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Research article



High contribution of an invasive macroalgae species to beach wrack CO_2 emissions

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A B S T R A C T

Accumulations of macroalgal wrack are important for adequate functioning of the beach ecosystem. However, the sudden beaching of seaweed masses smothers the coastline and forms decomposing piles on the shore, harming tourism-based economies, but also affecting the beach ecosystem metabolism. The decomposition of sudden pulses of wrack can modify the biogeochemistry of beach sands and increase greenhouse gas (GHG) emissions. The presence of invasive species in the wrack deposits can superimpose harmful effects on the beach functioning. We quantified the wrack biomass of *Rugulopteryx okamurae*, an invasive species of extreme impact, on five sandy beaches from the Atlantic coast of the Strait of Gibraltar (Spain), and we tested the effects on *in situ* respiratory CO_2 fluxes using an infrared gas analyser. All the beaches showed massive accumulations of *Rugulopteryx* wrack deposits. However, the biomass changed significantly between beaches, ranging (mean ± SE) from 968.3 ± 287.7 kg m^{-1} to 9210 ± 1279.4 kg m^{-1} of wet weight. Wrack supported high respiration rates, with CO_2 fluxes averaging (±SE) 19.15 ± 5.5 μmol CO_2 m^{-2} s^{-1} across beaches, reaching astounding maximum peaks of 291 μmol CO_2 m^{-2} s^{-1}. The within-beach variability was related to the distance of the wrack deposits from the shoreline, as the average metabolic rates tended to increase significantly from the swash to the drift line. Thicker wrack and a more degraded algae stage showed significantly higher CO_2 fluxes. We estimated that the annual CO_2 flux of *R. okamurae* in our study area ranged between 0.39 (±0.01) and 23.30 (±11.33) kg C m^{-2} y^{-1}. We suggest that massive amounts of beach wrack can become a globally significant contributor to GHG emissions that can offset any potential carbon-sink capacity of macroalgal forests. However, the piles of wrack located several meters above the drift line showed non-measurable CO_2 efflux. Transferring beach wrack from swash to drier upper-beach areas, a common practice in many coastal regions suffering from massive wrack accumulations, might help reduce GHG emissions while removing the wrack stockpiles from the intertidal. However, this practice is not necessarily suitable for all beaches and can create ecological and conservation problems in the dune system. There is an urgent need to implement practical and sustainable management practices for massive wrack deposits capable of presenting various solutions to achieve a balance between conservation and recreation actions, answering the consequences of a problem that links both, environmental and economic issues.

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1. Introduction

Brown macroalgal communities are key biogenic habitats that dominate primary production in coastal areas worldwide (Duarte et al., 2022). Annual senescence and/or extreme weather events lead to macroalgal biomass detachment from such ecosystems. Macroalgal forests export almost half of their C production within nearby depositional areas where they become a significant resource for adjacent communities (Duarte and Cebrián, 1996; Krause-Jensen and Duarte, 2016). Thus, part of the macroalgal C production can be stored in the sediments, exported to the deep sea, or washed up to the shore as beach wrack. Sandy beaches have little *in situ* primary production and the ecological functioning of these systems is highly dependent on these external inputs. Wrack deposits can create hotspots of microbial metabolism, secondary productivity, biodiversity and nutrient remineralization (Coupland et al., 2007; Rodil et al., 2019). However, the standing stock of wrack on beach habitats is highly dynamic, both in space and time. This is due to a combination of factors such as the variability of the physical forces (e.g. tides, currents, waves or wind), the geomorphology and landscape of the beach and the state of the donor system (Hyndes et al., 2022 and references therein). Therefore, quantifying the fate of the macroalgal primary production in coastal areas is complex, and in terms of exported carbon, the role of beach wrack currently is understudied.

Large amounts of the macroalgal biomass detached from rocky habitats during periods of high wave action end up as beach wrack, functionally linking the ocean with the land. The accumulation of wrack provides an external vector of organic carbon, influencing almost all levels of beach ecology, from species interactions to productivity, food-web stability, and population dynamics (see Hyndes et al., 2022). Most of the beach wrack is moved by tides and waves before being washed away, but drift lines of ageing wrack remain and decompose on the beach for several weeks. Thus, wrack debris undergoes physical processes that allow algal loss, including breakdown through solar radiation and tidal drying-rewetting, sedimentation, leaching, and eventually fragmentation, decomposition, and finally consumption and remineralization by bacteria and grazers (Orr et al., 2005; Lastra et al., 2008; Dugan et al., 2011; Lowman et al., 2019). The decay of wrack will release nutrients into the sediment stimulating microbial communities, supplying organic matter for the macrobenthos, and reducing O_2 exchange in the sediment (Rossi and Underwood, 2002; Rodil et al. 2015a, 2015b). During the initial stages of decomposition high CO_2 emissions from beach wrack occur by microbial activity (Coupland et al., 2007; Rodil et al., 2019).

Across the beach, wrack can be distributed into tidal bands from the extremely high water of spring tide to mean tidal levels or can be deposited along one or more drift lines. This process will affect the quality and the quantity of the detritus stranded on the beach, with larger and thicker piles of degraded wrack at and above the drift line and a more continuous renewal of fresh wrack closer to the water's edge. These dynamics are superimposed on the strong beach environmental gradients where the characteristics of the wrack (e.g. temperature and humidity) can vary intensively across the beach shore, suggesting that the dynamics of wrack deposits may vary greatly with distance to the swash (Coupland et al., 2007). In addition, the thickness of wrack deposits can also affect the characteristics of the materials, which can, in turn, affect metabolic rates and carbon processing (Coupland et al., 2007). The wrack washed up on a beach can also end up buried by sediment, sometimes after a period of decomposition on the surface, affecting the physical and chemical characteristics of the sediments (Rossi and Underwood, 2002; Rodil et al., 2019). The role of wrack in the beach community dynamics and nutrient cycling has been increasingly studied (reviewed by Hyndes et al., 2022). Recently, more studies have focused on the metabolic role of algal decay (e.g. Coupland et al., 2007; Lastra et al., 2018; Liu et al., 2019). However, fewer studies have focused on the driving factors of the metabolic role of macroalgal degradation.

The average biomass of wrack on beaches worldwide varies considerably, from 0.1 to 325 kg wet weight m^{-1} (Hyndes et al., 2022). However, massive biomass occurrences of seaweed can occur seasonally in many coastal regions (Smetacek and Zingone, 2013). Sudden pulses of wrack generate tonnes of algal accumulations that affect tourism-based economies and traditional fisheries, causing severe losses to the local economy, in addition to the costs of removing and disposing of thousands of tonnes of beached algae (Smetacek and Zingone, 2013; Krelling et al., 2017; Mogollón et al., 2024). The decomposition of sudden pulses of wrack can modify the biogeochemistry of beach sands, including dissolved O_2 consumption, increased sulfide reduction, CO_2, and CH_4 production (van Erk et al., 2020; Perkins et al., 2022). Recent studies showed that beach wrack can release larger amounts of CO_2 during the decomposition process than previously thought, and thus become a significant source of GHG emissions (Liu et al., 2019; Lanari et al., 2024). The degradation pathways of detrital subsidies are essential to understanding C and nutrient cycling in coastal systems. A significant shift of the macroalgal biomass contributing to the C import to nearshore ecosystems, e.g. massive wrack beaching, can stimulate nearshore metabolic activity, in terms of CO_2, affecting the global nearshore C-budget.

The coastal area between the Strait of Gibraltar (SoG) and the Gulf of Cádiz, a linking point between the Mediterranean and the Atlantic, is exposed to multiple environmental variations, which provide valuable information on the alterations caused by climate change, as well as the intrusion of potentially invasive species. In this context, *Rugulopteryx okamurae* (E.Y.Dawson) I.K.Hwang, W.J.Lee & H.S.Kim, 2009 (Dictyotales, Ochrophyta) has spread quickly and massively within the SoG and along the Atlantic coast. In a brief period, *R. okamurae* has come to be considered an invasive species with an overwhelming competitive capacity and growth, becoming a dominant species and a source of negative ecological and economic impacts. For instance, the high coverage of *R. okamurae* in the SoG region has caused the displacement of local benthic communities (García-Gómez et al., 2020), and generated costs of more than 3 million euros per year in the fishing sector and public administration (Mogollón et al., 2024). This situation results in the local municipalities and coastal administrators having to remove large amounts of beach wrack. In 2015, more than 5000 tonnes of algal biomass were extracted from the beaches of Ceuta with municipal cleaning machines (Ocaña et al., 2016), and since then, massive accumulations have been removed each summer in the area, with large economic expenses and ecological impacts. Furthermore, several studies have documented the effects of invasive macroalgae as detritus on the structure and functioning of sandy beaches (Rossi et al., 2010; Taylor et al., 2010; Rodil et al. 2015a, 2015b), including wrack metabolic rates (Rodil et al., 2019). To date, biomass accumulations of *R. okamurae* on beaches from the SoG have not been quantified, and the consequent increase in CO_2 wrack emissions has not been estimated yet.

Our first objective was to quantify the wrack biomass of *R. okamurae* deposited on five sandy beaches from the Atlantic coast of the SoG during the summer accumulation peak. We aimed to test whether this biomass differed between beaches and their relative deposition across the intertidal. Beach wrack may serve as an important part of the global C-budget, but how this detritus can enter into the budget of nearshore blue carbon remains overlooked. Therefore, our second objective was to quantify the metabolic activity (in terms of CO_2 efflux) of the accumulations of *R. okamurae* on the study beaches and to examine some of its potential driving factors. Wrack deposits in sandy beaches from this area are fully dominated by *R. okamurae* accumulations, potentially modifying the bare sediment metabolic activity of this habitat. We aim to confirm that the wrack deposits of *R. okamurae* are metabolic hot spots, defined as patches that show disproportionately high reaction rates relative to the surrounding area (McClain et al., 2003). We suggest that the sudden beaching of large amounts of biomass of *R. okamurae* and the degradation stage of the algae may change fundamental processes

related to the marine atmospheric transfer of GHG emissions. We hypothesize that increasing wrack accumulations and subsequent degradation will increase CO_2 beach wrack emissions. In general, macroalgal recently detached from their points of origin can resist degradation, maintaining primary production function and photosynthetic performance for a long time, depending on the light conditions (Frontier et al., 2021). Therefore, we suggest that the fresher the wrack deposit, the lower the degradation stage, and therefore we will find lower CO_2 emissions closer to the swash area. In contrast, the wrack deposits closer to the drift line will be in the initial and/or more advanced stages of the decomposition process and thus, they will emit high CO_2 fluxes.

2. Material and methods

2.1. Study sites

To test for differences in wrack biomass and metabolic rates (CO_2 fluxes), surveys across 5 sandy beaches were conducted during a spring-tide week in July 2023: Marisucia (36°11′3.63″ N; 6° 1′45.71″ O), El Pirata (36°11′7.24″ N; 6° 0′42.89″ O), and Hierbabuena (36°11′10.50″ N; 5°56′48.10″ O) in Caños de Meca-Barbate, and Punta Paloma (36° 3′32.77″ N; 5°42′35.23″ O), and Lances North (36° 3′5.85″ N; 5°38′58.11″ O) in Tarifa (Table 1, Fig. 1A). These beaches are located close to Tarifa

Table 1
Location of study sites, description of the beach characteristics, main wrack deposit characteristics, and infra-red gas analyzer (IRGA) measurements. Wrack deposits were located in the upper (UB) and middle (MB) bands (above and below the drift line, respectively), the lower band (LB) in the vicinity of the beach swash area and bare sand.

