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Patterns and drivers of macroalgal 'blue carbon' transport and deposition in near-shore coastal environments

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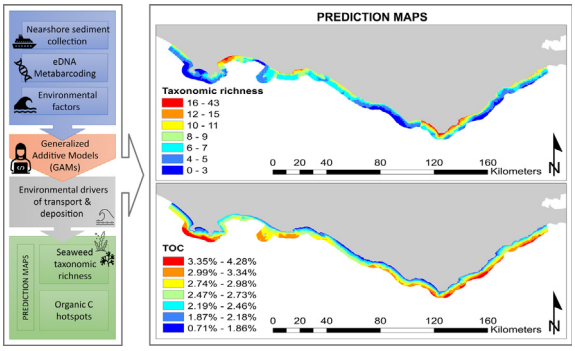
HIGHLIGHTS

- Genetic analyses identify macroalgal deposits in near-shore environments.
- Patterns of deposition are influenced by a range of environmental factors.
- Models predict the distribution of potential blue-carbon sinks.

GRAPHICAL ABSTRACT



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ABSTRACT

The role of macroalgae (seaweed) as a global contributor to carbon drawdown within marine sediments – termed 'blue carbon' – remains uncertain and controversial. While studies are needed to validate the potential for macroalgal-carbon sequestration in marine and coastal sediments, fundamental questions regarding the fate of dislodged macroalgal biomass need to be addressed. Evidence suggests macroalgal biomass may be advected and deposited within other vegetated coastal ecosystems and down to the deep ocean; however, contributions to near-shore sediments within coastal waters remain uncertain. In this study a combination of eDNA metabarcoding and surficial sediment sampling informed by seabed mapping from different physical environments was used to test for the presence of macroalgal carbon in near-shore coastal sediments in south-eastern Australia, and the physical factors influencing patterns of macroalgal transport and deposition. DNA products for a total of 68 macroalgal taxa, representing all major macroalgal groups (Phaeophyceae, Rhodophyta, and Chlorophyta) were successfully detected at 112 near-shore locations. These findings confirm the potential for macroalgal biomass to be exported into near-shore sediments and suggest macroalgal carbon donors could be both speciose and diverse. Modelling suggested that macroalgal transport and deposition, and total organic carbon (TOC), are influenced by complex interactions between several physical environmental factors including water depth, sediment grain size, wave orbital velocity, current speed, current direction, and the extent of the infralittoral zone around depositional areas. Extrapolation of the optimised model was used

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to predict spatial patterns of macroalgal deposition and TOC across the coastline and to identify potentially important carbon sinks. This study builds on recent studies providing empirical evidence for macroalgal biomass deposits in near-shore sediments, and a framework for predicting the spatial distribution of potential carbon sinks and informing future surveys aimed at determining the potential for long-term macroalgal carbon sequestration in marine sediments.

1. Introduction

The fate of macroalgal carbon is one of the most urgent questions in blue carbon research (Macreadie et al., 2019). Macroalgal communities occupy large areas of marine ecosystems in the infralittoral zone (Duarte, 2017; Duarte et al., 2022), producing biomass that vastly exceeds that of any other coastal vegetation type (Smith, 1981; Duarte et al., 2022). Globally, standing stocks of macroalgae store significant amounts of carbon, with 109.9 Tg C estimated to be temporarily stored in living macroalgal biomass in temperate Australia alone (Hill et al., 2015; Filbee-Dexter and Wernberg, 2020). At present, macroalgal contributions to blue carbon remain largely unknown due to a lack of empirical evidence for long-term sequestration in marine sediments. However, recent studies have shown that biological features associated with cell wall structure and composition are likely to aid the long-term preservation of macroalgal carbon in marine sediments (Wakeham and Canuel, 2006; Trevathan-Tackett et al., 2015). Specifically, refractory compounds in different macroalgal taxa have been shown to provide defence against microbial decomposition during early diagenesis (Wakeham and Canuel, 2006) and are expected to support the preservation of recalcitrant macroalgal carbon in marine sediments over extended time frames (Trevathan-Tackett et al., 2015). Understanding the potential for sequestration of macroalgal carbon is therefore essential for creating robust inventories of Greenhouse Gases (GHGs) in which key carbon donors are recognised. Likewise, there is a growing need to understand the sources and sinks of macroalgal carbon across the world's oceans, and the factors influencing patterns of macroalgal transport and deposition in marine sediments.

