



Changes in carbon metabolism and dissolved organic carbon fluxes on seagrass patches (*Halodule wrightii*) with different ages in Southern Gulf of California

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ABSTRACT

Seagrass meadows are highly dynamic, particularly in sites where extreme climatological events may produce a mosaic of patches with different ages. This study evaluates the community carbon metabolism, dissolved organic carbon (DOC) fluxes and associated fauna in patches of *Halodule wrightii* with different ages since establishment. Net community production declined as patch age increased, probably due to the increase in non-photosynthetic tissues, higher respiration rates of the community assemblage and a likely increase in self-shading of the canopy. The export of DOC was significantly higher in the youngest patches, mainly as a consequence of the lower seagrass net production recorded in older meadows. We concluded that ‘colonizers’ seagrass species may show higher production rates and DOC release during the first stages of colonization, which suggest that, the production, organic carbon exportation and their role as relevant blue carbon communities may be higher than expected.

1. Introduction

Seagrasses are marine foundation species that form one of the richest and most important coastal habitats (Short et al., 2011). They are globally distributed and well recognized by the ecosystem services they provide, including shoreline protection, suitable breeding habitats, biodiversity hotspots, and organic carbon sequestration (Campagne et al., 2015; Jiménez-Ramos et al., 2021). However, seagrass beds are currently decreasing on a global scale, mainly due to anthropogenic disturbances (Waycott et al., 2009) and also because of the increase in the frequency and intensity of extreme climatological events, which are expected to increase due to global climatic change (Fraser et al., 2014). Among extreme climatological events, storms, hurricanes and typhoons can impact positively, neutrally or negatively in seagrass communities. For example, these events may help seagrass to shear off aged and dead leaves, facilitating seagrass growth (Yang and Huang, 2011; Jiménez-Ramos et al., 2023a). However, most of previous studies

reported negative impacts of these extreme climatological events on seagrass meadows (e.g., Tomasko et al., 2020; Wilson et al., 2020). These negative impacts fall into two broad categories: i) physical; via burial, scouring and direct removal of plants and seed banks (Preen and Marsh, 1995; Campbell and McKenzie, 2004); and ii) physiological; via light limitation, nutrient excess and low salinity conditions (Ralph et al., 2007; Jiménez-Ramos et al., 2023b). As a consequence, both large and continuous seagrass meadows, and those that usually grow in a mosaic of patches such as *Halodule* spp. become more fragmented. This fragmentation can trigger seagrass patches with different ages cohabit in the same site (Côté-Laurin et al., 2017; Cuvillier et al., 2017). The patch age of seagrasses (i.e., time after establishment following a disturbance event) can affect the structure of the meadow (i.e., seagrass biomass, density, etc), biodiversity and productivity. Studies on seagrass colonization and recovery showed that relatively young seagrass meadows have different structural complexity, sediment stabilization capacity, carbon stocks and fauna assemblages in comparison with mature meadows (Williams, 1990;

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Barrón et al., 2004; Macreadie et al., 2014). Through the seagrass recovery process, aboveground and belowground biomass increase with time after patch establishment (Duarte and Sand-Jensen, 1990), triggering changes in seagrass production and yielding changes in hydrodynamic conditions (Fonseca et al., 2019; Schaefer and Nepf, 2022). Particle sedimentation and particle transference from the sediment to the water column can be affected by changes in hydrodynamic conditions during the process of patch growth (Morris et al., 2008; van Katwijk et al., 2010; Adhitya et al., 2016; Egea et al., 2023a), which may modify productivity and dissolved organic carbon (DOC) fluxes of seagrass communities (Peralta et al., 2006; Egea et al., 2018).

Changes in the carbon balance of seagrass meadows throughout patches with different ages may determine ecosystem recovery, as ecosystem functioning relies on the supply and cycling of energy and nutrients, with carbon as the main element in this transfer (Hyndes et al., 2014). A positive carbon balance is necessary to increase the carbon storage in the community, which is crucial for seagrass growth (Jiménez-Ramos et al., 2023b), to increase carbohydrate reserves (necessary to buffer stressful period; Brun et al., 2008) and to support biodiversity (Marczak et al., 2007; Egea et al., 2020). The high productivity of seagrasses contributes to the carbon uptake in the coast; carbon that can be stored, consumed, buried or exported to adjacent ecosystems as particulate or dissolved molecules (Duarte and Cebrián, 1996). Previous studies analysing differences in seagrass patch age have been mainly focused on spatial structure and associated biodiversity (Turner et al., 1999; Macreadie et al., 2009), whereas changes in community carbon metabolism and DOC export are still largely disregarded. The DOC exported by seagrass meadows accounts for up to 46% of their global net community production (NCP) (Barrón et al., 2014), and this DOC released may be critical to keep the annual high productivity and biodiversity of communities dominated by seagrass meadows (Navarro et al., 2004; Egea et al., 2019; Jiménez-Ramos et al., 2023b). DOC is one of the largest interchangeable organic carbon reserves in the marine environment, and it is a key factor in the global carbon cycle (Hansell, 2013). A significant fraction of DOC released from seagrasses is formed by bioavailable material (i.e., labile fraction), which is rapidly taken up by several heterotrophic and autotrophic organisms (Navarro et al., 2004; van Engeland et al., 2011; Egea et al., 2019). Otherwise, another fraction of DOC is less accessible to microbial degradation (i.e., recalcitrant fraction) and can be exported and sequestered into the deep ocean (Duarte and Krause-Jensen, 2017; Jiménez-Ramos et al., 2022; Egea et al., 2023b). The current understanding of carbon metabolism and DOC fluxes in seagrasses is limited by the little attention that has been given to these responses *in situ*, including the whole community, but also due to the uneven distribution of previous studies. Thus, there is still a substantial gap of information regarding metabolic rates and DOC fluxes in seagrass communities along the coasts of the Southern Hemisphere and North and West Pacific regions (Duarte et al., 2010; Barrón et al., 2014).