	Beach characteristics				Wrack							IRGA (wrack)	
Name	Width (m)	Total/ intertidal area (m^2)	T (°C)	Band	Density factor (kg l^{-1})	Distance to swash (m)	Humidity (%)	Biomass (kg m^{-2})	Biomass (kg m^{-1})	C:N	CO2 (µmol m-2 s^{-1})	T (°C)	Thickness (cm)
Marisucia (18/07/23)	74	2220/1332	28	UB	0.345	44.4	85.3 ± 0.7	4.04 ± 1.92	8694.6 ± 841.5	20.51 ± 2.32	10.62 ± 3.9	26.0 ± 0.2	3.0 ± 0.4
				MB		29.6	89.8 ± 0.6	36.92 ± 7.89		18.66 ± 0.62	22.50 ± 3.97	24.6 ± 0.3	11.0 ± 2.2
				LB		7.4	89.8 ± 0.3	24.02 ± 4.52		18.26 ± 0.55	11.33 ± 2.35	24.3 ± 0.3	7.3 ± 1.0
				Sand		44.4	78.4 ± 0.9	–		–	0.55 ± 0.04	–	–
				Buried[a]		29.6	85.0 ± 0.6	–		–	5.55 ± 0.42	26.5 ± 0.2	–
Pirata (18/07/23)	24.5	735/368	30	UB	0.428	12.3	86.8 ± 1.2	4.35 ± 2.05	968.3 ± 287.7	27.30 ± 0.44	5.38 ± 1.37	28.0 ± 0.0	2.0 ± 0.4
				MB		4.9	88.1 ± 1.4	8.39 ± 2.43		26.0 ± 1.63	3.52 ± 1.11	26.0 ± 0.0	6.3 ± 0.9
				LB		2.45	89.6 ± 0.2	26.28 ± 11.23		25.55 ± 1.52	2.04 ± 0.06	26.0 ± 0.0	8.3 ± 1.3
				Sand		12.3	88.7 ± 0.5	–		–	0.83 ± 0.09	–	–
Hierbabuena (19/07/23)	80	2400/1680	30	UB	0.418	56	80.0 ± 0.6	12.79 ± 8.23	3284.7 ± 1468.5	17.65 ± 0.33	16.02 ± 5.69	26.0 ± 0.2	8.0 ± 5.1
				MB		40	85.5 ± 1.0	6.11 ± 2.23		20.86 ± 0.76	3.96 ± 0.24	24.6 ± 0.3	2.5 ± 0.2
				LB		8	86.7 ± 1.1	2.50 ± 0.89		25.85 ± 1.71	2.74 ± 0.41	24.6 ± 0.3	1.6 ± 0.2
				Sand		56	85.2 ± 2.1	–		–	0.44 ± 0.03	–	–
				Outside pile[a]		60	70.7 ± 0.6	–		–	−7.22 ± 3.15	30.0 ± 0.0	23.7 ± 1.9
				Inside pile[a]		60	80.4 ± 0.5	–		–	123.69 ± 36.59	31.0 ± 0.0	
Punta Paloma (20/07/23)	34	1020/610	29	UB	0.285	20.4	84.7 ± 1.9	24.22 ± 9.72	9209.8 ± 1279.4	15.55 ± 0.38	123.14 ± 59.87	28.2 ± 0.2	52.0 ± 21.1
				MB		13.6	85.2 ± 1.1	187.5 ± 28.8		14.99 ± 0.10	7.75 ± 1.22	26.7 ± 0.3	8.0 ± 1.5
				LB		3.4	80.3 ± 0.7	12.27 ± 2.43		15.26 ± 0.40	14.09 ± 2.02	26.1 ± 0.3	8.5 ± 0.8
				Sand		20.4	61.2 ± 0.2	–		–	0.36 ± 0.07	–	–
				Buried[a]		13.6	67.4 ± 0.0	–		–	24.21 ± 0.0	29.3 ± 0.0	–
				Grey Sand[a]		3.4	71.2 ± 2.1	–		–	3.62 ± 0.33	–	–
Lances (21/07/23)	50	3	26	UB	0.365	25	85.2 ± 0.7	2.70 ± 0.90	1123.9 ± 379.3	17.20 ± 0.57	6.13 ± 1.13	21.8 ± 0.2	3.6 ± 0.2
				MB		20	85.8 ± 0.4	20.95 ± 8.84		19.32 ± 0.98	71.35 ± 24.43	22.9 ± 0.1	19.0 ± 1.5
				LB		5	85.9 ± 0.3	0.10 ± 0.05		22.15 ± 099	3.28 ± 0.52	22.5 ± 0.0	3.4 ± 0.2
				Sand		25	78.4 ± 0.9	–		–	0.55 ± 0.04	–	–
				Buried[a]		20	84.0 ± 1.1	–		–	3.06 ± 0.41	23.6 ± 0.4	–

[a] Other measurements were taken in the sand with algae buried beneath (Marisucia, Paloma and Lances), in bare grey sediment (Paloma), and in an old wrack pile (outside on the wrack surface layer of the pile and a few cm inside the pile) several meters above the UB.

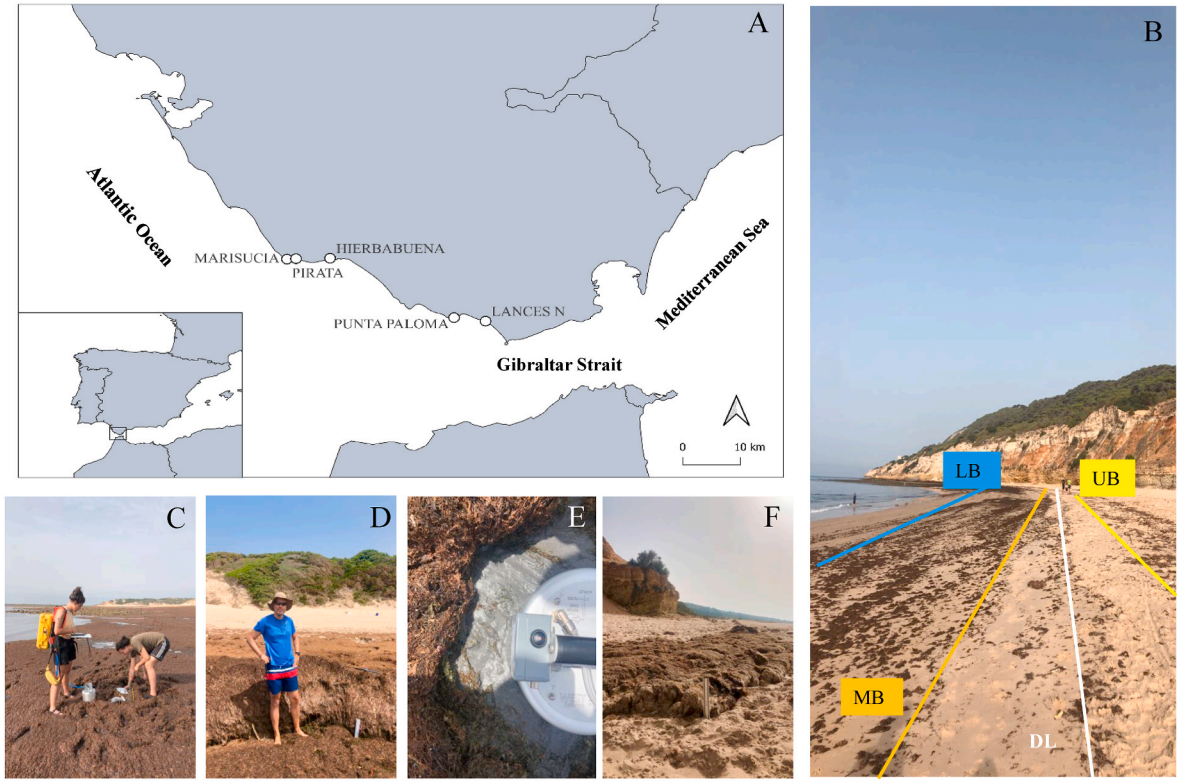


Fig. 1. Location of the five study beach sites in the vicinity of the Gibraltar Strait (A): Marisucia, Pirata and Hierbabuena (Caños de Meca-Barbate), and Paloma and Lances N (Tarifa). We measured metabolic rates (CO_2 and H_2S fluxes) in three wrack bands (upper, medium and lower bands, UB, MB, LB, respectively; n = 4) and bare sand in all beaches Drift line (DL) is the reference point (B). Four pictures showing: IRGA measurements in Marisucia (C), the largest wrack accumulation (D) and grey sediment (E) at Paloma Beach, and an old and dry wrack piled several meters above the drift line after successive tides and storms at Hierbabuena Beach (F).

and the SoG area (Fig. 1A) within the coastal range largely influenced by the presence of *R. okamurae* as beach wrack.

2.2. Quantification of the macroalgal wrack detritus

At all 5 beaches, 4 transects perpendicular to the shore were placed 20 m apart, extending from the lowest line of coastal vegetation, dune, or cliff to the swash area. Along each transect, 10 levels located at 10 m intervals (beach width) were established at low tide. At each level, 3 quadrats (0.25 m^2) were thrown randomly, and wrack volume was estimated (n = 30 quadrats per transect). Within each sampling quadrat, the wrack's total percentage cover (%) was estimated visually, and the depth (cm) was recorded by randomly inserting a metallic ruler 3 times into the wrack until the substratum was reached (Gilson et al., 2021). Wrack volume was then estimated by multiplying the area of wrack cover by the mean depth. Volume estimates were converted to biomass (wet weight) using a beach-specific density factor (kg l^{-1}), obtained by weighing wrack in each beach from all levels of the shore in a 10-l bucket (n = 100, total) (see Table 1). Care was taken to include wrack at all stages of degradation to account for any biomass change that may occur throughout the degradation process. We calculated the mean total (entire beach) and mean intertidal (from drift line to swash, as the main accumulation beach area) cover of the wrack per beach. Wrack wet biomass was estimated as mean densities (kg m^{-2}), where the biomass of wrack per quadrat is averaged by the number of quadrats sampled on the beach. We also estimated the wrack biomass per strip transect (BST, kg m^{-1}), i.e. within linear meters of the beach, to account for width differences among beach sites. The BST was estimated by averaging the biomass in each sampling quadrat (individuals m^{-2}) summed over meters of each transect and multiplying by the corresponding width of the surveyed area following a simple linear interpolation.