Because macroalgae primarily grow on hard substrata, it is unlikely that their biomass contributes to carbon sinks within local habitats (Duarte and Cebrián, 1996; Barrón and Duarte, 2015). Instead, dislodged macroalgal biomass is thought to be advected from the source location potentially contributing to allochthonous carbon sinks (Hill et al., 2015; Krause-Jensen and Duarte, 2016; Ortega et al., 2019). However, the fate of dislodged macroalgal biomass and its contribution to marine sediments is likely to be influenced by complex interactions between abiotic and biotic factors. Wind-driven Langmuir circulation has been identified as a key factor associated with export of floating macroalgal biomass to the deep ocean (Johnson and Richardson, 1977; Dierssen et al., 2009) with the dispersion of macroalgal biomass being spatially and temporally variable due to differences in surface and sub-surface hydrodynamic conditions both within and between ocean basins (Shi et al., 2015; Kokubu et al., 2019; Kwan et al., 2022). The potential for dispersion and deposition to the ocean floor is also likely to vary among macroalgal taxa, depending on morphological features (such as buoyancy) that influence passive transport (Johnson and Richardson, 1977; Fraser et al., 2022), sinking rates (Schoener and Rowe, 1970; Johnson and Richardson, 1977; Wernberg and Filbee-Dexter, 2018; Smale et al., 2021), and resistance to decomposition *en route* (Wakeham and Canuel, 2006; Pedersen et al., 2021; Li et al., 2022). Several studies to date have demonstrated the potential for macroalgal biomass to be advected to other vegetated coastal habitats (Ortega et al., 2020; Saavedra-Hortua et al., 2020; Hidayah et al., 2021) and offshore into deep water (Garden and Smith, 2015; Krause-Jensen and Duarte, 2016; Miyajima et al., 2022), however, contributions to near-shore environments within coastal waters have been largely overlooked. To address these uncertainties, research is needed to test for signatures of macroalgal carbon within near-shore coastal sediments and to understand the factors facilitating deposition and sequestration dynamics.

Although the potential for long-term sequestration of macroalgal carbon remains uncertain (Howard et al., 2017; Krause-Jensen et al., 2018; Chen and Xu, 2020) a key challenge associated with blue carbon research is the availability of survey tools that reliably allow for the detection and taxonomic discrimination of carbon sources in marine sediments. To date, several studies have attempted different techniques (stable isotopes, molecular compounds, environmental DNA (eDNA)) to discern the source of organic carbon in marine deposits, yet most traditional techniques are limited in the taxonomic resolution of potential carbon donors (Geraldi et al., 2019). Recently, eDNA has emerged as a powerful biomarker for resolving the taxonomic identity of biological material extracted from the environment. This technology is geared around the detection of species-specific DNA products from environmental samples using genetic assays and is providing greater taxonomic resolution compared to traditional biomarkers (Thomsen and Willerslev, 2015; Geraldi et al., 2019). Several studies have successfully used eDNA to assess the contribution of coastal angiosperms and macroalgal carbon to marine sediments (Queirós et al., 2019; Ortega et al., 2020; Hamaguchi et al., 2022; Ørberg et al., 2022). While these studies have successfully confirmed the presence of macroalgal carbon in some coastal sediments, more replicated spatial sampling of near-shore marine sediments is needed to test the generality of the findings and to identify environmental factors influencing patterns of macroalgal transport and deposition at local and regional scales. Such research is needed to help confirm that macroalgal biomass is regularly advected to near-shore sediments, to identify potential macroalgal carbon donor species, and to inform models aimed at predicting the spatial distribution of potential carbon sinks in marine environments.

