station, reflecting stronger edge productivity and the sensor depth at CC (4 m above the bottom), which can lead to underestimation of photosynthesis in relation to respiration.

4.2. Temporal evolution of DO in Ria Formosa in the last 40 years and future perspectives

From a temporal perspective, anticipating future changes in DO is crucial for minimizing hypoxia risks in Ria Formosa, reinforcing the need for continuous monitoring and management (Cravo et al., 2020; Newton et al., 2010; Rosa et al., 2022). Global observations and climate model projections indicate a general decline in oceanic DO, linked to rising temperatures, elevated CO₂, and increased nutrient inputs from human activities (Breitburg et al., 2018; Hull et al., 2000, 2008; Schmidt et al., 2019; Stramma et al., 2008). This resilience likely reflects the lagoon's strong tidal flushing, with six inlets promoting high water renewal, together with relatively low industrial and urban pressures. Improvements in wastewater treatment over recent decades have further reduced local stressors (Cravo et al., 2020, 2024; Rosa et al., 2022), which could justify the lack of decrease observed over the last 40 years (Fig. 8). Consequently, compared to microtidal lagoons or more heavily impacted coastal systems, Ria Formosa apparently is buffered against the broader global DO decrease trend. Rodrigues et al. (2021) considering a scenario of a future warming scenario of +1–1.5 °C in Ria Formosa found that DO would generally remain near saturation (~100 %), consistent with current observations of this study. Yet, local conditions may diverge in restricted areas where elevated nutrient inputs may stimulate phytoplankton growth, potentially disrupting DO balance. Predicting DO evolution is challenging, as it is largely governed by biological processes and by temperature variability. Water temperature plays a key role in modulating both DO and NEM. There is a direct effect of temperature on DO solubility and metabolism (according to Arrhenius's law; Laidler, 1984), as well as indirect effects such as modulation of phytoplankton dynamics and chlorophyll-a production.

Hydrodynamic constraints also represent a major vulnerability for DO dynamics. At the Cacela inlet, circulation is already reduced (as mentioned before), and further restriction could intensify sediment accretion, potentially leading to partial or total closure. Such changes may lengthen water residence times, enhance organic matter accumulation, and favour the development of phytoplankton and/or expansion of submerged vegetation. Under these conditions, night respiration could exceed oxygen replenishment, making episodic hypoxia more frequent likely at CV. The risk would be strengthened by future warming, which accelerates respiration and decreases oxygen solubility.

4.3. NEM at edges of the Ria Formosa - comparison of diel oxygen open-water vs. bottle incubation methods

In this study, metabolism was assessed by comparing the open-water diel method with bottle incubations. Results showed consistent discrepancies: bottle incubation method underestimated metabolism relative to diel oxygen open-water calculations, as also reported in Ria de Vigo (Seco, 2025) and other coastal systems (e.g. Europe – Denmark, France and Germany- and USA; Gazeau et al., 2005; Kennish and Paerl, 2010; Soulié et al., 2021). These differences arise from physical limitations in bottles, such as lack of water exchange, confinement effects, light attenuation, exclusion of benthic and advective processes, and absence of wind-driven mixing (Berg et al., 2003; Gazeau et al., 2005; Giordano et al., 2012). Consequently, bottle-based estimates may fail to capture full metabolic activity of the community (Bender et al., 1987).

Hydrodynamics further influenced NEM patterns as observed in other systems using Aquatic Eddy Covariance, such as in Ria de Vigo (Seco, 2025) and in Europe (Scotland), and in USA (West Falmouth Harbor and Oregon Attard et al., 2015; Berg et al., 2013; Glud et al., 2016; Reimers et al., 2016). In Ria Formosa, tidal reversals and current velocity changes led to episodic nighttime positive BDO during flooding, particularly during spring tidal conditions (Fig. 5 B), and negative BDO during the day, on the ebbing time (from high tide to low tide) (Fig. 5E and F). This leads to the highest NEM observed at PF under spring tides in autumn (215 mmol O₂ m⁻² d⁻¹; Table 4) with NR positive (45 mmol

O₂ m⁻² d⁻¹; Table 4), suggesting that the incoming waters are enriched with more oxygen. These high values were not directly linked to chlorophyll peaks, but rather to tidal-driven oxygen inputs and enhanced mixing (Lucas and Cloern, 2002; McLaughlin et al., 2020). Short residence time, mainly during spring tides, can flush the water so rapidly that biological activity has little or no effect on gases concentrations (Gazeau et al., 2005). Wind also contributed to oxygenation, particularly during summer campaigns at PF (Table SM 1), regardless the lower contribution of FO₂ compared to BDO (Fig. 5). This effect cannot be caught by the light-dark oxygen bottles method.