The Gulf of California in northwestern Mexico is a relatively overlooked region regarding seagrass studies, despite the fact that first records were several decades ago and it is inhabited by almost a third of the seagrass species found in North America (Pérez-Estrada et al., 2021). The south of the Baja California Peninsula is usually exposed to tropical storms and hurricanes (Jauregui, 2003). The impact of hurricanes and the recovery of affected ecosystems have been mainly focused to terrestrial vegetation, mangroves and coral reefs (e.g., Piñon-Gimate et al., 2020; Shiba-Reyes et al., 2020; Yao et al., 2021) whereas seagrass meadows have received little attention. *Halodule wrightii* Ascherson (shoalgrass) is a globally distributed tropical and subtropical seagrass species inhabiting this region and considered as an important primary producer and 'early colonizer' after environmental disturbances (Ferreira et al., 2017; Darnell et al., 2021). This makes this species a desirable candidate for assessing the changes in carbon metabolism and DOC fluxes during the early stages of meadow growth following disturbance. Bahía Balandra is a protected natural area in the south of Baja California Peninsula, with a degree of protection and uniqueness (see Materials and method section for more

information) that make it an ideal natural laboratory to evaluate *in situ* the objectives of this study. This study aimed to explore the structural (i.e., seagrass biomass and density), metabolic (i.e., community production and DOC export) and community-associated (i.e., biodiversity) changes among patches of the seagrass *Halodule wrightii* with different ages (2, 4 and 6 years old). We hypothesized that the gross community production and DOC fluxes will increase with patch age. Additionally, changes in the metabolic balance should be expected in older patches due a high structural complexity with higher respiration rates due to expected greater fauna and organic matter content within the sediment.

2. Material and methods

2.1. Study site

The study was carried out in April 2016 in Bahía Balandra, at the subtidal site called la Poza (24°19'0.54"NN, 110°19'30.53"W) and during the period of maximum growth of the seagrass *Halodule wrightii*. Bahía Balandra is a shallow coastal wetland located in the southern Gulf of California, Mexico (24°18'54.8" N; 110°19'39.3" W) (Fig. 1). It covers approximately 52.5 ha which includes a coastal lagoon, mangroves, rocky reefs and *H. wrightii* seagrass meadows. The site belongs to the RAMSAR International Wetland Convention since 2008. It was declared a Protected Area in 2012 by the Mexican Government and a World Heritage Site by the UNESCO in 2013 (Comisión Nacional de Áreas Naturales Protegidas, 2016). The tides are semidiurnal, with an average tidal range of 1–1.5 m, depth varies from 0.5 m in the southern part to 25 m at the inlet (Domínguez-Orozco, 1996). The average current velocity in the area during ebb tide is 0.141 m s⁻¹ (Gutiérrez Sánchez, 1987). The climate is considered as a subtropical arid zone (Zeitzschel, 1969), with seawater temperature reaching minimum values during winter and peaking in summer (on average, 22.8 °C and 27.3 °C, respectively; Pérez-Estrada et al., 2021). Salinity shows low annual variation, ranging between 34.4 and 35 PSU (Urquidí-Gaume, 2012). The sandy sea bottom is mostly composed of the remaining invertebrate shells hash (Torres-Alfaro, 2010) and monospecific patches of *H. wrightii* with a scattered distribution (Pérez-Estrada et al., 2021). For detailed information of the study area, see previous description in Pérez-Estrada et al. (2021). Extreme climatological events, such as tropical cyclones or hurricanes with a wide range of frequencies and intensities, usually occur in the area (Luja and Rodríguez-Estrella, 2010). Previous to our experimental period, during 2015–2016 "Godzilla El Niño" event took place (Coria-Monter et al., 2018), and in September 2016, Hurricane Newton (category 1 on the Saffir-Simpson scale) reached the southern peninsula of Baja California, causing maximum sustained winds between 85 and 140 km/h and precipitation of 55.8 mm (Berg, 2017; Instituto Nacional de Estadística y Geografía, 2017).

A monitoring program focused on the dynamic of the establishment and growth of patches of *H. wrightii* in the area started in 2010. As part of the monitoring program, three main zones were surveyed every six months, and every *H. wrightii* patch (those previously identified and new ones) was measured and GPS-referenced during the following 7 years. This monitoring was carried out visiting the area, using aerial photographs, taking new photographs in the area, measuring directly the area of the patches and collecting samples of biomass (more details in Pérez-Estrada et al., 2021). This allowed to have a large dataset, including location, size and establishment time for each patch. During the experimental period, a total of 59 patches with a scattered distribution were established in the area, covering a surface of approximately 4420 m² (Pérez-Estrada et al., 2021).

Four types of subtidal populations were selected: i) patches established in 2010 (6-years), ii) patches established in 2012 (4-years), iii) patches established in 2014 (2-years) and iv) unvegetated areas surrounding the patches (i.e., areas without vegetation during the 6 years of the monitoring program). The different patches were spaced at least 7 m far away each other and were all allocated at a similar depth (2 m during high tide).