The southern coast of Australia is recognised as the world's greatest biodiversity hotspot for marine macroalgae (Kerswell, 2006; Keith et al., 2014; Huisman and Baldock, 2018), supporting at least 1150 formally recognised macroalgal taxa described to species and high levels of endemism (Phillips, 2001). The coastline is recognised as a highly energetic region with strong ocean currents and high wave exposure (Hemer and Griffin, 2010; Flocard et al., 2016). Here, dislodged macroalgal biomass is substantial and typically associated with extensive accumulations of wrack on coastal beaches (Hyndes et al., 2022). South-eastern Australia is also recognised as a climate-change hotspot, a region prone to marine heatwaves (Oliver et al., 2017), and where ocean warming is occurring at four times the global average (Frusher et al., 2013; Hobday and Pecl, 2014). Recent studies have demonstrated that many macroalgal species are showing signs of climate stress with changes in the physical marine climate triggering widespread declines in dominant and ecologically important species in the region, including *Macrocystis pyrifera*, *Phyllospora comosa* and *Ecklonia radiata* (Layton et al., 2020; Eger et al., 2022; Young et al., 2022). These declines are raising significant concerns for the structure and function of marine ecosystems in the region due to their contributions to detrital food webs, nutrient cycling, primary productivity, and habitats (Vergés and Wernberg, 2019). Further, these declines are also threatening important commercial fisheries due to disruptions to critical habitat and trophic interactions supporting fishing stocks (Ling, 2008; Johnson et al., 2011; Holland et al., 2021). However, at this stage it is uncertain if these declines are also likely to directly threaten macroalgae-derived detrital carbon, sequestration dynamics and ocean carbon budgets in the region.

This study aimed to investigate the fate of dislodged macroalgal biomass in south-eastern Australia by assessing spatial patterns and the diversity of macroalgal carbon products in near-shore sediments, and physical drivers of macroalgal transport and deposition dynamics in the region. An eDNA metabarcoding approach was used to test for evidence of macroalgal carbon in near-shore coastal surficial sediments (top ~7 cm) collected from 100 locations in water depths up to 55 m. This allowed for the identification

of key physical and spatial factors influencing the distribution, taxonomic richness, and relative abundances of macroalgal material and total organic carbon (TOC) in near-shore marine sediments, and the modelling of macroalgal and potential carbon deposits beyond the sampling locations. This study represents the most comprehensive investigation of macroalgal contributions to near-shore coastal sediments and provides an important resource for identifying potential macroalgal carbon donors and the distribution of potential carbon sinks. Finally, this study provides a framework for prioritising future research aimed at validating long-term sequestration of macroalgal carbon in near-shore marine sediments and quantifying the contributions of macroalgae to blue carbon stocks.

2. Material and methods

2.1. Collection and analysis of sediment

To investigate the prevalence of macroalgal eDNA in near-shore sediments, a total of 112 surficial sediment samples were collected from near-shore coastal waters (to 5.6 km (3 nm) offshore) of Victoria, south-eastern Australia, between July 2019 to November 2020 (Fig. 1, Supplementary Table S1) in waters depths between 4 and 55 m. Sampling was informed by a 10-m continuous seamless topographic-bathymetry Digital Elevation Model (DEM), which is the best available, seamless depth data available for the study area (Allemand et al., 2017), with a derived consolidated (compacted) / unconsolidated (loosely arranged and/or unstratified) substrate GIS layer. Sediments were collected from the top 70 mm of the seafloor using a Shipek grab sampler (Bingham et al., 1982) deployed from a research vessel along a series of transects spaced 1.5–3 km apart. This grab sampler allowed the recovery of sediment from the top seven centimetres of the seafloor (Carvalho et al., 2022). The sampling sites spanned across seven marine biounits (Edmunds and Flynn, 2018), including Glenelg (GL), Discovery Bay (DB), Cape Nelson (CN), Shipwreck Coast (SWC), Cape Otway (CO), Surf Coast (SFC), Bellarine-Mornington (BM) (Fig. 1). Study sites were grouped as biounits, which were characterised by one or more dominant physiographical settings such as discrete ecophysiological features, distinct ecological properties, intrinsic ecological functions and values by using natural (instead of administrative) boundaries where possible (Edmunds and Flynn, 2018). Given only a single sample was collected from the GL biounit and only two samples from the BM, they were included into their nearest biounit (DB and SF, respectively) in data analysis (Fig. 1) to avoid imbalanced data among the biounits which may result in biased output of analysis. For statistical analysis, the sampling sites were grouped into two depth categories (<30 m and ≥30 m) based on common habitat zonation of macroalgal communities that are highly affected by the gradient of natural light intensity (Dawes, 1981). Each depth category included 54 and 58 sites, respectively.