2.3. Metabolic measurements of beach wrack depositions

At each beach transect (n = 4), estimates of CO_2 and H_2S (μmoles m^{-2} s^{-1}) from random patches were measured *in situ* using a portable accumulation chamber with an infrared gas analyzer (IRGA, WEST Systems Portable Soil CO_2 Flux Meter (Parkinson, 1981). This device, which includes a metallic cylindrical respiration chamber (base area 317 cm^2), allows measurement of fluxes in 3 min based on the rate of accumulation of CO_2 within the chamber. Placement of the chamber in the wrack was made randomly at three bands relative to the typical beach wrack deposition drift line site (Fig. 1B). A band is defined here as a line parallel to the tide covered by an algal wrack. Wrack deposits stranded on beaches during the last highest spring tide and located above (1–2 m) the current high tide drift line were the upper wrack band (UB). Meanwhile, the middle wrack band (MB) is formed at the last high tide and located right below the current drift line (1–2 m). The most seaward band affected by wrack accumulations (2–3 m above the swash area) was also sampled, namely the lower wrack band (LB). Generally, upper bands are composed of aged wrack, desiccated by exposure to air and sun for several days, while lower bands are composed of fresh material deposited during the last high tide before the sampling. In total, we measured 12 wrack patches per beach. The chamber was inserted (~2 cm) into the wrack deposit by applying gentle pressure to the top of the chamber. The proper wrack deposit around the chamber acted as an insulator for the measurements, and the base of the chamber was sealed with an extra layer of algae to prevent any flux loss (Fig. 1C). The distance of the chamber from the water's edge at low tide was determined using a tape measure. The respiration chamber provides temperature, pressure, and humidity data. Ambient and wrack temperatures were simultaneously measured with alcohol thermometers (°C). The depth of the wrack deposit within the chamber (i.e., thickness) was measured using a steel ruler. The composition of the wrack deposits was

annotated. Metabolic measurements (CO_2 and H_2S) were also recorded in bare sand. Metabolic measurements were taken at low tide to allow access to the entire wrack accumulations along each beach at similar timing (approx. from 9:00 to 12:00). Each beach site was surveyed for approximately 1.30 h in total.

At three transects per beach, we randomly collected algal samples (>10 g) from the three wrack bands for biochemical composition analyses (n = 9). Samples were dried (60 °C for 48 h), ground to a fine powder, and stored in a freezer (−40 °C). Total carbon and nitrogen algal content (%) were determined (2.7 ± 0.16 g of dry mass) using a CHN elemental analyzer. The C:N ratio was estimated and used as a good predictor of the degradation stage for macroalgal detritus (Rodil et al. 2015a, 2015b).

2.4. Beach-specific metabolic measurements: buried wrack and long-term accumulations

Beach-specific metabolic measurements were recorded from some beaches (Marisucia, Lances N, and Paloma). In these three beaches, bare sand was metabolically very active (high CO_2 fluxes) differing from a typical non-metabolically active bare sand (see Rodil et al., 2019). This was caused by a large accumulation of buried algae (buried). Therefore, we took measurements for sand without buried algae (n = 4 per beach, sand) and for sand with associated buried algae (n = 4 per beach, buried) (see Table 1). Another beach (Hierbabuena) showed very thick (>30 cm) old piles of wrack located several meters above the drift line most likely accumulated after several high tides and summer storms (Fig. 1D). We measured the dry surface layer (chamber inserted 1 cm, pile surface) after long exposure to the sun, and a deeper more humid wrack layer by peeling off the first 5 cm of the wrack (n = 3, pile inside) for comparison. Finally, we measured one sediment area (with no buried algae) full of wrack and close to the swash in Paloma Beach that changed the typical sediment colour of the beach to grey sediment, probably due to the leaching of the huge piles of wrack in this particular beach (Fig. 1E).

2.5. Statistical analyses

Univariate data was analyzed using a permutational multivariate analysis of variance (PERMANOVA) based on Euclidean distances. PERMANOVA was used to test for differences in the total and intertidal wrack cover (%), total and intertidal biomass (kg m^{-2}), and biomass per strip transect (kg m^{-1}) among beaches (5 levels, fixed, n = 4), separately (log (x+1) transformed data. The statistical significance (i.e. *p*-value) of each term was estimated using an unrestricted permutation (4999) of raw data as recommended when there is only a single factor (Anderson et al., 2008). When the number of unique permutations was low (<100), the Monte Carlo *p*-value was used instead. A 2-way PERMANOVA model (same as above) was used to test for differences in CO_2 and H_2S wrack fluxes (μmol C m^{-2} s^{-1}) between beaches (5 levels, fixed) and across bands (4 levels: UB, MB, LB and sand, fixed), separately. Significant effects ($p \leq 0.05$) were further investigated through pairwise comparisons. The permutational analysis of multivariate dispersions (PERMDISP) was applied to quantify the degree of sample-point deviation from the respective centroids defined by the variability across beach sites.

The metabolic rate effects of the large wrack piles accumulated above the drift line in Hierbabuena were measured with one-way PERMANOVA (Euclidean distance, unrestricted permutation). We used the wrack band as a fixed factor (7 levels: UB, MB, LB, outside pile, inside pile, and sand). The metabolic rate effects of wrack patches buried under sand occurring on two beaches (Marisucia and Lances) were tested using a two-way PERMANOVA. We used beach (2 levels, fixed) and wrack band (5 levels: UB, MB, LB, sand, buried wrack). All multivariate analyses were conducted in PRIMER v7.0 (Clarke and Gorley, 2015).

A general linear model was used to estimate drivers of metabolic CO_2 rates. Distance from shore as a proxy for wrack band (m), the thickness of the deposits (cm), overlaying air and wrack temperature (°C), humidity (%), TC (%), TN (%), and CN ratio of the wrack were included in the original model. We also included the wrack wet biomass (kg m^{-2}) as a proxy for the average biomass per wrack band. We checked the data correlation (Pearson). Highly correlated variables were not used simultaneously in the regression model. We only retained the significant variables in the final model. The explained deviance (adjusted- R^2) and Akaike's Information Criterion (AIC) were used to evaluate each regression-based model fit and parsimony. The normality (Shapiro test) and homogeneity (Durbin Watson test) of the residuals were estimated. Regression analyses were fitted in R 4.3.1. (R Development Core Team, 2023).

3. Results

3.1. Quantification of the macroalgal wrack deposits

All the beaches showed large accumulations of wrack, mainly *R. okamurae* (>98 % of the biomass). Most of the wrack cover (%) and biomass (kg m^{-2}) were found in the intertidal area, from the drift line to the swash, with several peaks in biomass observed a few meters above and below the drift line in most of the beaches (Fig. 2). The total (pseudo-$F_{4,15}$ = 17.82) and intertidal (pseudo-$F_{4,15}$ = 17.02) wrack cover varied significantly ($p < 0.001$) among beaches (Fig. 2). The highest wrack cover was found in the intertidal, ranging (mean ± SE) from 23.4 ± 5.2 (Lances N) to 96.0 ± 3.2 % (Paloma) of the sampled area (Fig. 2). The largest average biomass (kg m^{-2}) in both, the total beach (pseudo-$F_{4,15}$ = 13.16; $p < 0.001$) and intertidal (pseudo-$F_{4,15}$ = 13.3; $p < 0.001$) areas was found in Paloma (Fig. 3A and B). However, the estimated BST (kg m^{-1}), i.e. accounting for width differences among beach sites, showed no significant differences (t = 0.238; p = 0.826) between Paloma and Marisucia (Fig. 3C–Table 1). Both beaches showed the significantly (pseudo-$F_{4,15}$ = 12.68; $p < 0.001$) largest BST, with 8.70 ± 0.84 and 9.21 ± 1.28 tons per strip transect, respectively. However, Marisucia is a much larger across-shore beach than Paloma where the wrack piled up in a smaller area (Fig. 2, Table 1).

3.2. Metabolic measurements of beach wrack depositions: CO_2 flux rates

The wrack patches supported high metabolic rates, with CO_2 fluxes averaging (±SE) 19.15 ± 5.5 μmol CO_2 m^{-2} s^{-1} compared to the mean value of 0.55 ± 0.07 μmol CO_2 m^{-2} s^{-1} for the sand (Supplementary data, Table S1). Wrack metabolic rates ranged 80-fold across beaches, from a minimum of 1.31 (El Pirata, LB) to a maximum of 291.04 (Paloma, UB) μmol CO_2 m^{-2} s^{-1} (Table S1), and average rates from 2.04 ± 0.06 to 123.1 ± 59.87 μmol CO_2 m^{-2} s^{-1} (Table 1). There was considerable variability in the metabolic rates supported by the wrack within any single beach (Fig. 4A). The within-beach variability was related to the distance of the wrack band deposits from the shoreline, as the average metabolic rates tended to increase significantly (pseudo-$F_{3,60}$ = 90.2; $p < 0.001$) from the swash to the drift line, with maximum rates in the UB and MB levels (Fig. 4A–Table 1). However, this pattern was significantly different in some of the beaches (i.e. beach × band interaction; pseudo-$F_{12,60}$ = 11.53; $p < 0.001$) (Fig. 4A). Paloma Beach showed the highest CO_2 fluxes in the UB compared to the other bands, and at Lances the CO_2 fluxes in the MB were significantly higher than in UB and LB (Fig. 4A). Although differences in multivariate dispersion were found between wrack bands (PERMDISP, $p < 0.05$), the centroids corresponding to the three wrack bands and the bare sand within each beach site differed in location (Supplementary data, Fig. S1; PCO), indicating that the statistical significance is likely due to differences in wrack metabolic rates rather than dispersion effects (Anderson, 2017).

Interestingly, bare sand from Marisucia (pseudo-$P_{4,15}$ = 34.91; $p < 0.001$) and Lances (pseudo-$P_{4,15}$ = 83.09; $p < 0.001$) showed relatively high CO_2 rates (Fig. 4A), and at Paloma, we even recorded significantly (pseudo-$P_{5,15}$ = 18.71; $p < 0.001$) higher CO_2 rates (24.21 ± 0.0 μmol