Seasonal analysis also highlighted the influence of coastal upwelling on lagoon metabolism at PF in the summer campaign resulting in autotrophic conditions (maximum NEM: 191 mmol O₂ m⁻² d⁻¹ diel oxygen open-water method and 25 mmol O₂ m⁻² d⁻¹ bottle incubation; Table 4). Chlorophyll concentrations were also significantly higher at this station (Fig. SM 3A), justifying the highest NEP and reinforcing autotrophy. At CV, autotrophy was only found in the winter campaign (under upwelling influence, as referred before), supporting that autotrophy in coastal lagoons can be common in winter (Bas-Silvestre, 2021). However, this period may also match the onset of the typical spring phytoplankton bloom, leading to an increase of primary production (Caffrey et al., 1998).

Both NEM methods showed CV as predominantly heterotrophic, with lower NEP and NR than PF, contrasting with the autotrophic or near-equilibrium behaviour reported for many coastal lagoons (Giordano et al., 2012; Thébault et al., 2008). Weak hydrodynamic conditions and longer residence time at this shallow station, as mentioned before, favoured respiration. There, BDO values were among the lowest values (<20 mmol O₂ m⁻² h⁻¹, Fig. 5 G), since the water column is minimum and the variation in tidal height is considered in this estimation.

Overall, these results illustrate that understanding ecosystem metabolism requires integrating physical (hydrodynamics, tides, upwelling) with biological and chemical processes. Short 24-h measurements provide only snapshots, while long-term, high-frequency monitoring (as at inner station) is essential for reliable NEM estimation. Santos et al. (2004) in the western sector of Ria Formosa, relatively close to PF, in two areas of high water renewal (Ancão inlet and Ramalhete Channel), conducted during the summer season (July 2002), using light and dark bottles during a tidal cycle, showed that both sites of Ria Formosa were in metabolic equilibrium and that net plankton production was autotrophic. Comparing to other systems, Ria Formosa's maximum NEM value (~191 mmol O₂ m⁻² d⁻¹ at PF) was relatively lower than those in Ria de Vigo (~300 mmol O₂ m⁻² d⁻¹; Alonso-Pérez et al., 2015) and much lower than that in the Thames Estuary (485 mmol O₂ m⁻² d⁻¹; Hull et al., 2016).

4.4. NEM at inner station in the Ria Formosa, using a high frequency monitoring approach

Continuous high frequency DO monitoring is essential for evaluating trophic status and net ecosystem metabolism of aquatic ecosystems. High-frequency data capture diurnal, tidal, seasonal, and interannual variability, enabling robust NEM estimates and the detection of short-term shifts between autotrophy and heterotrophy are often missed by discrete sampling, such as rapid shifts in respiration/decomposition of organic matter or phytoplankton blooms (Bas-Silvestre, 2021; Caffrey, 2004; Cravo et al., 2020; Duarte and Prairie, 2005; Gomez-Castillo et al., 2023; Jankowski et al., 2021; Odum, 1956; Soulié et al., 2021).

Such datasets provide valuable indicators for the management of coastal ecosystems under anthropogenic and climatic changes pressures.

This study presents the first long-term high-frequency DO record in Ria Formosa (2.5 years, 15-min intervals), allowing estimation of FO₂, BDO, NEP, NR, and NEM (Fig. 7). Results reveal distinct processes operating at multiple timescales, not captured by one-day surveys. NEP and NR showed clear seasonality, with higher values in spring–summer, highlighting the pivotal role of biological processes. Seasonal NEM

values over 1002 days ($-894 \text{ mmol O}_2 \text{ m}^{-2}$) indicate a generally heterotrophic system (mean NEM = $-0.9 \text{ mmol O}_2 \text{ m}^{-2} \text{ d}^{-1}$), though close to metabolic balance, characterizing the study area as a slight sink for organic matter (Lee et al., 2017). Seasonal biological processes were likely stronger at edges than at inner station, leading to more pronounced autotrophic or heterotrophic conditions. Given the deeper water column at inner station, similar process intensity should have resulted in higher NEM values according to the NEM formula, yet this was not observed. Instead, inner station displayed episodic shifts from heterotrophy to net autotrophy during late spring–summer, a pattern typical of systems with balanced metabolism (Bas-Silvestre, 2021). These shifts were linked to enhanced phytoplankton growth during neap tides, whereas spring tides often drove the system back to heterotrophy (Gomez-Castillo et al., 2023).

Heterotrophy at inner areas results from both internal processes and external organic matter inputs (Caffrey, 2004; Camacho et al., 2016; Giordano et al., 2012; Rewrie et al., 2025). Station 3, located in WB2 and subject to strong anthropogenic pressure from Faro and Olhão, is particularly influenced by land runoff near the saltmarshes where organic matter accumulates (Santos et al., 2004), and transported at deeper levels where the DO sensor was deployed. Additional contributions of organic matter come from respiration and remineralization in the water column and benthic fluxes (Alonso-Pérez et al., 2015; Seco, 2025). These processes are dynamic and modulated by environmental drivers as reported in section 5.1. The heterotrophic pattern at inner station is consistent with earlier studies in inner areas of Ria Formosa (Barbosa, 2006) and with observations from estuaries worldwide, where heterotrophy is common (Caffrey, 2004), including Mediterranean lagoons (Bas-Silvestre, 2021), the Southampton Water estuary in the UK (Gomez-Castillo et al., 2023), and the Patos Lagoon estuary in Brazil (Bordin et al., 2024).