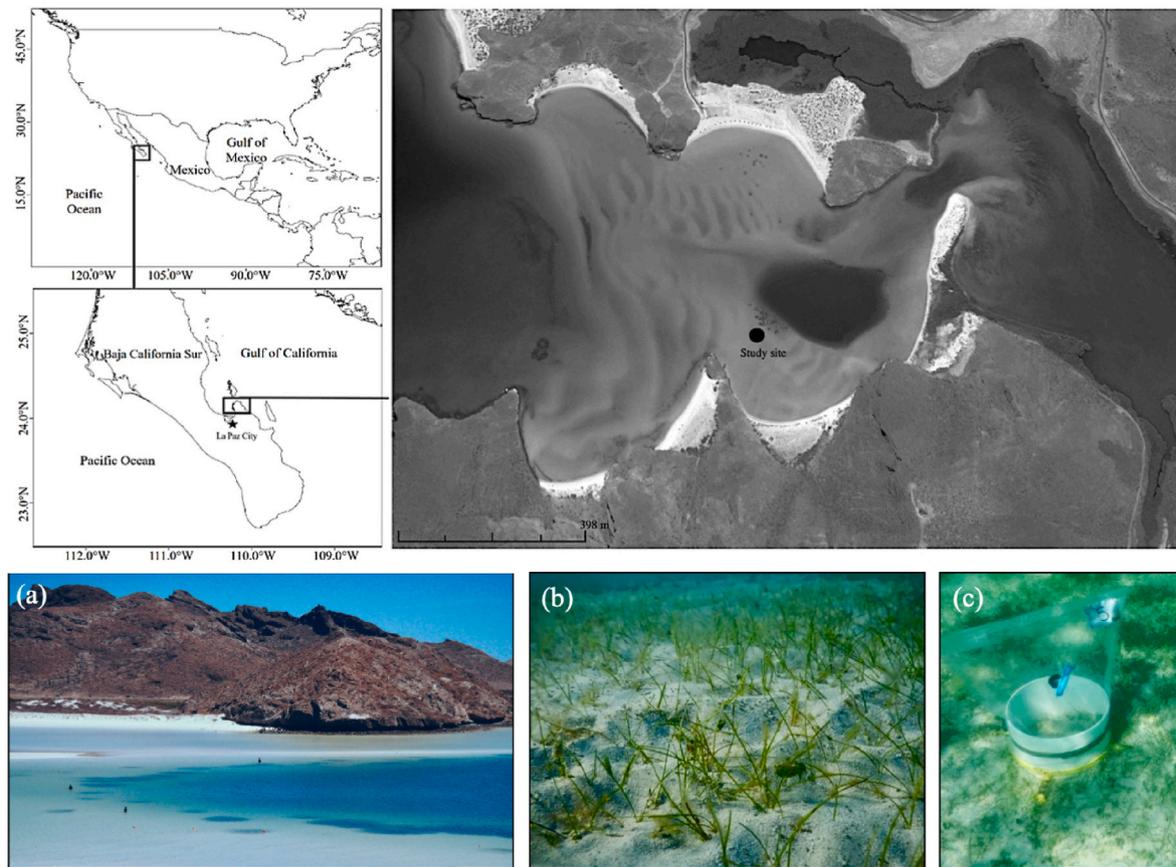


Fig. 1. Study site in Bahía Balandra, southern Gulf of California, Mexico and pictures of (a) the sampling area (black areas around deeper water represent *H. wrightii* patches); (b) one representative patch of the youngest meadow; and (c) one representative *in situ* incubation.

2.2. Experimental setup

We followed the methodology described in Egea et al. (2019) and Jiménez-Ramos et al. (2022) to estimate community carbon metabolism and DOC fluxes, using *in situ* benthic chambers (called incubations from here on), which were placed by scuba diving. The incubation period lasted ca. 19 h, from about 2 h before sunset until about 4 h after the sunrise of the next day. Three *H. wrightii* patches from each selected age (i.e., 2-, 4- and 6-years), with an average size of 4.1 ± 1.2 , 20.5 ± 4.6 and 36.2 ± 10.7 m², respectively, and three unvegetated areas located near patches were randomly selected as independent replicates ($n = 3$). Although the vegetated community was dominated by *H. wrightii*, it is composed by an assemblage of several biological components, such as plankton, epiphytes, macroalgae, infauna and sediment microbes. Therefore, the results from this study integrate the whole community, which produces a more realistic approach. Incubations consisted of a rigid cylinder made of a polyvinyl chloride (diameter = 19.5 cm; height = 17 cm) with a sharpened lower end firmly inserted into the sediment (15 cm) with only 2 cm of the cylinder above the sediment, which was the minimum necessary to fit the air-tight polyethylene plastic bag (height \approx 22 cm; width \approx 33 cm) over the upper end-part of the cylinder. Each bag was provided with a sampling port located in the upper half of the bag (\approx 15 cm) to withdraw water samples. The walls of the bags (wall thickness \approx 0.07 mm) were flexible enough to allow their movement with the hydrodynamics, preventing water stagnation. An additional structure consisting of a metal ring (diameter = 20.7 cm) with four legs (height = 25 cm; width = 1.3 cm; thickness = 0.3 cm) inserted in the sediment was installed surrounding the rigid polyvinyl chloride cylinder to increase the anchoring of the incubation in the sediment. Light penetration measured inside the incubations was circa $99.15 \pm 0.01\%$ ($n = 6$) of incident light outside the bag. Oxygen diffusion controls were

run and demonstrated no oxygen permeability of the plastic bags. All incubations were initiated at the same time in the evening, a few hours before nightfall, and they were placed randomly in the central part of the patches. To avoid the collection of resuspended material resulting from the physical disturbance during installation of the incubations, the first sample was taken 2h after setting up.

To measure community carbon metabolism and DOC fluxes, water enclosed within each incubation was collected through the sampling port using a 50-mL acid-washed syringe (standard plastic previously subjected to blank control) at three moments during the day: i) just before sunset (S1), ii) right after sunrise (S2) and iii) 6 h after sunrise (S3). In this way, community carbon metabolism and DOC flux in dark and light periods can be distinguished (Egea et al., 2019). To calculate the water volume in each incubation, 20 mL of a 0.1 M uranine solution (sodium fluorescein, C₂₀H₁₀Na₂O₅) was injected into each incubation bag at the end of the experimental period, allowing 15 min for mixing. The bag was shaken manually to favour the quick mixing of the solution. Thereafter, water samples were collected and kept frozen until spectrophotometric determination according to Egea et al. (2019). The mean volume of water enclosed in each incubation was 9.8 ± 0.03 L ($n = 12$). Finally, during the process of disassembling incubations, the whole community inside the incubations were carefully harvested (including belowground biomass and fauna) and kept in darkness and refrigerated until laboratory analysis. Temperature (°C) and light (lumens m⁻²) were continuously monitored during the sampling period with HOBO data loggers (UA-002-64) set within the seagrass canopy and in unvegetated areas close to the experimental incubations ($n = 3$). Light intensity was converted from HOBO values in Lux (lumens m⁻²) to $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$ according to a previous calibration with a LiCor light sensor (LI-1400, LiCor Biosciences, United States) under laboratory conditions.

2.3. Laboratory analysis

Community carbon metabolism was estimated through changes in dissolved oxygen (DO) concentration. Water samples (15 mL) for DO concentration were fixed immediately after collection, kept in darkness, refrigerated, and determined using a spectrophotometric modification of the Winkler titration method (Pai et al., 1993; Egea et al., 2019). Hourly rates of community respiration (CR_h), net community production (NCP_h) and gross primary production (GPP_h) were calculated using the following formulas:

$$CR_h \left(\frac{mmolO_2}{m^2 d} \right) = \frac{DO_{S2} \left(\frac{mgO_2}{l} \right) - DO_{S1} \left(\frac{mgO_2}{l} \right) * Vol(l) * \frac{1}{32} \frac{mmolO_2}{mgO_2}}{\Delta T_{T_{S1}-T_{S2}}(h) Area(m^2)} \quad (1)$$

$$NCP_h \left(\frac{mmolO_2}{m^2 d} \right) = \frac{DO_{S3} \left(\frac{mgO_2}{l} \right) - DO_{S2} \left(\frac{mgO_2}{l} \right) * Vol(l) * \frac{1}{32} \frac{mmolO_2}{mgO_2}}{\Delta T_{S2-S3}(h) Area(m^2)} \quad (2)$$

$$GPP_h \left(\frac{mmolO_2}{m^2 d} \right) = CR_h \left(\frac{mmolO_2}{m^2 d} \right) + NCP_h \left(\frac{mmolO_2}{m^2 d} \right) \quad (3)$$

where DO_{S1-S3} are the dissolved oxygen concentrations at times $S1-S3$, ΔT is the elapsed time between sampling events and “Vol” and “Area” are the volume and area of the benthic incubation respectively.