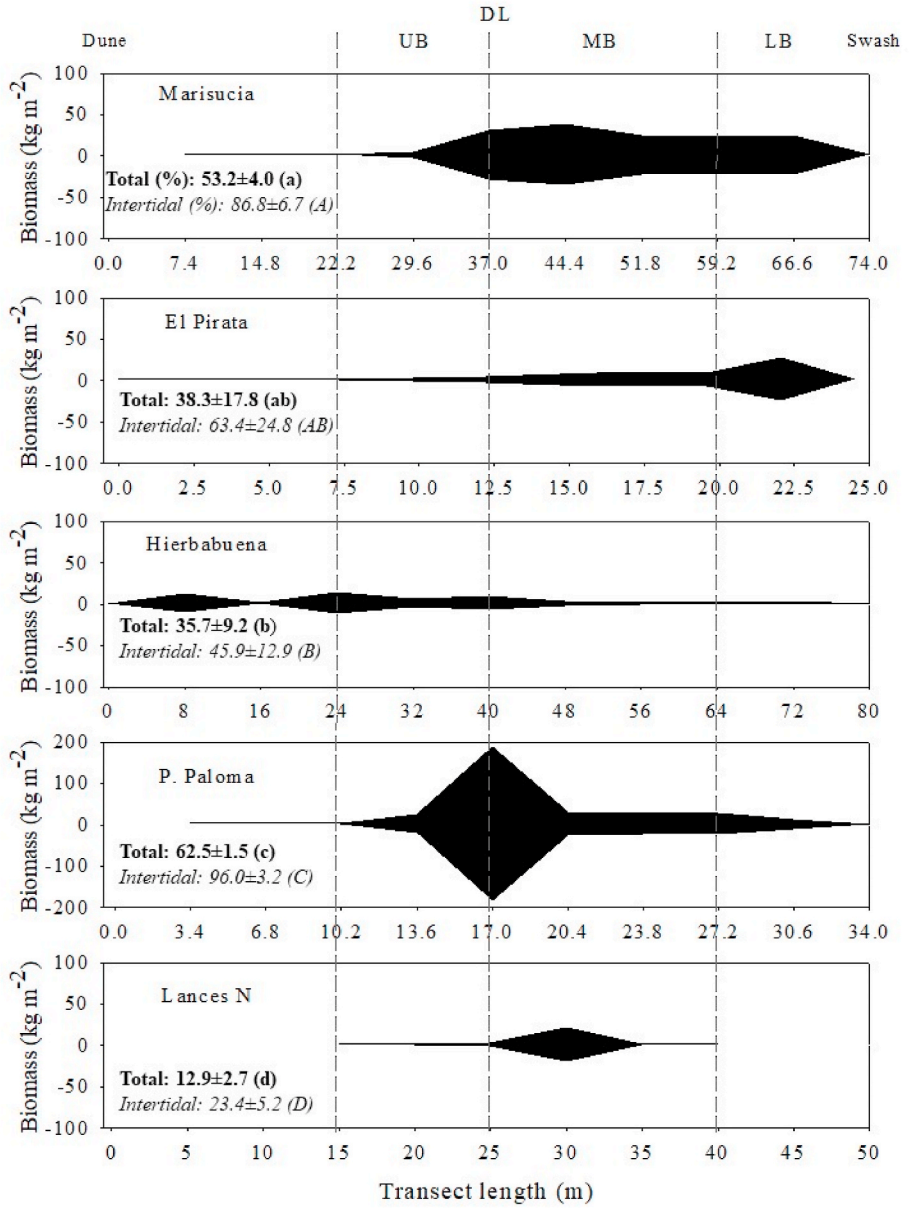


Fig. 2. Kite diagrams show the average across-shore distribution (m) of the wrack biomass (kg m^{-2}) in the five beach sites. Different letters in brackets show significant differences in total (lowercase) and intertidal (uppercase) wrack cover (%, mean ± SE) across-shore distribution. UB: upper band; MB: medium band; LB: lower band; DL: drift line.

CO_2 m^{-2} s^{-1}) in some bare sand than in the MB wrack band (pairwise comparison; $p < 0.05$) (Fig. 4A–Table 1). However, the high CO_2 rates measured from these non-typical bare sand (6.52 ± 2.26 μmol CO_2 m^{-2} s^{-1}) were due to the presence of buried wrack mixed with the sediment, thus there was no proper bare sand (named "buried"). At Paloma Beach, we recorded CO_2 rates from "grey sediment" (Fig. 1E) significantly higher (pairwise test, t = 13.7; $p < 0.001$) than the typical bare sand (Fig. 4A). At Hierbabuena Beach we measured an old wrack pile (23.7 ± 1.9 cm height) located several meters above the drift line (Figs. 1F and 5). We tested the CO_2 rates on the drier outside part of the pile and inside the pile after peeling off the first 5 cm of the pile (Table 1) for a comparison (Fig. 5). While non-measurable CO_2 rates were recorded from the surface, the inside of the pile showed significantly large CO_2 rates (pseudo-$F_{5,18}$ = 54.07; $p < 0.001$) compared to the rest of the wrack bands from Hierbabuena (Fig. 5, Table 1).

The H_2S flux rates from the wrack were highly variable, and relatively low compared to the CO_2 fluxes, ranging on average from 0.05 to 4.26 mmol m^{-2} s^{-1} (Table S1). There were significantly higher H_2S fluxes in some of the wrack patches (pseudo-$F_{12,60}$ = 2.45; $p < 0.01$; PERMDISP, p = 0.219) from Pirata, Hierbabuena, and Paloma beaches (Fig. 4B). No significant H_2S flux differences between wrack and bare sand except in Pirata and Hierbabuena (Fig. 4B). However, exceptionally high H_2S flux rates (i.e. 2.69 ± 0.92 μmol m^{-2} s^{-1}) were measured in the grey sediment from Paloma Beach (Fig. 5, Table S1) compared to all the wrack band and all the beaches (pseudo-$F_{5,15}$ = 12.6; $p < 0.001$). There was a high and positive correlation (Pearson r = 0.456) between CO_2 and H_2S fluxes (Supplementary data, Table S2).

3.3. Modelling the relationship between wrack characteristics and CO_2 flux rates

The C:N ratio ranged from 14.8 to 29.2 across wrack bands (Table 1, Table S1), with significant low values (i.e. high degradation stage) in the upper area of the beach (pseudo-$F_{2,30}$ = 49.32; $p < 0.05$)

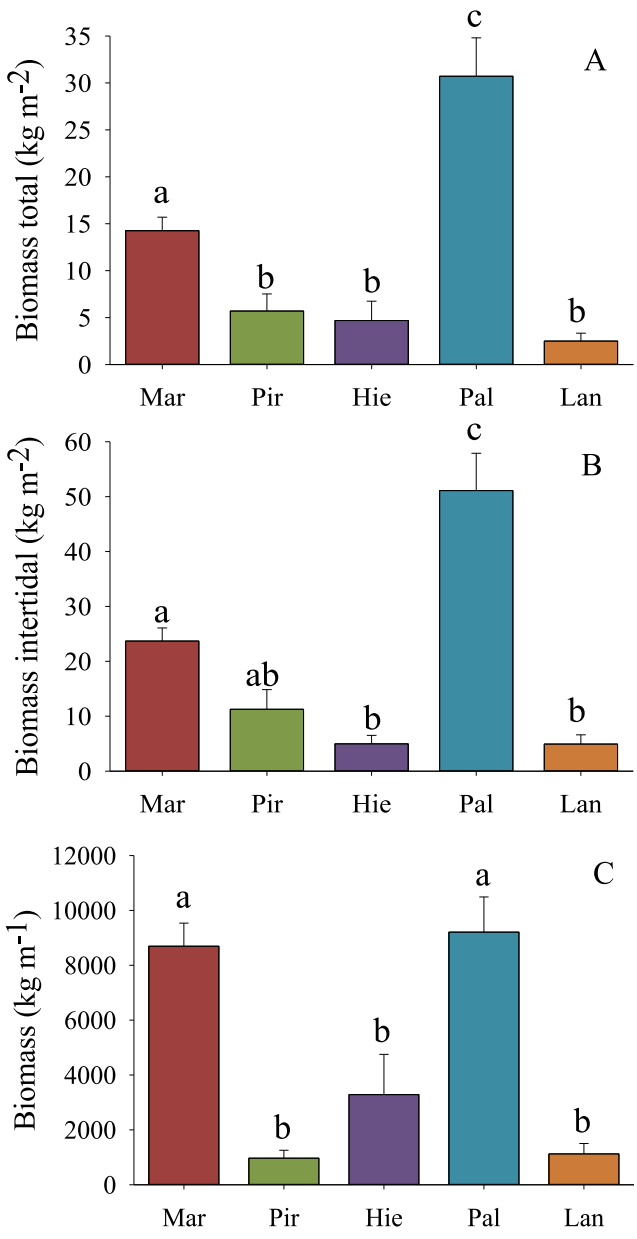


Fig. 3. Wrack biomass (kg m^{-2}) across the total beach (A) the intertidal area (B), and wrack biomass per strip transect (kg m^{-1}), i.e., within linear meters of beach, to account for width differences among beach sites. Beach sites: Marisucia (Mar), Pirata (Pir), Hierbabuena (Hie), Paloma (Pal), Lances (Lan). Different letters correspond to significant differences ($p < 0.05$) between beaches.

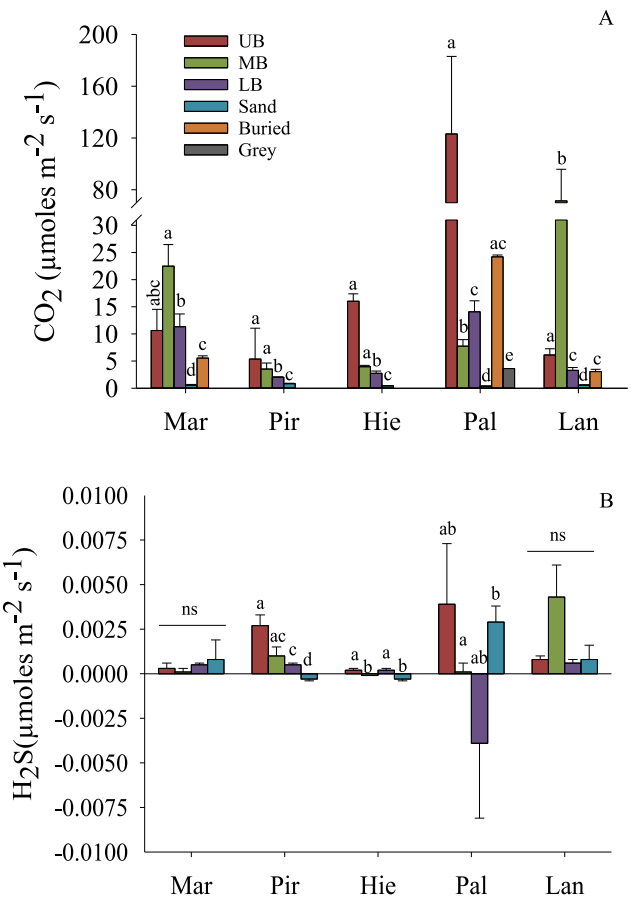


Fig. 4. Mean (±SE) CO_2 (A) and H_2S (B) effluxes from beach wrack bands (UB: upper band, MB: medium band, LB: lower band) made of *Rugulopteryx okamurare* and bare sand across sandy beaches: Marisucia (Mar), Pirata (Pir), Hierbabuena (Hie), Paloma (Pal), Lances (Lan). Some CO_2 efflux measurements were obtained from beaches with buried algae (Marisucia, Paloma and Lances) and grey sediment due to high wrack biomass concentration (Paloma). Negative values mean no efflux. Different letters correspond to significant differences ($p < 0.05$) between wrack bands across beaches.

(Supplementary data, Fig. S2). However, this pattern was significant at Hierbabuena and Lances (i.e. beach × band interaction, pseudo-$F_{8,30}$ = 4.99; $p < 0.01$). Also, differences in multivariate dispersion (PERMDISP <0.05) were found, reflecting a high variability between wrack bands (Fig. S2). In general, fresher and less degraded wrack (high C:N) was found closer to the swash (Supplementary data, Table S2, Fig. S3).

The wrack patch characteristics differed greatly in their thickness, from 1.6 to 52.0 cm, and biomass, from 0.10 to 29.74 kg m^{-2} across beaches (Table 1, Table S1). Both variables were highly correlated (r = 0.888) (Table S2, Fig. S3), and a maximum thickness of 93 cm (=254.3 kg m^{-2}) was recorded at Paloma Beach (Fig. 1D–Table S1). Therefore, we can use wrack thickness as a proxy of wrack biomass to explain the metabolic rates in the models. Thicker and larger biomass accumulations were typically found at the lower beach bands (Table 1), also with higher wrack temperatures (Table S2, Fig. S3).

The best linear model analysis (AIC = 16.87) showed that the thickness and the C:N ratio of the wrack were significant sources of variance in the CO_2 rates of the beach wrack (Fig. 6). Therefore, thicker wrack combined with a lower C:N ratio showed significantly higher CO_2 fluxes (Fig. 6). The second-best model (AIC = 20.58) showed that both thickness and distance to swash explained a high variability of the metabolic rates (Fig. 6). A similar model with wrack biomass and distance also explained a high variability of the metabolic rates (Fig. 6).