Overall, inner station highlights the value of high frequency DO monitoring for identifying drivers of metabolism in inner lagoon areas. In the context of global changes, understanding the current state and NEM dynamics of coastal lagoons like Ria Formosa is crucial for anticipating future scenarios, especially at stations most vulnerable either due to limited water renewal, shallow depth or increased anthropogenic pressure. It is known that the main channel sites, with strong tidal flushing, remain near DO saturation (Alcântara et al., 2012; Cravo et al., 2014, 2019, 2024, 2019; Rosa et al., 2019, 2022) and consequently in and metabolic balance, as found by Santos et al. (2004) at Ancão inlet. Understanding the processes that regulate NEM is critical for anticipating responses to climate change, including warmer and drier conditions that can be expected in the future close to the Mediterranean, and increased frequency of extreme weather events. These changes would affect the hydrological regime, subsequently altering input loadings and dynamics (Hallett et al., 2018; IPCC, 2014; Pesce et al., 2018) which could ultimately affect the ecosystem's metabolism. Such knowledge is crucial for informing effective management and conservation of these complex, vulnerable coastal systems (Caffrey et al., 2014).

5. Conclusions

- Dissolved oxygen in Ria Formosa exhibited clear spatial and temporal heterogeneity, with a pronounced seasonal pattern consistently observed across all three sampling sites.
- Occasional low DO concentrations ($\leq 2 \text{ mg L}^{-1}$) indicative of hypoxia may induce stress in marine organisms; however, these events were sporadic and currently do not pose significant ecological concern.
- The system's metabolism was strongly influenced by seasonal biological processes, particularly photosynthesis and respiration, and by the coupling between benthic and pelagic processes, especially during spring and summer. Tidal dynamics and hydrodynamic conditions also play an important role in modulating these processes.
- The edges are characterized by dense submerged vegetation (macroalgae and salt marshes), exhibited enhanced biological activity,

resulting in greater DO variability, with higher values during daylight and decreases at night.

- NEM revealed distinct spatial patterns: PF was predominantly autotrophic, CV mainly heterotrophic—likely reflecting differences in hydrodynamics and water exchange, particularly after the recent relocation of the Cabela inlet. Inner station was slightly heterotrophic over 2.5 years, with weaker biological activity; hydrodynamics, tidal exchange, and depth also contributed to its metabolic balance. Overall, Ria Formosa exhibits nearly balanced or slightly autotrophic metabolism where hydrodynamic conditions and water circulation are favorable.
- The lagoon responded sensitively to coastal oceanographic processes such as upwelling, which during flood periods can influence local water characteristics. Biological production in autotrophic areas may be exported to the adjacent ocean during ebb tide, contributing to coastal fertilization and supporting higher trophic levels. High-frequency oxygen monitoring at inner station proved essential to capture short-term variability, transient hypoxic events, and long-term trends, providing a more accurate assessment of metabolic processes in this dynamic system.
- Continuous long-term monitoring substantially improves understanding of ecosystem dynamics, supporting more effective management and conservation strategies compared to classical short-term or single 24-h surveys.
- NEM estimates are more robust when derived from long-term datasets rather than single snapshots, although short-term measurements remain useful for assessing ecosystem status at specific times.
- Methodological differences in NEM estimation can lead to divergent results; for instance, bottle incubation techniques may underestimate NEM, as considering a different rationale, it does not account for hydrodynamic effects.
- Understanding the current metabolic behavior of Ria Formosa, especially in its more confined areas, is critical for predicting responses to global change. Insights into spatial heterogeneity and ecosystem functioning can inform conservation and management strategies, and the findings may be applicable to similar mesotidal coastal lagoons.

CRedit authorship contribution statement

Cátia Correia: Writing – review & editing, Writing – original draft, Visualization, Validation, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **José Jacob:** Writing – review & editing, Writing – original draft, Supervision, Methodology, Investigation. **Alexandra Cravo:** Writing – review & editing, Writing – original draft, Supervision, Methodology, Investigation, Conceptualization.

Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Catia Correia reports financial support was provided by Foundation for Science and Technology, Portugal. Alexandra Cravo reports administrative support and equipment, drugs, or supplies were provided by Foundation for Science and Technology, Portugal. Jose Jacob reports administrative support and equipment, drugs, or supplies were provided by Foundation for Science and Technology, Portugal. If there are other authors, they 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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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.marenvres.2025.107761>.

Data availability

Data will be made available on request.

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