Finally, daily rates of gross primary production (GPP_d), community respiration (CR_d) and net community production (NCP_d) were estimated following the upcoming calculations (where photoperiod corresponded to the number of sunlit hours measured in each sampling day):

$$GPP_d = GPP_h * Photoperiod (h) \quad (4)$$

$$CR_d = CR_h * 24 h \quad (5)$$

$$NCP_d = GPP_d - CR_d \quad (6)$$

Metabolic rates in DO units were converted to carbon units assuming photosynthetic (PQ = moles O_2 :moles CO_2) and respiratory quotients (RQ) of 1, values used widely in seagrasses studies (Barrón et al., 2004; Jiménez-Ramos et al., 2022).

DOC fluxes were estimated by changes in DOC concentration during light and dark periods. Water samples (20 mL) from benthic chambers were filtered through pre-combusted (450 °C for 4 h) Whatman GF/F filters (0.7 μm) and were kept with 0.08 mL of H_3PO_4 (diluted 30%) at 4 °C in acid-washed material (glass vials encapsulated with silicone-PTE caps) until analyses. Concentrations of DOC were derived by catalytic oxidation at high temperature (720 °C) and measured via NDIR detector using a Shimadzu TOC-VCPH analyzer. DOC-certified reference material (Low and Deep), provided by D. A. Hansell and W. Chen (University of Miami), of 41–45 μmol DOC and 1 μmol DOC were used to assess the accuracy of the estimations. The instrument blank ranged between 0 and 12 μmol DOC l^{-1} across the different analytical batches. DOC flux at night or daylight were calculated (according to Egea et al., 2019) as the difference between the final and the initial DOC concentrations in the water samples for each period. Then, the DOC flux was calculated using the following formula:

$$DOC \text{ flux} \left(\frac{mmolC}{m^2 h} \right) = \frac{DOC_f \left(\frac{mgC}{l} \right) - DOC_0 \left(\frac{mgC}{l} \right) * Vol(l) * \frac{1}{12} \frac{mmolC}{mgC}}{\Delta T_{T_0-T_f}(h) Area(m^2)} \quad (7)$$

where DOC_f and DOC_0 are the DOC concentrations at final (T_f) and

initial (T_0) times, ΔT is the time elapsed between sampling times, “Vol” and “Area” are the volume and area of the incubation respectively.

Daily rates of DOC fluxes were calculated by the sum of the hourly DOC fluxes at daylight multiplied by photoperiod and the hourly DOC fluxes at night multiplied by night hours. Thus, when net DOC flux was positive, the community was considered to act as a net DOC producer (i. e., source). When net DOC flux was negative, however, the community was considered to act as a net DOC consumer (i. e., sink).

Community biomass (including *H. wrightii*, epiphytes and macroalgae) within incubations were weighed (fresh weight; FW). Seagrasses were split into leaves (aboveground, AG) and rhizomes/roots (belowground, BG), and weighed to calculate the AG/BG ratio. Samples for sediment organic matter (SOM) close to the incubations ($n = 3$) were also collected (height ≈ 5 cm; diameter ≈ 2.5 cm) and measured by a standard combustion procedure (Howard et al., 2014). Macroalgae and fauna-associated with seagrass were identified to the lowest possible taxon level (usually to class or order level) counted, dried (48 h at 60 °C) and weighed. Number of taxa, abundance and diversity index of Shannon–Wiener (H') (Shannon and Weaver, 1963) and equitativity were calculated. H' and equitativity were calculated according to the following formulae:

$$H' = - \sum (\rho_i) \ln (\rho_i) \quad (8)$$

$$Equitativity = \frac{\ln (s)}{H'} \quad (9)$$

where ρ_i is the relative abundance and s is the number of taxa.

2.4. Data and statistical analysis

Data are presented as mean and standard error (SE). Generalized linear models (GLMs) were used to test the effects of response variables among patch age categories. Gaussian distribution with identity link were used to model the response variables. The goodness of fit of each model was assessed by checking the normality and homoscedasticity of the residuals with the Shapiro-Wilk and Levene’s test, respectively. When the models were significant, pairwise comparisons were tested using estimated marginal means with a Bonferroni correction (“emmeans” R package; Lenth et al., 2019). The significance level (α) set in all tests performed was 0.05. Statistical analyses were computed with R statistical software 4.0.2 (R Development Core Team, 2020).

3. Results

3.1. Description of the benthic communities

Average water temperature measured during the study period was 23.2 ± 0.03 °C during the night time and 23.5 ± 0.12 °C during the day. Mean underwater daily irradiance reaching the bottom of *H. wrightii* patches at midday was 160 ± 23 μmol photons $m^{-2} s^{-1}$, while higher values were recorded in unvegetated areas (590 ± 120 μmol photons $m^{-2} s^{-1}$). The average community biomass (i. e., the sum of seagrass, epiphyte and macroalgae weights) and shoot density were significantly lower ($p < 0.05$) in the youngest patches than in the other two patches (2.8 and 2-fold higher for community biomass and 1.7 and 2.5-fold

Table 1

Characteristics of the patches of *H. wrightii* in Bahía Balandra with different ages and unvegetated sediment. Data are mean \pm SE ($n = 3$). Superscript letters indicate significant differences among communities. NP = no presence or negligible.