Sediment samples were immediately transferred from the grab to plastic bags, placed on ice, and transferred to the laboratory within <12 h. In the laboratory, an approximately 15-g subsample from each sediment sample was transferred into a 50-ml Falcon tube and stored at −80 °C while 200 g was bagged and stored at −20 °C for organic carbon analysis. Total organic carbon (TOC) was estimated for each sediment sample through loss on ignition (LOI) by oven-drying ~4-g subsamples at 105 °C for 24 h, followed by combustion at 550 °C for 4 h (Heiri et al., 2001; Kennedy and Woods, 2013). Sediment samples were washed in fresh water and dried at 60 °C. Grain size texture was determined through a combination of mechanical sieving for particles > 1.8-mm diameter and laser diffraction analysis using a Beckman Coulter LP 133230 for the remaining sand and mud fractions. Due to disturbance of the sediment occurring during grab sampling, dry bulk density of the in-situ sea floor sediment could not be undertaken.

2.2. DNA extraction and amplification

Total genomic DNA was extracted from ~2.5 g (WW) of homogenised sediment from each sample using the NucleoSpin® 96 Plant II protocol (Macherey-Nagel Inc.) and quantified using the QuantiFluor® dsDNA System (Promega Inc). Negative extraction controls, involving all steps above but with no sediment sample, were performed in parallel with all total genomic DNA extractions to control for potential cross-sample contamination. Quantitative Polymerase Chain Reactions (qPCR) targeting a 100–110 base pair hypervariable of nuclear 18S rRNA gene v7 region fragment was performed on total genomic DNA extractions. qPCRs were performed in triplicate for each sample 10-μL reactions consisting of 5-μL SsoAdvanced™ Universal SYBR Green Supermix (BIO-RAD), 1-μL each of forward (TTTG TCTGSTTAATTSCG) and reverse (CACAGACCTGTTATTGC) primer (Guardiola et al., 2015), 1-μL DNA template, and 2-μL autoclaved Milli-Q water. Additionally, three negative template qPCR controls (no DNA extract