4. Discussion

4.1. Quantification of the macroalgal wrack depositions

Our study showed massive wrack detritus accumulations (between 1 and 9 t m^{-1}) made of *Rugulopteryx okamurae* (>95 % biomass) across all beaches, occupying most of the intertidal and confirming the dominance and extent of this invasive species in this coastal area. However, there were significant differences in the amount of wrack biomass between beaches, with Paloma Beach's standing biomass (kg m^{-2}) significantly peaking compared to any other beach. This is the only beach with no mechanical grooming in the area due to limited land access to the beach

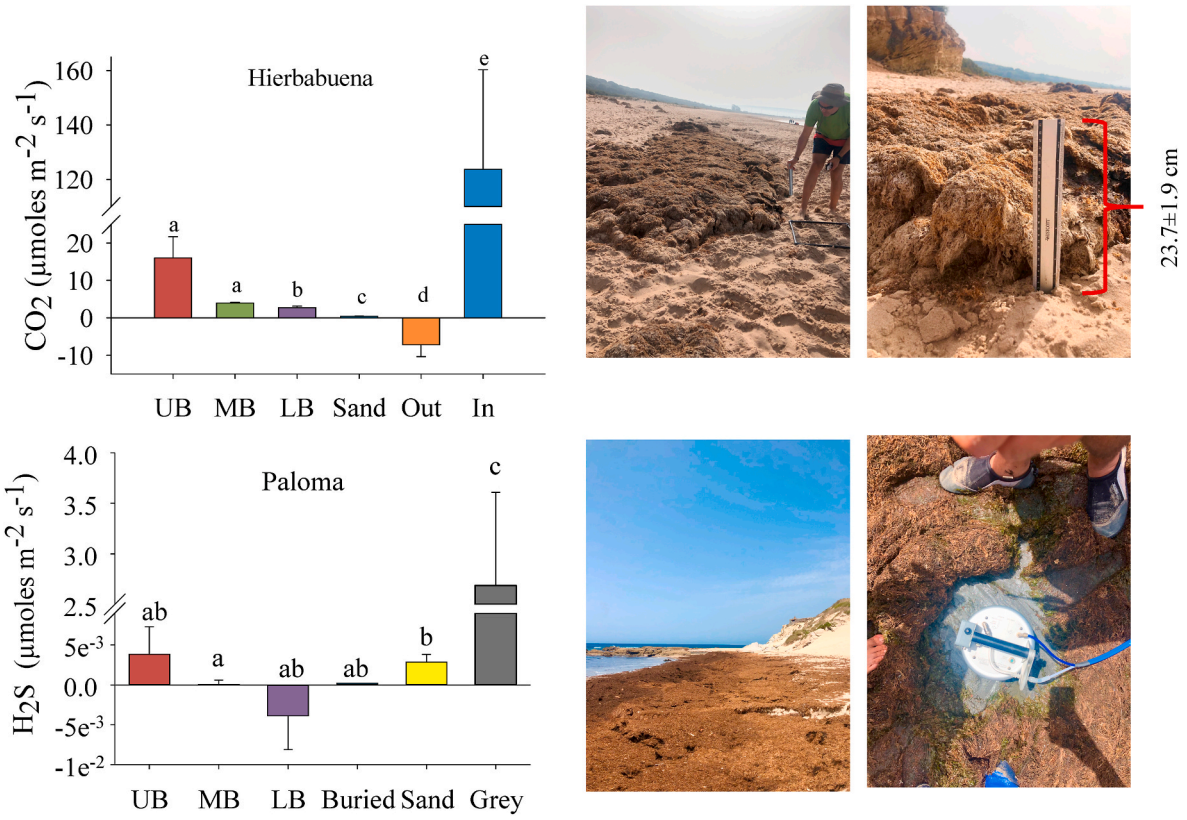


Fig. 5. Mean (±SE) CO_2 efflux (A) from wrack bands (UB: upper band, MB: medium band, LB: lower band), bare sand and a wrack pile (outside and inside) 10 m above the drift line at Hierbabuena Beach (A) and H_2S efflux from wrack bands, bare sand, buried wrack beneath sand and bare grey sediment at Paloma Beach (B). Negative values mean no efflux. Different letters correspond to significant differences ($p < 0.05$) between wrack bands across beaches.

for cleaning activities (surrounded by cliffs and no entrance for vehicles). However, when accounting for width differences among beach sites, Marisucia showed similar wrack biomass (kg m^{-1}) as Paloma, but twice the across-shore intertidal width. Marisucia was one of the most affected beaches in this area, with extensive follow-up in local and national media.

Seasonal wrack biomass is a complex and variable process with some studies registering higher standing biomass during autumn and winter (Gómez et al., 2013; Gilson et al., 2021), when macrophytes senescence and increased wind and storm frequency pile up the macroalgal biomass on the shore, while other studies registering higher wrack biomass in autumn and summer (Mateo, 2010; Barreiro et al., 2011). In general, high rates of beach wrack accumulation are affected by changes in wind, waves and tidal currents (Orr et al., 2005). Tarifa coastal area is well-known for its powerful local easterly and westerly winds, influencing beaching events. However, the daily mean wave height and wind speed recorded during July were similar among beaches and relatively low, the mean ranging from 0.2 to 0.86 m and from 0.55 to 6.86 m/s, respectively (https://www.puertos.es/es-es/oceanografia/Paginas/portus.aspx). The natural occurrence of *R. okamurae* in the Pacific peaks during the summer months as the thallus is reduced to a basal system of perennial rhizoids in winter (Hwang et al., 2009), similar to the waters of the SoG (García-Gómez et al., 2020). The annual sea temperature in the SoG, with a monthly average of approximately 15 °C, is ideal for temperate to subtropical species such as *R. okamurae* (Verlaque et al., 2009; El Aamri et al., 2018). Water temperature in the coastal area is typically high during summer, and it has been increasing steadily for the last 40 years (T_{mean} = 0.029 °C/year; T_{max} = 0.028 °C/year) (Fig. 7A). The explosive growth of *R. okamurae* documented in the study area in 2015 coincided with the maximum sea surface temperature in the SoG and nearby areas in the period 2000–2015, peaking at 24.7 °C in July 2015 during a heat-wave event (Fig. 7B). In July 2023, during this study, the average water temperature for all the beaches was 22.9 ± 0.46 °C, peaking at 23.7 °C due to a heatwave event as a function of the climatology (Fig. 7C). During these extreme events, invasive species such as *R. okamurae* can present a potential metabolic advantage, enhancing the growth and thus, outperforming native communities (Mercado et al., 2022). The temperature of summer peaks together with high nitrogen concentrations, are likely the key factors for the blooming of this species in the SoG (García-Gómez et al., 2020; Mercado et al., 2022). Similarly, green and golden tides worldwide tend to occur regularly during summer, associated with eutrophication processes and high temperatures (Smetacek and Zingone, 2013; Wang et al., 2020; García-Sánchez et al., 2020). Importantly, the number of this type of accumulation in previously unaffected areas has increased in recent years, mainly related to anthropogenic waste and global warming (Smetacek and Zingone, 2013; Gao et al., 2017; Wang et al., 2020).

The proliferation of *R. okamurae* in the SoG area is promoting seasonal accumulations of thousands of tons of algae on beaches affecting local inhabitants and tourism. Cleaning activities and mechanical grooming from local municipalities in the area are continuous during summer (Fig. 8) with significant detrimental effects on the local budgets of the city halls from the affected littoral. With a budget of 340,000 euros, 25 % more than the previous year, the Provincial Council of Cádiz launched in 2024 a support program ("340.000 euros en ayudas", 2024) for the coastal municipalities affected by the invasive algae (a total of 736,827.09 € in the last three years). This budget is meant to cover beach grooming and the disposal of the algal wrack in the affected localities, including the five beaches in our study. However, mechanical grooming is known to have a detrimental effect on the beach macrofauna and wildlife communities (Dugan et al., 2003), alter the coastal morphodynamic (Lima et al., 2020), and excavate a huge amount of sand from the beaches (Defeo et al., 2009), affecting both biodiversity and the beach sandbank.

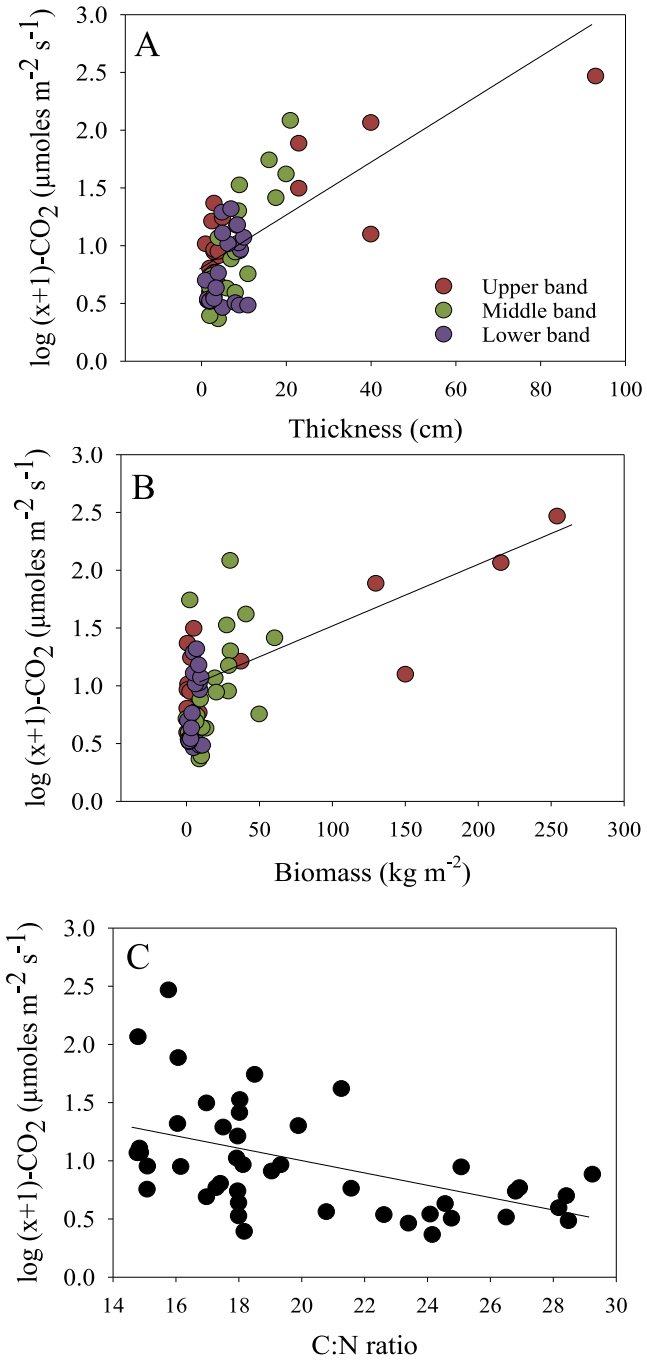


Fig. 6. Significant responses of the CO_2 efflux to wrack thickness (A), wrack biomass (B), and wrack C:N ratio (C) between wrack bands (increasing distance from the upper to the swash beach area) across the five study beaches based on the following linear regression models: Model 1 (AIC = 16.87, R^2_{adj} = 0.653): $logCO_2 = 1.43$ ($p < 0.001$) + 0.02 Thickness ($p < 0.001$) - 0.03CN ($p < 0.01$); Model 2 (AIC = 20.58; R^2_{adj} = 0.520): $logCO_2 = 0.64$ ($p < 0.001$) + 0.023Thickness ($p < 0.001$) + 0.006 Distance ($p < 0.05$); adjusted-R^2 = 0.52; Model 3 (AIC = 36.26, R^2_{adj} = 0.425): $logCO_2 = 0.69$ ($p < 0.001$) + 0.006 Biomass ($p < 0.001$) + 0.007 Distance ($p < 0.05$); adjusted-R^2 = 0.425.