Community	Seagrass biomass (g FW m^{-2})	Macroalgae and cyanobacteria biomass (%)	Shoot density (shoot m^{-2})	AG/BG biomass ratio	SOM (g DW m^{-2})	SOM (%)
Unvegetated (6-years)	NP	NP	NP	NP	3.8 ± 1.5	0.24 ± 0.08
<i>H. wrightii</i> (2-years)	125 ± 26^a	0.01 ± 0.004	3400 ± 700^a	0.44 ± 0.14	6.6 ± 0.9	0.37 ± 0.04
<i>H. wrightii</i> (4-years)	364 ± 77^b	0.07 ± 0.058	$6000 \pm 1,700^b$	0.30 ± 0.08	5.2 ± 0.6	0.31 ± 0.07
<i>H. wrightii</i> (6-years)	257 ± 61^b	0.07 ± 0.061	$8600 \pm 2,200^b$	0.24 ± 0.09	7 ± 0.9	0.39 ± 0.01

Table 2

Mean values of carbon community metabolism in patches of *H. wrightii* in Bahía Balandra with different ages and unvegetated sediment. Data are mean \pm SE ($n = 3$). GPP_d: Daily rate of Gross Primary Production; CR_d: Daily rate of Community Respiration; NCP_d: Daily rate of Net Community Production. P:R: Productivity:Respiration ratio. Superscript letters indicate significant differences among communities.

Community	GPP _d (mmolC m ⁻² d ⁻¹)	CR _d (mmolC m ⁻² d ⁻¹)	NCP _d (mmolC m ⁻² d ⁻¹)	P:R
Unvegetated (6-years)	25.5 \pm 7.0 ^a	-17.4 \pm 3.9 ^a	8.1 \pm 10.9	1.9 \pm 1.0
<i>H. wrightii</i> (2-years)	165.1 \pm 40.2 ^b	-62.6 \pm 9.6 ^b	102.4 \pm 31.5	2.6 \pm 0.3
<i>H. wrightii</i> (4-years)	110.9 \pm 28.1 ^a	-38.4 \pm 4.6 ^{a,b}	72.5 \pm 27.9	3.0 \pm 0.7
<i>H. wrightii</i> (6-years)	112.1 \pm 4.2 ^a	-51.5 \pm 6.1 ^b	60.7 \pm 4.7	2.2 \pm 0.2

higher for shoot density in the 4-years and 6-years patches, respectively) (Table 1). In terms of biomass, seagrass was the dominant macrophyte in the community, while macroalgae (*Polysiphonia* sp., *Ceramium* sp., *Acanthophora spicifera*, *Caulerpa sertularioides* and *Spyridia filamentosa*) and cyanobacteria (probably *Lyngbya* sp. or *Dapis* sp.) recorded in the three patches were negligible (<0.1% FW), even in unvegetated areas. The above- and belowground biomass ratio (AG/BG) decreased with patch age, indicating a tendency to increase belowground tissues with patch age. The sediment organic matter (SOM) was very low (<0.4% in all patches), with no significant differences between patch ages (Table 1).

3.2. Community metabolism

Overall, daily community metabolism in the communities dominated by seagrasses were significantly higher (5, 3 and 9-fold higher for GPP_d, CR_d and NCP_d, respectively) than unvegetated ones ($p < 0.01$) (Tables 2 and 5). In addition, there were significant differences between patches of different ages. Thus, the GPP_d, CR_d and NCP_d in the youngest patches were ca. 1.5-fold higher than the average of the other two older patches (Table 2). This difference turned into significant when data was normalized by biomass. GPP_d, CR_d and NCP_d in the youngest patches were more than 3-fold higher than the average of the other two patches (Fig. 2, Table 5). No significant differences were found between 4-years and 6-years old patches.

3.3. DOC fluxes

The youngest patches showed the greatest net DOC production (44.2 \pm 3 mmol C m⁻² d⁻¹) with values significantly higher than the average of the other communities (4-years, 6-years patches and unvegetated sediment; Fig. 3, Table 5). Unvegetated areas and 4-years old patches were also net DOC producers, but at lower rates (3.2 \pm 6.7 mmol C m⁻² d⁻¹ and 1.6 \pm 1.1 mmol C m⁻² d⁻¹, respectively). In contrast, 6-years old patches were net DOC consumers (-5.6 \pm 5.3 mmol C m⁻² d⁻¹).

3.4. Biodiversity

The youngest patches showed the lowest number of taxa and density of individuals, while 4- and 6-years old patches showed similar number of taxa and density of individuals (Table 3). The number of taxa was circa 1.6 to 1.9 higher, while the density of individuals was 3–4 times higher in 4-year and 6-year old patches when compared to the youngest ones. The oldest patches showed the highest Shannon diversity index and equitativity (Tables 3 and 5). The most abundant taxa in all the patches were Cnidaria, followed by Annelida, but these taxa decreased with patch age. Mollusca and Crustacea were relatively abundant as well. Echinodermata and Chordata were only found in the youngest patches, whereas Nematoda was the phylum less represented among the patches. In fact, taxa of this phylum were absent in the youngest patches (Table 4).