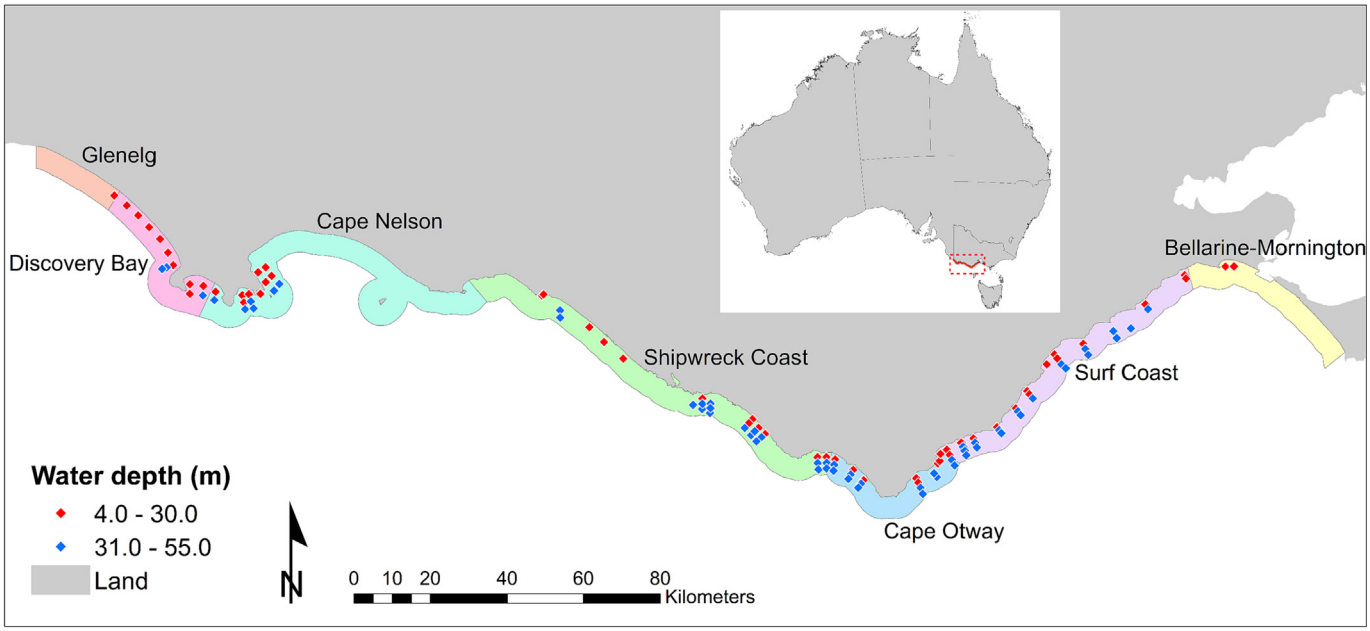

Fig. 1. Location of study sites spanning seven biounits along south-west coast of Victoria, Australia. Blue and red dots represent sediment collection sites at water depths < 30 m and ≥ 30 m, respectively, along line transects extending offshore and perpendicular to the coastline. Different coloured bands running parallel to the coastline represent seven marine biounits described by Edmunds and Flynn (2018)

added), three negative controls (extract from negative extractions) and three positive controls of known samples were run on each 96-PCR sample plate and used in each step of the metabarcoding process through to sequencing. All PCR primer combinations were modified to include Illumina adapter tails at their 5′ ends (TCG TCG GCA GCG TCA GAT GTG TAT AAG AGA CAG and GTC TCG TGG GCT CGG AGA TGT GTA TAA GAG ACA G for forward and reverse primers, respectively) to enable the addition of Illumina dual index barcodes for downstream metabarcoding analysis. qPCRs were performed on a Bio-Rad qPCR Thermocycler (BioRad, California) with cycling conditions involving an initial denaturing step at 95 °C for 10 min, followed by 35 cycles of 94 °C for 30, 55 °C for 30 s, and 72 °C for 30 s, with a final extension of 72 °C for 10 min. Positive amplification was confirmed by visualising the digital outputs from each qPCR reaction and assessing a subset of PCR amplicons via electrophoresis on a 2 % agarose gel (2 g agarose in 100 mL TAE) with stained with 10-μL GelRed® nucleic acid gel stain (Biotium, California) and visualized under UV light on a BioRad Gel Doc XR imaging system (BioRad, California). PCR amplicons were then purified using 0.8 × volume of AmpureBead XP buffer (Beckman Coulter) and then used as the template for indexing.

2.3. DNA metabarcoding library preparation and sequencing

Index PCRs were performed in 20 μL reaction matrices consisting of 10 μL of Bioline MyTaq™ Red Mix, 2 μL of purified PCR product, 4 μL of autoclaved Milli-Q water, and 0.4 μM of forward and reverse index primers. Forward and reverse index primers provided dual indices in unique combinations, allowing demultiplexing of pooled products, and Illumina sequencing adapters. Indexing PCR conditions consisted of 95 °C for 3 min followed by eight cycles of 95 °C for 15 s, 57 °C for 15 s and 68 °C for 30 s, and a final extension step of 68 °C for 2 min. A subset of PCR amplicons was subsequently visualized by electrophoresis (as outlined above) to confirm the addition of adapter sequences. PCR products were purified again using 0.8 × volume of AmpureBead XP (Beckman Coulter) and quantified using Qubit dsDNA BR Assay Kit (Invitrogen). Indexed PCR products were then normalized and pooled equimolar for sequencing. The pooled PCR library was subsequently denatured and sequenced on the Illumina MiSeq® platform using the MiSeq® Version 3 kit (300 bp paired-end) allowing for an average read depth of 1×10^{-5} DNA sequence reads per sample.

2.4. Reference library development

A reference DNA sequence library for the 18S rRNA PCR assays was constructed by searching for publicly available DNA sequences from the National Centre for Biotechnology Information's (NCBI) nucleotide database. The search query was limited to the 18S rRNA gene region for "Rhodophyta, Chlorophyta, Phaeophyceae, Magnoliopsida" resulting in 148,782 reference sequences producing a library consisting of 16,990 Chlorophyta (11.4 %), 1458 Phaeophyceae (1.0 %), 3179 Rhodophyta (2.12 %), and 127,155 Magnoliopsida (85.5 %) taxa. The reference library was enhanced by generating and adding 18S haplotype sequences for a range of macroalgal species common to the study region. A total of 24 specimens representing native red (Rhodophyta), brown (Phaeophyceae, Ochrophyta), and green (Chlorophyta) macroalgal species (Supplementary Table S2) were collected from fresh beach wrack at Lady Bay, Warrnambool, Victoria (−38.400748°, 142.476652°). In addition, common Victorian angiosperms, including *Zostera muelleri* (seagrass) and *Sarcocornia* sp. (saltmarsh), were collected from Griffith Island (−38.392452°, 142.244302°) and *Avicennia marina* (mangrove) from Western Port Bay, Victoria (−38.344505°, 145.246337°). Additional samples representing 22 coastal macrophytes (5 macroalgal, 3 mangrove, 6 saltmarsh, and 8 seagrass species, Supplementary Table S2) were collected from a range of temperate and subtropical locations spanning the Australian coastline for genetic analysis. All samples were morphologically identified to the lowest taxonomic level possible (genus or below), then stored at −20 °C prior to genetic analysis. Total genomic DNA was extracted from all tissues and sequenced using the protocol outlined above.