4.2. Metabolic measurements of beach wrack depositions: CO_2 flux rates

Quantifying the fate of the macroalgal primary production in coastal areas is complex, and in terms of exported C, the role of beach wrack is both understudied and underestimated. Our results showed that wrack

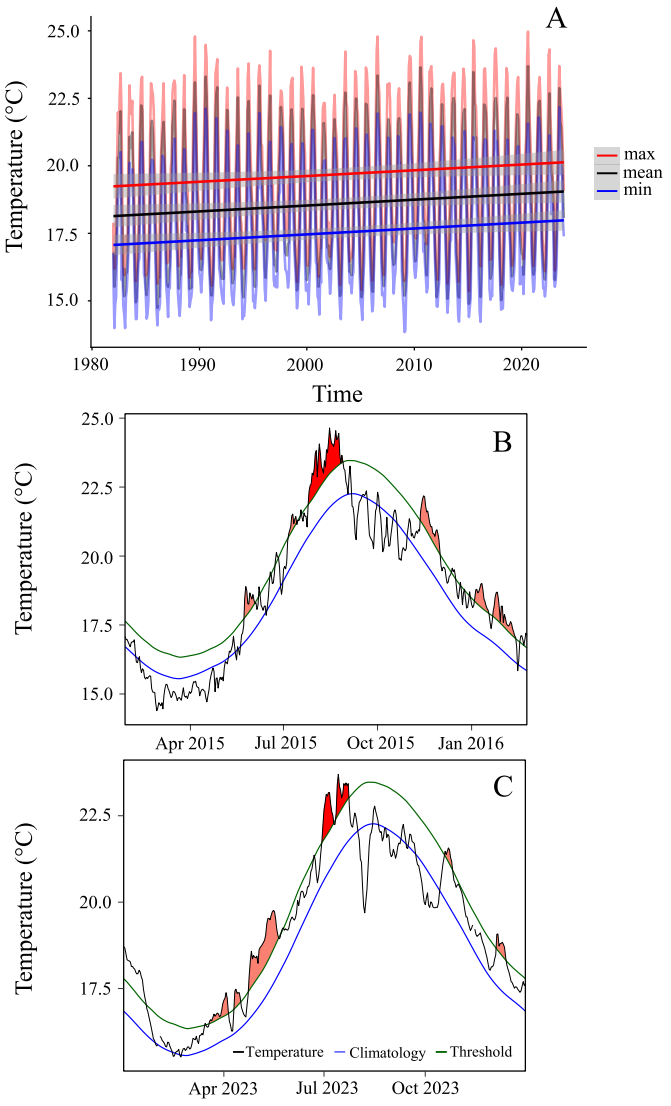


Fig. 7. Monthly means (black line), maximums (red line), and minimums (blue line) of sea surface temperature (sst) in the Strait of Gibraltar area (95% confidence interval in grey) from the years 1980–2024 (A). Heatwaves from 2015 (B) and 2023 during this study (C) were recorded. The blue line indicates the seasonal climatology. The green line indicates the seasonally varying threshold (90th threshold) for identifying mean heat waves. The black line indicates the satellite-driven sst (https://coastwatch.pfeg.noaa.gov/erddap/). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

deposits of *R. okamurae* are metabolically very active, supporting intense CO_2 fluxes during the wrack degradation process. However, these emissions varied greatly among (see 4.3) and within beaches. The within-beach variability was related to the distance of the wrack band deposits from the shoreline, as the average metabolic rates tended to increase significantly from the swash area towards the drift line. Similarly, Coupland et al. (2007) found that wrack CO_2 flux rates tended to increase significantly from the shoreline to reach maximum rates at about 10 m from the water's edge, declining further from the swash. This trend agrees with our hypothesis that closer to the swash area, the wrack deposits are fresher, photosynthetically active once detached from the substrate (Frontier et al., 2021; Mateo-Ramírez et al., 2023), and more often washed away from the beach compared to the wrack deposits in the vicinity of the drift line with longer residence time for degradation. Wrack bands close to the drift line (f.i. MB) are more exposed to tidal cycles of drying-rewetting, accelerating the decomposition of the algae,



Fig. 8. Pictures of the (A) wrack accumulations in Punta Paloma, (B, C) cleaning activities in Barbate (Fig. 1) leading to (D) artificial piles of wrack transported by the cleaning services (E) from the swash to the dune area (blue arrow) where they are left to dry for several weeks before final disposal. Photo credits: I. Gestoso (A), A. Malia (B, C, D), and F. Soccio (E). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

and stimulating the CO_2 flux (Liu et al., 2019)

In our study, further above the drift line, the wrack deposits were very small patches of fully dried algae compared to the intertidal. Occasionally, very old wrack was piled several meters above the drift line due to progressive algal accumulation between tidal cycles pushed upward through cumulative wind and wave action (e.g. Hierbabuena; Fig. 1F). The dry surface of the old pile on Hierbabuena showed non-measurable CO_2 rates, while the inner part of the pile, still moist and metabolically active, showed CO_2 rates similar to the rest of the wrack bands once the first cm of the crustose surface layer was peeled off (Fig. 5). Similarly, a previous laboratory study showed that seagrass cast high up on beaches that remained dry had 72% lower emissions than wrack that was subjected to intertidal repeated wetting (Liu et al., 2019). Our field study supports the conclusion from these authors that the relocation of wrack from the swash area to drier upper-beach areas can help to reduce atmospheric CO_2 emissions, potentially helping to mitigate GHG coastal budgets. The relocation of wrack to the dune area is a frequent practice of coastal managers in many places to consolidate fore-dune stability or coastal protection purposes (Chubarenko et al., 2021; Pal and Hogland, 2022). Some local municipalities in the SoG area are relocating the wrack to the upper-beach area to deal with the massive accumulations of *R. okamurae* (Fig. 8). This practice might facilitate later disposal of the wrack in landfills or waste treatment plants because dry wrack is lighter than fresh wrack (less water), and sand is potentially easier to remove from the dry wrack. Moreover, the removal of sand from the wrack will serve as a first step for wrack reutilization in industrial activities such as compost preparation or biofuel generation (Pal and Hogland, 2022). However, the transfer of wrack to the upper beach and dune areas might generate serious ecological and conservation problems on some of the beaches. Importantly, mechanical grooming is known to have a detrimental effect on beach macrofauna and wildlife communities (Dugan et al., 2003; Defeo et al., 2009; Schlacher et al., 2017). Ideally, from an environmental conservation perspective, the non-removal of wrack is the best option, especially in protected beaches and for low or moderately-used beaches to avoid affecting the beach habitat. Wrack removal activities should be carried out only in specific cases of episodic massive accumulations and in highly used or urbanized beaches, always trying to reduce the frequency of the activity (Zielinski et al., 2019). When feasible, manual cleaning should replace mechanical grooming as a friendly-ecological and economic option (Zielinski et al., 2019; Robbe et al., 2021). If grooming is considered necessary to provide clean beaches for recreation, mitigation strategies combining areas of non-groomed with groomed sections have been proposed (Defeo et al., 2009). From a management perspective, it is fundamental to develop best practice protocols for ecologically friendly beach cleaning activities that simultaneously reduce the recreational impacts of these massive accumulations and the costs of the cleaning operations.

Wrack metabolic rates have been rarely estimated in the field. For example, Coupland et al. (2007) in Australia recorded an emission mean rate of 6.62 ± 0.88 μmol CO_2 m^{-2} s^{-1} from mixed wrack deposits of seagrass and macroalgae. However, wrack composition can produce significant differences in CO_2 rates. For instance, experimental studies using manipulated wrack macroalgae buried in beaches in the North of Spain (Rodil et al., 2019) recorded large emissions of CO_2 highly dependent on the macroalgae species, ranging from 1.4 ± 0.2 (*Cystoseira baccata*, native species) to 8.3 ± 1.5 (*Undaria pinnatifida*, non-indigenous species) μmol CO_2 m^{-2} s^{-1}. In both field studies, the maximum flux rates recorded were average values of 20.9 ± 5.1 μmol CO_2 m^{-2} s^{-1} (Coupland et al., 2007) and cumulative values of 25.8 μmol CO_2 m^{-2} s^{-1} after 12 days of macroalgae left on the beach (Rodil et al., 2019). We quantified even larger CO_2 rates, ranging from 2.04 ± 0.06 to 123.14 ± 59.87 μmol CO_2 m^{-2} s^{-1} (Table 1). The mean average (±SE) across all the wrack bands and beaches of 19.15 ± 5.50 μmol C m^{-2} s^{-1}

is > 6 times as high as that of tropical rain forests (>3 μmol C m^{-2} s^{-1}; see Coupland et al., 2007). The maximum wrack metabolic rate recorded was an astonishing high flux of 291 μmol CO_2 m^{-2} s^{-1}. This value is almost 2 orders of magnitude higher than the most metabolically active terrestrial biomes (i.e. tropical rain forests).

Brown macroalgal communities dominate coastal primary production worldwide with mean productivity rates of 600 g C m^{-2} $year^{-1}$ and maximum reported averaged values well exceeding 2 kg C m^{-2} $year^{-1}$ (Pedersen et al., 2020; Duarte et al., 2022). We estimated that the annual CO_2 flux of *R. okamurae* in the beach wrack from our study area ranged between 0.39 (±0.01) and 23.30 (±11.33) kg C m^{-2} y^{-1}. These calculations are estimated for only 6 months, from April to September, when the maximal growth of *R. okamurae* is reached and the main beach depositions occur, especially in July–August (García-Gómez et al., 2020; Mercado et al., 2022). Interestingly, we estimated very significant CO_2 emissions (i.e. 1.23 kg C m^{-2} y^{-1}) from beach sand containing buried wrack. This result challenges the idea that buried algae can represent the contribution of wrack macroalgae to blue carbon storage (Perkins et al., 2022). Further research is needed to estimate whether the buried wrack persists in the sediment for sufficiently long periods to allow an accumulation of wrack carbon in the sediment that counterbalances the CO_2 flux emissions.

Seasonal or annual studies are needed to estimate accurately the *R. okamurae* CO_2 fluxes and their potential contribution to global GHG emissions in which wrack residency times, and wrack rates of burial and degradation within the sediment are investigated over time. Unmanned aerial vehicles and satellites have been proven useful in monitoring and quantifying beach wrack (Pan et al., 2021; Roca et al., 2022). This methodology can be used to effectively upscale wrack estimates of annual CO_2 fluxes and estimate with precision the coastal GHG budgets. Similarly, they can be used to monitor the distribution and abundance of the *R. okamurae* populations of origin (Roca et al., 2022), to track nearshore drifting macroalgae and predict when and where massive beaching episodes might occur (Smetacek and Zingone, 2013). These methods could be implemented to report the expected beaching amount of *R. okamurae* to wrack to the local authorities, helping to develop early warning systems in the affected areas and assisting in implementing environmental management strategies and solutions.