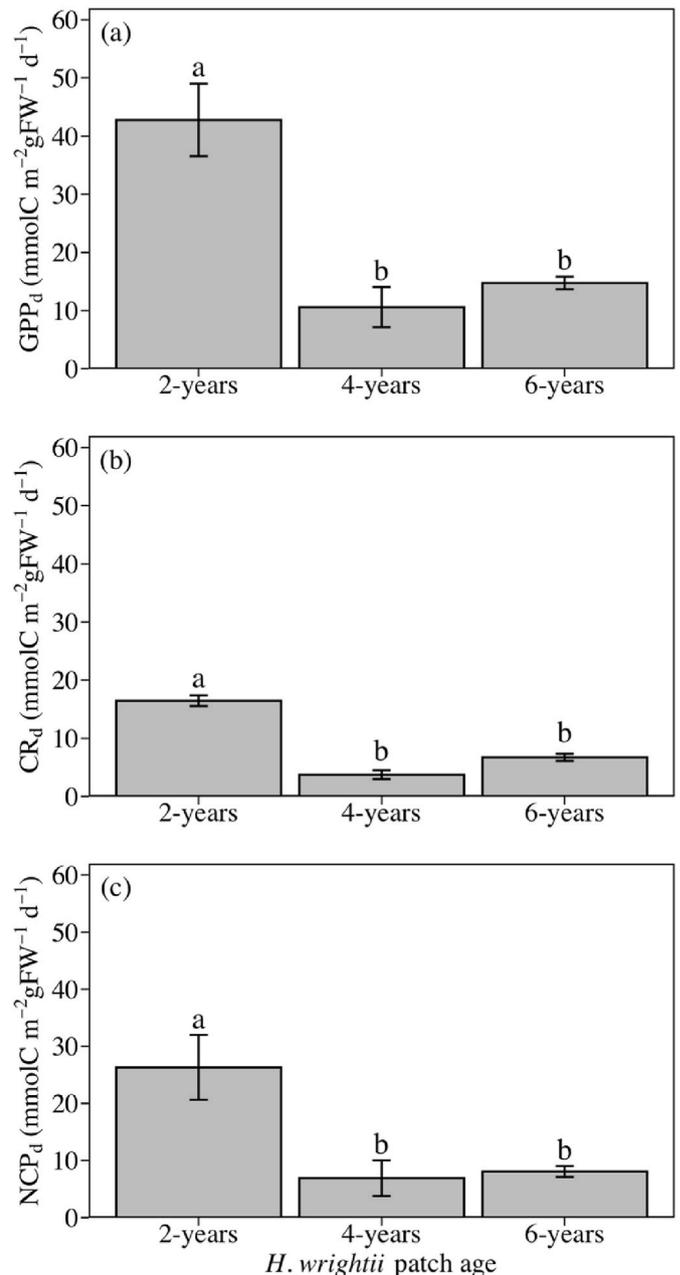


Fig. 2. Carbon community metabolism in patches of *H. wrightii* in Bahía Balandra with different ages normalized by the community biomass. (a) Daily rate of Gross Primary Production (GPP_d), (b) Daily rate of Community Respiration (CR_d) and (c) Daily rate of Net Community Production (NCP_d). Different letters indicate significant differences between patches. Data are presented and mean \pm SE ($n = 3$).

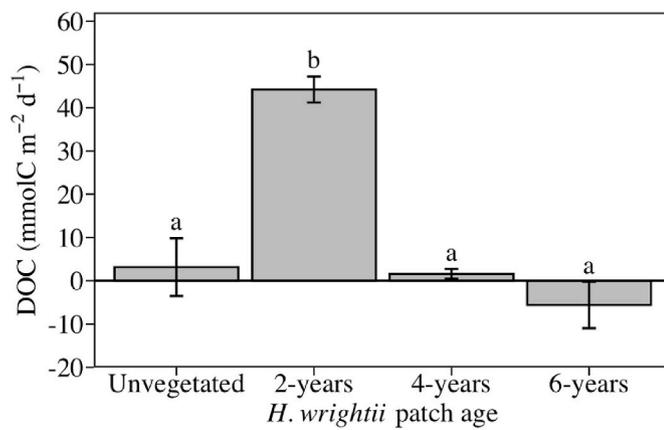


Fig. 3. Net DOC fluxes in unvegetated sediments and *H. wrightii* patches in Bahía Balandra with different ages. Different letters indicate significant differences between patches. Data are showed as mean \pm SE ($n = 3$).

Table 3

Number of taxa, abundance, diversity and equitativity in patches of *H. wrightii* in Bahía Balandra with different ages. Data are presented as mean \pm SE ($n = 3$). Superscript letters indicate significant differences between patches.

Response variable	<i>H. wrightii</i> (2-years)	<i>H. wrightii</i> (4-years)	<i>H. wrightii</i> (6-years)
Number of taxa	10 \pm 1 ^a	16 \pm 2 ^{ab}	19 \pm 1 ^b
Abundance (ind m ⁻²)	1697 \pm 708 ^a	6596 \pm 567 ^b	5603 \pm 1,625 ^{ab}
Shannon-Wiener Index (H)	1.07 \pm 0.13 ^{ab}	0.82 \pm 0.07 ^a	1.42 \pm 0.12 ^b
Equitativity	0.46 \pm 0.03 ^a	0.30 \pm 0.02 ^b	0.49 \pm 0.04 ^a

Table 4

Relative abundance of taxa (%) in patches of *H. wrightii* in Bahía Balandra with different ages. Data are presented as mean \pm SE ($n = 3$). n.f. = taxon not found.

Taxa	<i>H. wrightii</i> (2-years)	<i>H. wrightii</i> (4-years)	<i>H. wrightii</i> (6-years)
Cnidaria	50 \pm 25	85 \pm 1	72 \pm 4
Annelida	17 \pm 4	6 \pm 1	8 \pm 1
Mollusca	12 \pm 4	5 \pm 1	11 \pm 3
Crustacea	11 \pm 7	4 \pm 1	8 \pm 3
Echinodermata	5 \pm 4	n.f.	n.f.
Chordata	6 \pm 6	n.f.	n.f.
Nematoda	n.f.	1 \pm 1	2 \pm 0

Table 5

Results of GLM analysis to test the effects of *H. wrightii* patch ages on each response variable. FW: fresh weigh; GPP_d: Daily rate of Community Gross Primary Production; CR_d: Daily rate of Community Respiration; NCP_d: Daily rate of Net Community Production; DOC: Dissolved Organic Carbon. Symbols indicate significant differences at $\alpha < 0.05$ (*); $\alpha < 0.01$ (**); $\alpha < 0.001$ (***)

Response variable (units)	Estimate	SE	t value	Pr (> t)
Seagrass biomass (g FW m ⁻²)	40.1	8.03	5.00	0.0024**
Shoot density (shoot m ⁻²)	-1189.0	380.14	-3.13	0.0107*
GPP _d (mmolC m ⁻² d ⁻¹)	18.2	5.34	3.42	0.0142*
CR _d (mmolC m ⁻² d ⁻¹)	34.1	9.09	3.75	0.0056**
NCP _d (mmolC m ⁻² d ⁻¹)	-52.5	30.90	-1.70	0.1274
GPP _d (mmolC m ⁻² g FW ⁻¹ d ⁻¹)	28.0	5.88	4.76	0.0031**
CR _d (mmolC m ⁻² g FW ⁻¹ d ⁻¹)	3.0	1.11	2.71	0.0349*
NCP _d (mmolC m ⁻² g FW ⁻¹ d ⁻¹)	18.2	5.34	3.42	0.0142*
DOC (mmolC m ⁻² d ⁻¹)	49.8	6.46	7.71	<0.001***
Number of taxa	8.33	2.11	3.95	0.0075**
Abundance (ind m ⁻²)	116.67	45.38	2.57	0.0423*
Shannon Index (H)	0.60	0.16	3.81	0.0088**
Equitativity	-0.16	0.04	-3.69	0.0102*

4. Discussion

This study demonstrated that community composition (i.e., seagrass biomass and density, fauna and flora assemblages), carbon community metabolism (i.e., NCP_d, GPP_d and CR_d) and DOC fluxes in seagrass communities dominated by *Halodule wrightii* in Bahía Balandra were affected significantly by the patch age (i.e., time after establishment following a disturbance event). The community dominated by *H. wrightii* was highly autotrophic independently of the patch age, since all patches showed P:R ratios higher than 1 and also significantly higher than unvegetated sediments (Table 2). Regarding net DOC fluxes, communities dominated by *H. wrightii* generally acted as a net DOC source, although patch age shifted DOC flux from net producers in young patches to net DOC consumers in older ones. Moreover, this is the first *in situ* study on *H. wrightii* in the Gulf of California accounting for its community carbon metabolism and DOC fluxes, assessing its consequences on the biodiversity, services and ecosystem functions.