2.5. Bioinformatic analysis

Bioinformatic analyses were performed using a modified version of the analytical pipeline outlined by Holland et al. (2021). In brief, demultiplexed paired-end sequence reads in FASTQ format were trimmed using the *Trimmomatic* v0.39 command line tool to remove the forward and reverse index sequences. Trimmed FASTQ files were imported into the 'DADA2' R package (Callahan et al., 2016) where further data filtering was performed using the *filterAndTrim* function with forward and reverse truncation set (TruncLen = 110, 110) to retain reads with a Phred score > 20, followed by a calculation of error rates using *learnErrors*. Dereplication of data and amplicon sequence variant (ASV) inference was performed using the *derepFastq* and *dada* functions, respectively. Paired-end reads were then merged using the *mergePairs* function and chimeras were removed using the r*emoveBimeraDenovo* function. ASVs with <1000 reads were filtered to reduce the inclusion of non-informative ASVs and potential contaminant sequences. Finally, ASVs were written to ASV table in FASTA format and sequence table formats including read counts. FASTA-derived ASV sequences were aligned against the reference DNA sequence library using BLASTn v2.6.0 (Altschul et al., 1990), restricting hits to a 90 % minimum query length cover. Alignments were imported into MEtaGenome ANalyser (MEGAN V6.23.2) (Huson et al., 2016) where ASVs were assigned to the lowest taxonomic rank possible using the LCA (lowest common ancestor) parameters outlined in Port et al. (2016). Taxonomic assignments were referred back to the DADA2-derived sequences table and DNA sequence read counts per each taxon per sample were summarized. ASV sequences of dominant taxa and those expected to be off-targets were manually verified using the NCBI nucleotide database Basic Local Alignment Search Tool (BLAST). A cladogram depicting all detected macroalgal taxa was generated using MEGAN then modified in FigTree v1.4.4 (Rambaut, 2018).

2.6. Acquisition of environmental and taxonomic data for predictive modelling

Spatial oceanographic data were extracted from GIS layers, consisting of the yearly average and maximum wave orbital velocity (2010–2014), yearly average- (2000–2014) and maximum- (2010–2014) current speeds, current direction for the maximum current speeds, bathymetry (10-m resolution) and slope (10-m resolution). Averaging across several years of hydrodynamic data from these models helped to characterise the variability in the wave and current conditions over the study area since more contemporary hydrodynamic models were not available. Information on the source of the hydrodynamic layers (waves and currents) can be found in (Ierodiaconou et al., 2018) and the 10-m resolution interpolated bathymetry layer in Allemand et al. (2017). An open-coast biotope layer of Victoria was retrieved from the portal of SEAMAP Australia (Ierodiaconou et al., 2007, Lucieer et al., 2019). The distance of sampling sites to coastline and total area of 1) reef, 2) mixed reef-sediment, 3) infralittoral and 4) circalittoral around each site, were then extracted from this biotopes layer. Infralittoral and circalittoral data were both derived from the habitat categories of this layer, where infralittoral is defined as the algal-dominated zone while circalittoral is defined as the area below the infralittoral algal zone and is dominated by invertebrates. 'Proximity Analysis' tool was used to create three scales (5, 15, and 30 km) of buffer areas surrounding each sampling site using ArcMap (v10.7.1). Mean and standard deviation (SD) values were extracted from all GIS layers from each site within the radius of each scale to be used in the model.