4.3. The relationship between wrack characteristics and CO_2 flux rates

The average CO_2 flux rates of the wrack made by *R. okamurae* increased significantly with increasing wrack thickness (and biomass). The thickness of wrack, which has insulating properties (Kirkman and Kendrick, 1997), and the species-specific properties of the algae (Rodil et al., 2008) are known to affect the degradation, biochemistry, temperature, and moisture of the materials, which can, in turn, affect the CO_2 fluxes and the sedimentary composition (Coupland et al., 2007; Lastra et al., 2018; Rodil et al., 2019; this study). In our study, there was a correlation between wrack temperature and thickness (and biomass) that could influence the higher metabolic rates of the thicker beach deposits. The differences in wrack biomass and thickness among beaches can explain the across-beach variability of the CO_2 flux rates recorded. The thicker and larger wrack biomass tended to occur close to the beach drift line, reaching a maximum of 93 cm (and 250 kg m^{-2}) in Paloma Beach. The lower C:N ratio of the wrack deposits from the drift line compared to the swash indicates higher wrack degradation (Rodil et al. 2015a, 2015b). These results indicate longer residency times of the wrack detritus accumulating on the beach that may increase the potential for burial of macroalgal-derived detritus and CO_2 emissions from the shore. In addition, there was a significant and positive relationship between CO_2 fluxes and the degradation stage (Fig. 6). This means that those wrack patches with a lower C:N ratio (i.e. more degraded algae) were emitting higher flux rates of CO_2, likely through microbial activity. Therefore, thicker (and larger) wrack patches combined with a lower C:N ratio showed significantly higher CO_2 fluxes.

Long-term large depositions of macroalgal detritus may have detrimental effects on species distribution and abundance on beaches by creating areas of anoxia, low pH, or high H_2S concentration (Colombini and Chelazzi, 2003). We recorded drastic physical sedimentary changes and metabolic changes such as a significant increase in H_2S emissions and a change in sedimentary colour in Paloma Beach (Fig. 1E), potentially due to anoxic conditions as a consequence of the high residency times of the wrack accumulations in this beach. These sedimentary changes might have significant consequences on the structure of the benthic communities. Massive wrack deposits can have negative effects on beach fauna communities, such as shorebirds, fish and turtles (Hendy et al., 2021; Maurer et al., 2021), and long periods of macroalgal degradation can cause hypoxia, potentially affecting macroinvertebrates (Olabarria et al., 2010; Quillien et al., 2015). We need to further investigate the effects of *R. okamurae* massive accumulations on the beach fauna communities. The presence of sand hoppers, typical wrack-associated macroinvertebrates (Lastra et al., 2008), was evident and abundant in some of the beaches such as Hierbabuena or Paloma (pers. observation). Hierbabuena is within the limits of a natural park and Paloma is a beach with difficult access for vehicles also in a natural park. Limited beach grooming or non-cleaning activities are performed on these two beaches, which could explain, at least partially, the abundance of sand hoppers. Seasonal studies showing variable wrack amount inputs (i.e. from low to large accumulations) in different beaches are needed to disentangle the potential positive or negative effects of *R. okamurae* on beach fauna, including fish, shorebirds and macrofauna.

5. Conclusions

Most of the studies on the role of macroalgal detritus in the global C-budget have focused on the deep areas and fewer studies have focused on the nearshore environment. However, only a fraction of detached macroalgal biomass in the POC form (ca. 15%) is exported to the deep seas potentially contributing to carbon sequestration, while the majority (ca. 85 %) is retained in nearshore environments such as sandy beaches (Krause-Jensen and Duarte, 2016; Filbee-Dexter et al., 2024). There it can be consumed, buried or remineralized with a feasible return of CO_2 to the atmosphere (Filbee-Dexter et al., 2024). We need to quantify how much of the macroalgal forest production ends up in the deep sites compared to nearshore environments, including beaches, and how much is consumed, buried or remineralized to achieve a full and accurate nearshore C-budget. Recent findings have shown that beach wrack accumulations may lead to significant GHG emissions such as CO_2, CH_4, and N_2O (Liu et al., 2019; Björk et al., 2023; Lanari et al., 2024). Our study confirms the high contribution of the wrack *R. okamurae* to CO_2 emissions, even while buried in the sand. We need to include these estimates when building global nearshore C-budgets. Any potential carbon-sink capacity of the macroalgal forests could be offset through the degradation of the large standing stock of beach wrack biomass, eventually effluxed into the atmosphere as a GHG (Liu et al., 2019; Lanari et al., 2024). The global increase of massive accumulations of beach wrack in recent years, including the beaching of a very successful invasive species such as *R. okamurae*, is especially concerning in the context of global warming. Increasing temperatures can enhance the degradation rate of beach wrack stimulating GHG emissions. Recent estimates (Lastra et al., 2018) predicted an increase of 8.2 % in CO_2 wrack emissions as a direct response to increasing beach sediment temperature within the range predicted by the IPCC (0.5–1.5 °C) for western Europe. Further studies on how temperature and/or radiation can affect the wrack degradation and posterior GHG emissions are needed. There is an urgent need to implement sustainable management practices for beach wrack deposits capable of answering the consequences of a problem linked with environmental and economic issues.

CRediT authorship contribution statement

Iván Franco Rodil: Writing – original draft, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Valle Perez Rodriguez:** Writing – review & editing, Methodology, Investigation, Data curation. **Alejandro Bernal-Ibáñez:** Writing – review & editing, Methodology, Formal analysis, Conceptualization. **Mauro Pardiello:** Writing – review & editing, Methodology, Investigation, Data curation. **Federica Soccio:** Writing – review & editing, Methodology, Investigation, Data curation. **Ignacio Gestoso:** Writing – review & editing, Methodology, Investigation, Conceptualization.

Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests:

IFR reports financial support was provided by Government of Andalusia. IFR reports financial support was provided by Spain Ministry of Science and Innovation. IFR reports financial support was provided by European Social Fund. IG reports financial support was provided by Government of Spain Ministry of Universities. ABI reports was provided by European Maritime and Fisheries Fund. IFR reports equipment, drugs, or supplies was provided by European Regional Development Fund. 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.

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

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References

Anderson, M.J., 2017. Permutational Multivariate Analysis of Variance (PERMANOVA). Wiley StatsRef: Statistics Reference Online, pp. 1–15. https://doi.org/10.1002/9781118445112.stat07841.

Anderson, M.J., Gorley, R.N., Clarke, K.R., 2008. PERMANOVA+ for PRIMER: Guide to Software and Statistical Methods. PRIMER-E, Plymouth, UK.

Barreiro, F., Gómez, M., Lastra, M., López, J., De la Huz, R., 2011. Annual cycle of wrack supply to sandy beaches: effect of the physical environment. Mar. Ecol. Prog. Ser. 433, 65–74.

Björk, M., Rosenqvist, G., Gröndahl, F., et al., 2023. Methane emissions from macrophyte beach wrack on Baltic seashores. Ambio 52, 171–181. https://doi.org/10.1007/s13280-022-01774-4.

Chubarenko, B, Woelfel, J, Hofmann, J, Aldag, S, Beldowski, J, Burlakovs, J, et al., 2021. Converting beach wrack into a resource as a challenge for the Baltic Sea (an overview). Ocean. Coast. Manag. 200, 105413.

Clarke, K.R., Gorley, R.N., 2015. PRIMER V7: User Manual/Tutorial. PRIMER-E, Plymouth, UK.

Colombini, I., Chelazzi, L., 2003. Influence of marine allochthonous input on sandy beach communities. Oceanogr. Mar. Biol. Annu. Rev. 41, 115159.

Coupland, G.T., Duarte, C.M., Walker, D.I., 2007. High metabolic rates in beach cast communities. Ecosystems 10, 1341–1350.

Defeo, O., McLachlan, A., Schoeman, D.S., Schlacher, T.A., Dugan, J., Jones, A., Lastra, M., Scapini, F., 2009. Threats to sandy beach ecosystems: a review. Estuar. Coast Shelf Sci. 81, 1–12.

Duarte, C.M., Cebrián, J., 1996. The fate of marine autotrophic production. Limnol. Oceanogr. 41, 1758–1766. https://doi.org/10.4319/lo.1996.41.8.1758.

Duarte, C.M., Gattuso, J., Hancke, K., Gundersen, H., Filbee-Dexter, K., 2022. Global estimates of the extent and production of macroalgal forests. Glob. Ecol. Biogeogr. 31, 1422–1439.

Dugan, J.E., Hubbard, D.M., McCrary, M.D., Pierson, M.O., 2003. The response of macrofauna communities and shorebirds to macrophyte wrack subsidies on exposed sandy beaches of southern California. Estuar. Coast. Shelf. S. 58, 25–40.

Dugan, J.E., Hubbard, D.M., Page, H.M., Schimel, J.P., 2011. Marine macrophyte wrack inputs and dissolved nutrients in beach sands. Estuar. Coast 34, 839–850.

El Aamri, F., Idhalla, M., Tamsouri, M.N., 2018. Occurrence of the invasive brown seaweed *Rugulopteryx okamurae* (EY dawson) Ik Wang, WJ lee and HS kim (dictyotales, phaeophyta) in Morocco (mediterranean sea). MedFAR 1, 92–96.

340.000 euros en ayudas para combatir los efectos del alga invasora. https://www.dipucadiz.es/transicion-ecologica-y-desarrollo-urbano-sostenible/destacados/340.000-euros-en-ayudas-para-combatir-los-efectos-del-alga-invasora, 2024–. (Accessed 20 June 2024).

Filbee-Dexter, K., Pessarrodona, A., Pedersen, M.F., et al., 2024. Carbon export from seaweed forests to deep ocean sinks. Nat. Geosci. https://doi.org/10.1038/s41561-024-01449-7.

Frontier, N., de Bettignies, F., Foggo, A., Davoult, D., 2021. Sustained productivity and respiration of degrading kelp detritus in the shallow benthos: detached or broken, but not dead. Mar. Environ. Res. 166, 105277.

Gao, G., Clare, A.S., Rose, C., Caldwell, G.S., 2017. Eutrophication and warming-driven green tides (*Ulva rigida*) are predicted to increase under future climate change scenarios. Mar. Pollut. Bull. 114, 439–447. https://doi.org/10.1016/j.marpolbul.2016.10.003.

García-Gómez, J.C., Sempere-Valverde, J., González, A.R., Martínez-Chacón, M., Olaya-Ponzone, L., Sánchez-Moyano, E., et al., 2020. From exotic to invasive in record time: the extreme impact of *Rugulopteryx okamurae* (Dictyotales, Ochrophyta) in the strait of Gibraltar. Sci. Total Environ. 704, 135408 https://doi.org/10.1016/j.scitotenv.2019.135408.

García-Sánchez, M, Graham, C, Vera, E, Escalante-Mancera, E, Álvarez-Filip, L, van Tussenbroek, BI., 2020. Temporal changes in the composition and biomass of beached pelagic Sargassum species in the Mexican Caribbean. Aquatic Botany 167, 103275. https://10.1016/j.aquabot.2020.10327.

Gilson, A., Smale, D., Burrows, M., O'Connor, N., 2021. Spatio-temporal variability in the deposition of beach-cast kelp (wrack) and inter-specific differences in degradation rates. Mar. Ecol. Prog. Ser. 674, 89–102. https://doi.org/10.3354/meps13825.

Gómez, M., Barreiro, F., López, J., Lastra, M., de la Huz, R., 2013. Deposition patterns of algal wrack species on estuarine beaches. Aquat. Bot. 105, 25–33. https://doi.org/10.1016/j.aquabot.2012.12.001.