4.1. Community carbon metabolism

The results showed that daily net community production (NCP_d) decreased with patch age as a consequence of the reduction in daily gross primary production (GPP_d) (Table 2; Fig. 2), despite that seagrass biomass was significantly higher in older patches, and therefore higher GPP_d values should be expected. By contrast, many studies in terrestrial ecosystems reported that NCP_d is usually reduced during the first stages of the succession, such as in the arctic (Rocha and Shaver, 2011), boreal tundra (Goulden et al., 2011) and temperate forests (Martínez-García et al., 2017). The highest NCP_d was usually found in intermediate successional stages and somewhat reduced in older ages because of the increase in the decomposition rates of the organic matter settled in the floor (Goulden et al., 2011). In the present study, a GPP_d increase in older patches would be expected, since macrophyte biomass and shoot density increased significantly with patch age. However, the youngest patches were significantly more productive per biomass unit (Fig. 2). This can be attributed to the sum of several processes. Firstly, the AG/BG biomass ratio was higher in the youngest patches, indicating a tendency to increase the proportion of non-photosynthetic tissues with patch age and, therefore, in the respiratory demand. Secondly, a shift in the community (i.e., diversity and organisms' abundance) with patch age was also recorded. The diversity of fauna and the abundance of organisms increased with patch age (Table 3), in agreement with the pattern found in previous studies showing the interweave of fauna and seagrasses with time after colonization (e.g., Gartner et al., 2015; Mckimming et al., 2016). Previous studies in other macrophyte-based systems have found lower NCP_d than expected, in part, as a consequence of the higher abundance of the faunal component (e.g., Santos et al., 2004). As the community hold a greater macrofauna assemblage, the NCP_d decreased because of the concomitant increase in respiration rates. Finally, we hypothesize that the relatively higher aboveground biomass and density in 4- and 6-years old patches respect to the youngest patches may trigger the self-shading of the canopy, which may reduce the productivity of the meadow per biomass unit (Fonseca and Koehl, 2006; Jiménez-Ramos et al., 2023b). Furthermore, although all the *H. wrightii* patches evaluated were located in the same area and subjected to the same hydrodynamic conditions, we suggested that the water flow within the canopy could be relatively higher in the youngest patches, since it showed significantly lower biomass and density (González-Ortiz et al., 2014; Morris et al., 2008). A higher volumetric flow rate crossing throughout the canopy may benefit plants by increasing nutrient uptake and therefore productivity (Morris et al., 2008, 2013). In addition, the oxygenation of the rhizosphere could be promoted, due to the higher productivity levels of the plants (Villazán et al., 2016) which may increase oxidative reactions and water-sediment fluxes (Folmer et al., 2012). Unfortunately, due to the complexity of the experimental design employed in this study, we were unable to record *in situ* hydrodynamic

data. This aspect should be considered in future experiments.

4.2. Dissolved organic carbon fluxes

A high variability in net dissolved organic carbon (DOC) fluxes was found depending on the patch age. The net DOC flux ranged from highly DOC producers in the youngest patches ($44.2 \pm 3 \text{ mmol C m}^{-2} \text{ d}^{-1}$, which represented the 43% of their NCP_d) to net DOC consumers in the oldest ones ($-5.6 \pm 5.3 \text{ mmol C m}^{-2} \text{ d}^{-1}$). Meanwhile patches of 4-years old had a nearly balanced net DOC flux, tending to be slightly positive ($1.6 \pm 1.1 \text{ mmol C m}^{-2} \text{ d}^{-1}$, which represented only 2% of their NCP_d). Although seagrasses typically act as a net source of DOC (i.e., positive net DOC flux) to the marine environment when they are highly productive, they can also act as a net DOC consumer (i.e., negative net DOC flux), especially under low productivity conditions (Barrón et al., 2014; Egea et al., 2019). Multiple components of the community (including microbes, cyanobacteria, metazoans, macroalgae and plants) might be responsible for a net DOC uptake in seagrass communities. For example, the relatively higher proportion of cyanobacteria in older patches (Table 1) could increase the uptake of DOC. This could be especially significant under low primary production in these communities, as were previously recorded in some seagrass systems (Navarro et al., 2004). The relatively higher proportion of fauna in older patches may imply a decrease in DOC since important amounts of DOC can be transferred through heterotrophic bacteria to higher trophic levels (Azam, 1998; Mostajir et al., 2015). Moreover, some studies using stable isotopes have reported that macroalgae and seagrasses can also take up dissolved organic carbon and nitrogen under particular conditions (van Engeland et al., 2011, 2013). Likewise, the high net DOC release in the youngest patches may be explained by the sum of different processes. Firstly, because of the linear relationship between seagrass production and DOC released estimated in the area ($r^2 = 0.97$; $p = 0.09$), which is in line with previous studies (Egea et al., 2019; Jiménez-Ramos et al., 2023b). Moreover, the characteristics of the associated community may also contribute to the pattern observed here, since different faunal components were recorded among patches, and their differential behaviour may produce large differences in DOC fluxes. For instance, bioturbator organisms may influence the transformation and retention of organic matter settled on the seafloor and enhance benthic fluxes to the water column (Josefson et al., 2012; Thomson et al., 2019). This can be the case for the youngest patches, where Annelida were more abundant and may increase the release of DOC as a consequence of a bioturbation process (e.g., when digging their galleries to feed on organic matter), as it has been recently highlighted in previous work with this phylum (Sun et al., 2018; Tian et al., 2019). Finally, we also hypothesize that the possible higher hydrodynamic flux within the youngest patches, as a consequence of the lower aboveground biomass and density, may prompt an increase in the DOC transference from the sediment to the water column (Chipman et al., 2010; Egea et al., 2023a), as also happens with the flux of nutrients to the water column (Corbett, 2010; Adhitya et al., 2016). As we noted previously, we were unable to measure *in situ* hydrodynamic conditions because of the complexity of the experimental design employed in this study. This aspect should be considered in future experiments.