Hendy, I.W., Woolford, K., Vincent-Piper, A., Burt, O., Schaefer, M., Cragg, S.M., et al., 2021. Climate-driven golden tides are reshaping coastal communities in Quintana Roo, Mexico. Clim. Change Ecol. 2, 100033 https://doi.org/10.1016/j.ecochg.2021.100033.

Hwang, I.K., Lee, W.J., Kim, H.S., De Clerck, O., 2009. Taxonomic reappraisal of Dilophus okamurae (Dictyotales, Phaeophyta) from the western Pacific Ocean. Phycologia 48, 1–12.

Hyndes, G.A., Berdan, E.L., Duarte, C., Dugan, J.E., Emery, K.A., Hambäck, P.A., et al., 2022. The Role of Inputs of Marine Wrack and Carrion in Sandy-beach Ecosystems: A Global Review, vol. 97, pp. 2127–2161. https://doi.org/10.1111/brv.12886.

Kirkman, H., Kendrick, G.A., 1997. Ecological significance and commercial harvesting of drifting and beach-cast macro-algae and seagrasses in Australia: a review. J. Appl. Phycol. 9, 311–326. https://doi.org/10.1023/A:1007965506873.

Krause-Jensen, D., Duarte, C.M., 2016. Substantial role of macroalgae in marine carbon sequestration. Nat. Geosci. 9, 737–742.

Krelling, A.P., Williams, A.T., Turra, A., 2017. Differences in perception and reaction of tourist groups to beach marine debris that can influence a loss of tourism revenue in coastal areas. Mar. Pol. 85, 87–99. https://doi.org/10.1016/j.marpol.2017.08.021.

Lanari, M., Busk, T., Holmer, M., Möller-Radi, T., Torn, K., Schubert, H., Quintana, C.O., 2024. From sink to source: dynamic of greenhouse gases emissions from beach wrack accumulations in a temperate coastal bay. Sci. Total Environ. 925, 171783 https://doi.org/10.1016/j.scitotenv.2024.171783.

Lastra, M., Page, H.M., Dugan, J.E., Hubbard, D.M., Rodil, I.F., 2008. Processing of allochthonous macrophyte subsidies by sandy beach consumers: estimates of feeding rates and impacts on food resources. Mar. Biol. 154, 163–174.

Lastra, M., López, J., Rodil, I.F., 2018. Warming intensify CO2 flux and nutrient release from algal wrack subsidies on sandy beaches. Glob. Change. Biol. 24, 3766–3779.
Lima, M.D.A.C., Ward, R.D., Joyce, C.B., 2020. Environmental drivers of sediment carbon storage in temperate beach wrack meadows. Hydrobiologia 847, 1773–1792. https://doi.org/10.1007/s10750-019-04153-5.
Liu, S., Trevathaackett, S.M., Ewers Lewis, C.J., Ollivier, Q.R., Jiang, Z., Huang, X., Macreadie, P.I., 2019. Beach-cast seagrass wrack contributes substantially to global greenhouse gas emissions. J. Environ. Manag. 231, 329–335. https://doi.org/10.1016/j.jenvman.2018.10.047.
Lowman, H.E., Emery, K.A., Kubler-Dudgeon, L., Dugan, J.E., Melack, J.M., 2019. Contribution of macroalgal wrack consumers to dissolved inorganic nitrogen concentrations in intertidal pore waters of sandy beaches. Estuar. Coast. Shelf 219, 363–371.
Mateo, M.A., 2010. Beach-cast *Cymodocea nodosa* along the shore of a semienclosed bay: sampling and elements to assess its ecological implications. J. Coast Res. 283–291. https://doi.org/10.2112/08-1100.1.
Mateo-Ramírez, Á., Iñiguez, C., Fernández-Salas, L.M., Sánchez-Leal, R.F., Farias, C., Bellanco, M., et al., 2023. Healthy thalli of the invasive seaweed *Rugulopteryx okamurae* (Phaeophyceae) being massively dragged into deep-sea bottoms by the Mediterranean OutflowWater. Phycologia 62, 99–108.
Maurer, A.S., Stapleton, S.P., Layman, C.A., Burford Reiskind, M.A., 2021. The Atlantic *Sargassum* invasion impedes beach access for nesting sea turtles. Clim. Change Ecol. 2, 100034 https://doi.org/10.1016/j.ecochg.2021.100034.
McClain, M.E., Boyer, E.W., Dent, C.L., Gergel, S.E., Grimm, N.B., Groffman, P.M., et al., 2003. Biogeochemical hotspots and hot moments at the interface of terrestrial and aquatic ecosystems. Ecosystems 6, 310–312.
Mercado, J.M., Gómez-Jakobsen, F., Korbee, N., Aviles, A., Bonomi-Barufi, J., Muñoz, M., et al., 2022. Analyzing environmental factors that favor the growth of the invasive brown macroalga Rugulopteryx okamurae (Ochrophyta): the probable role of the nutrient excess. Mar. Pollut. Bull. 174, 113315 https://doi.org/10.1016/j.marpolbul.2021.113315.
Mogollón, S.L., Zilio, M.I., Buitrago, E.M., Caraballo, M.A., Yñiguez, R., 2024. Economic impact of *Rugulopteryx okamurae* (dictyotales, Ochrophyta) along the andalusian coastline: the case of Tarifa, Spain. Wetl. Ecol. Manag. 32, 19–32. https://doi.org/10.1007/s11273-023-09951-2.
Ocaña, O., Afonso-Carrillo, J., Ballesteros, E., 2016. Massive proliferation of a dictyotalean species (phaeophyceae, Ochrophyta) through the Strait of Gibraltar (research note). Rev. Acad. Canar. Cienc. 28, 165–170.
Olabarria, C., Incera, M., Garrido, J., Rossi, F., 2010. The effect of wrack composition and diversity on macrofaunal assemblages in intertidal marine sediments. J. Exp. Mar. Bio. Ecol. 396, 18–26.
Orr, M., Zimmer, M., Jelinski, D.E., Mews, M., 2005. Wrack deposition on different beach types: spatial and temporal variation in the pattern of subsidy. Ecology 86, 1496–1507.
Pal, D., Hogland, W., 2022. An overview and assessment of the existing technological options for management and resource recovery from beach wrack and dredged sediments: an environmental and economic perspective. J. Environ. Manag. 302, 113971.
Pan, Y., Flindt, M., Schneider-Kamp, P., Holmer, M., 2021. Beach wrack mapping using unmanned aerial vehicles for coastal environmental management. Ocean Coast Manag. 213, 105843 https://doi.org/10.1016/j.ocecoaman.2021.105843.
Parkinson, K.J., 1981. An improved method for measuring oil respiration in the field. J. Appl. Ecol. 18, 221–228. https://doi.org/10.2307/2402491.
Pedersen, M.F., Filbee-Dexte, K., Norderhaug, K.M., Fredriksen, S., Frisk, N.L., Fagerli, C. W., Wernberg, T., 2020. Detrital carbon production and export in high latitude kelp forests. Oecologia 192, 227–239.
Perkins, A.K., Santos, I.R., Rose, A.L., Schulz, K.G., Grossart, H.P., Eyre, B.D., et al., 2022. Production of dissolved carbon and alkalinity during macroalgal wrack degradation on beaches: a mesocosm experiment with implications for blue carbon. Biogeochemistry 160, 159–175. https://doi.org/10.1007/s10533-022-00946-4.
Quillien, N., Nordström, M.C., Guyonnet, B., Maguer, M., Le Garrec, V., Bonsdorff, E., Grall, J., 2015. Large-scale effects of green tides on macrotidal sandy beaches: habitat-specific responses of zoobenthos. Estuar. Coast Shelf Sci. 164, 379–391.
R Development Core Team, 2023. R: A Language and Environment for Statistical Computing_. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org.
Robbe, E., Woelfel, J., Balčiūnas, A., Schernewski, G., 2021. An impact assessment of beach wrack and litter on beach ecosystem services to support coastal management at the Baltic Sea. Env. Manag. 68, 835–859. https://doi.org/10.1007/s00267-021-01533-3.
Roca, M., Dunbar, M.B., Román, A., Caballero, I., Zoffoli, M.L., Gernez, P., Navarro, G., 2022. Monitoring the marine invasive alien species Rugulopteryx okamurae using unmanned aerial vehicles and satellites. Front. Mar. Sci. 9 https://doi.org/10.3389/fmars.2022.1004012.
Rodil, I.F., Olabarria, C., Lastra, M., López, J., 2008. Differential effects of native and invasive algal wrack on macrofaunal assemblages inhabiting exposed sandy beaches. J. Exp. Mar. Biol. Ecol. 358, 1–13.
Rodil, I.F., Olabarria, C., Lastra, M., Arenas, F., 2015a. Combined effects of wrack identity and solar radiation on associated beach macrofaunal assemblages. Mar. Ecol. Prog. Ser. 531, 167–178.
Rodil, I.F., Fernandes, J.P., Mucha, A.P., 2015b. Disentangling the effects of solar radiation, wrack macroalgae and beach macrofauna on associated bacterial assemblages. Mar. Environ. Res. 112, 104–112.
Rodil, I.F., Lastra, M., López, J., Mucha, A.P., Fernandes, J.P., Fernandes, S.V., Olabarria, C., 2019. Sandy beaches as biogeochemical hotspots: the metabolic role of macroalgal wrack on low-productive shores. Ecosystems 22, 49–63.
Rossi, F., Underwood, A.J., 2002. Small-scale disturbance and increased nutrients as influences on intertidal macrobenthic assemblages: experimental burial of wrack in different intertidal environments. Mar. Ecol. Prog. Ser. 241, 29–39. https://doi.org/10.3354/meps241029.
Rossi, F., Olabarria, C., Incera, M., Garrido, J., 2010. The trophic significance of the invasive seaweed Sargassum muticum in sandy beaches. J. Sea. Res. 63, 52–61.
Schlacher, T.A., Hutton, B.M., Gilby, B.L., Porch, N., Maguire, G.S., Maslo, B., et al., 2017. Algal subsidies enhance invertebrate prey for threatened shorebirds: a novel conservation tool on ocean beaches? Estuar. Coast Shelf Sci. 191, 28–38.
Smetacek, V., Zingone, A., 2013. Green and golden seaweed tides on the rise. Nature 504, 84–88.
Taylor, S.L., Bishop, M.J., Kelaher, B.P., Glasby, T.M., 2010. Impacts of detritus from the invasive alga *Caulerpa taxifolia* on a soft sediment community. Mar. Ecol. Prog. Ser. 420, 73–81.
van Erk, M.R., Meier, D.v., Ferdelman, T., Harder, J., Bussmann, I., de Beer, D., 2020. Kelp deposition changes mineralization pathways and microbial communities in a sandy beach. Limnol. Oceanogr. 65 (12), 3066–3084. https://doi.org/10.1002/lno.11574.
Verlaque, M., Steen, F., De Clerck, O., 2009. *Rugulopteryx* (dictyotales, phaeophyceae), a genus recently introduced to the mediterranean. Phycologia 48, 536–542.
Wang, H., Wang, G., Gu, W., 2020. Macroalgal blooms caused by marine nutrient changes resulting from human activities. J. Appl. Ecol. 57, 766–776.
Zielinski, S., Botero, C.M., Yanes, A., 2019. To clean or not to clean? A critical review of beach cleaning methods and impacts. Mar. Poll. Bull. 139, 390–401.