4.3. Limitations of the *in situ* incubation methodology

The reported values in this study (on average, $129.4 \pm 16.8 \text{ mmol C m}^{-2} \text{ d}^{-1}$ for GPP_d and $13.4 \pm 8 \text{ mmol C m}^{-2} \text{ d}^{-1}$ for DOC export) are within the same range of values given by Duarte et al. (2010) for GPP_d ($186 \pm 41.2 \text{ mmol C m}^{-2} \text{ d}^{-1}$) and Barrón et al. (2014) for DOC exportation ($21.7 \pm 32.1 \text{ mmol C m}^{-2} \text{ d}^{-1}$) in this seagrass species. The methodology deployed in this experiment has been widely utilized in previous studies (e.g., Jiménez-Ramos et al., 2022), because it allows an effective approach to the *in situ* metabolic responses of the whole community, but it has also some limitations (Egea et al., 2019). In our

experimental set-up, the NCP_d was estimated during 5–6 h after sunrise, which may underestimate up to 25% the NCP_d of the benthic communities (Olivé et al., 2016). However, given that the objective of the study is to compare populations in the same area, using the same methodology, the possible NCP_d underestimation or overestimation does not affect the conclusions obtained throughout the study. On the other hand, the methodology does not allow to distinguish the relative contribution of each component of the community to the total net DOC exported (e.g., plants, macroalgae, epiphytic community, benthic microalgae, phytoplankton, plant litter, metazoans, exchange from sediment–water interface, etc.), which is, therefore, an open question that requires further attention. DOC transference from the sediment to the water column can be an important source of DOC in this ecosystem (Burdige and Komada, 2015; Adhitya et al., 2016), which could show significant differences among patches with different ages since the hydrodynamic regime inside the meadow can be deeply affected by seagrass density and patch age (Mazarrasa et al., 2018; Marin-Diaz et al., 2020). Likewise, the role of epiphytes in these communities, which also could show significant differences among patches with different ages (Lavery and Vanderklift, 2002), can be highly relevant to support the community metabolism (Cox et al., 2020) and the DOC fluxes (Apostolaki et al., 2011). The importance of DOC sediment–water exchange and DOC export from epiphytes among patches of different ages should be further assessed in future researches.

4.4. Ecological implications and conclusions

Seagrass ecosystems are lost each year through habitat destruction, eutrophication, and other anthropogenic stressors (Waycott et al., 2009). Consequently, seagrass restoration is increasing to help mitigate the loss of habitat as well as increasing carbon stocks and sinks in coastal waters (Greiner et al., 2013). However, the differences in sediment organic carbon stocks among seagrass species, makes that most management, monitoring and restoration programs focus on larger species such as *Posidonia oceanica* (Kilminster et al., 2015; IUCN, 2021), which typically exhibit higher sediment carbon deposits (Mazarrasa et al., 2018). The study presented here adds arguments to include also smaller seagrass species, usually considered as ‘colonizers’ (Mazarrasa et al., 2018). Although they sequester minor organic carbon than larger seagrass species, our results showed that they can be relatively more productive during early successional states. Besides boosting biodiversity (Duffy, 2006), this high production may trigger an important source of organic carbon (i.e., seagrass litter) that can be exported to adjacent ecosystems or deep sea (Duarte and Krause-Jensen, 2017; Trevañtan-Tackett et al., 2020). In addition, our results evidenced a high DOC export in early successional states. This has important ecological implications, since DOC released by seagrass communities can act as a quick transfer of carbon stimulating microbial activity and shifting the metabolic balance of aquatic ecosystems (Gattuso et al., 1998; Chen et al., 2020). Besides affecting to the trophic web, DOC can help to counteract climate change through the release of recalcitrant DOC that can be exported to deep waters (Duarte and Krause-Jensen, 2017; Jiménez-Ramos et al., 2022; Egea et al., 2023b). The present study evidenced that young patches released more DOC, so we suggest that future studies should further evaluate the final fate of this carbon fraction (i.e., whether it is rapidly taken up by heterotrophic microbes –labile– or be exported and sequestered in the deep ocean –recalcitrant–). However, it is important to note that our research did not consider the prolonged effect of degradation and recovery of the seagrass communities as a consequence of a higher frequency of extreme climatological events, which could affect or modify the patterns observed here. Moreover, the present study has focused on one ‘colonizer’ species, whereas long-living and more persistent species (e.g., *Posidonia* spp. and *Thalassia* spp.) could produce different results as they evidence marked differences in the carbon metabolism and the community structure (Mazarrasa et al., 2018). Those knowledge gaps

regarding seagrass habitats as blue carbon sinks should be further explored in order to make better predictions and improve future management actions in these ecosystems.

In summary, the present study demonstrates that the community production, DOC exportation and the diversity (i.e., abundance and taxa richness) associated with *Halodule wrightii* are highly influenced by the age of the patch. Older patches exhibited a decrease in NCP_d as a consequence of the increase in the proportion of non-photosynthetic tissues, higher respiration rates of the community, and probably a higher self-shading of the canopy. The DOC released also decreased with the patch age, mainly as a consequence of the lower seagrass production in older meadows. Finally, this study suggests that ‘colonizer’ seagrass species may show higher production rates and DOC release during early stages of colonization, which implies that the production, organic carbon exportation and their role as relevant blue carbon sinks may be higher than expected.

CRedit authorship contribution statement

Luis G. Egea: Conceptualization, Methodology, Investigation, Formal analysis, Writing - original draft, Writing - review & editing. **Claudia J. Pérez-Estrada:** Methodology, Investigation, Formal analysis, Resources, Writing - review & editing. **Rocío Jiménez-Ramos:** Methodology, Investigation, Formal analysis, Writing - review & editing. **Ignacio Hernández:** Conceptualization, Writing - review & editing, Supervision. **Silverio López-López:** Resources, Writing - review & editing, Supervision. **Fernando G. Brun:** Conceptualization, Writing - review & editing, Supervision, Project administration, Funding acquisition.

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.

Data availability

All relevant data are within the paper.

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