To compare the relative abundances of macroalgal eDNA (hereafter abundance) among samples, DNA sequence reads were standardised using logarithmic transformation after Anderson et al. (2006): $\log_{10}(x) + 1$ for $x > 0$, where zeros are left as zeros. Taxonomic richness was summarized as the total number of taxa identified in each sample. Both the abundance and taxonomic richness of macroalgal-eDNA were, then, assessed at two different resolutions: (1) the lowest taxonomic level identified through metabarcoding (*fine resolution*) and (2) at the broader

taxonomic levels of Rhodophyta (red), Phaeophyceae (brown), and Chlorophyta (green) (*coarse resolution*).

2.7. Statistical analyses

2.7.1. Macroalgal diversity in near-shore sediments

The taxonomic composition of macroalgae genetically identified across sediment samples was explored using multivariate statistical analyses. Prior to analysis, the read-count data were transformed into a presence-absence matrix with "1" for present and "0" for absent. A resemblance matrix was then generated using a Jaccard similarity measure (Schroeder and Jenkins, 2018). PERmutational Multivariate ANalyses Of Variance (PERMANOVA) and PERmutational analysis of Multivariate DISPersions (PERMDISP) were performed in PRIMER v7.0.21.0 using the PERMANOVA+ add-on (Anderson, 2005; Clarke and Gorley, 2015). These multivariate analyses were performed to explore the effects of categorical factors including biounit (seven biounits), water depth (<30 m-shallow, ≥30 m-deep), and sediment grain-size (fine, very fine, medium, coarse, very coarse) on the taxonomic composition of macroalgae detected in sediment samples. Following a significant *biounit* × *depth* interaction in PERMANOVA, pairwise tests on the interaction term compared biounits within each depth category, and significance was assessed using the *P*-value based on Monte Carlo random draws *P(MC) at* $\alpha = 0.05$ (Anderson et al., 2008). The frequency of occurrence (FOO) and relative read abundance (RRA) of all detected taxa (assigned to at least order level) was summarized graphically using the 'ggplot2' R package (Wickham, 2016). FOO is calculated as the number of samples that contain a given taxon divided by the total number of samples, while RRA was determined as the proportional summary of filtered sequence read counts among taxa within a sample, with both expressed as percentages (Deagle et al., 2019). To identify the most abundant and commonly occurring macroalgal taxa across samples, taxa were filtered based on read count using a threshold set at >1000, and the results were graphically presented using 'ggplot2' in the R package.

2.7.2. Multiscale drivers of carbon and macroalgal transportation and deposition in near-shore environments

To assess the oceanographic and environmental drivers of transport and deposition of macroalgal biomass, and the potential distribution of carbon sinks in near-shore sediments, 1) preliminary data exploration (testing multicollinearity among environmental variables) was initially performed, then 2) Generalized Additive Models (GAMs) were used to examine the relationships between environmental variables (predictors; Supplementary Table S3) and each of the ecological response variables (taxonomic richness, abundance, and TOC). This modelling approach was used as ecosystem components do not always respond linearly to environmental drivers, where small variations in drivers may stimulate moderate to excessive ecological responses (Hunsicker et al., 2016). The preliminary analysis assessed the presence of outliers and multicollinearity among environmental variables through a matrix of scatter plots and Pearson correlations. Highly correlated ($r > 0.70$; $P < 0.05$) environmental variables were excluded, leaving 12 final predictors out of an initial set of 25 environmental variables (Supplementary Table S3). Given the environmental drivers of macroalgal biomass transport and deposition are poorly studied, modelling begun by including all 12 uncorrelated variables (hereafter full-models) and then selected only the significant variables from full-models for subsequent reduced models (hereafter SV-models). Both, full- and SV-models were performed for each single scale (5 km, 15 km, 30 km) and then ran for multiscale data by combining significant predictors obtained from all single-scale models. A generalized mixed-effects model with the Gaussian family (link function: identity) was used for TOC (continuous data) models, while the taxonomic richness (count data) models followed the Poisson family with two link functions (log and square root) tested (Crawley, 2013).

Data were partitioned into training (75 %) and test (25 %) datasets to enable cross-validation and test the predictive performance of the models. Single and multiscale GAMs were trained to observe the possible drivers of macroalgal eDNA abundance, taxonomic richness, and TOC measured across the study area (near-shore environment). In addition to environmental variables (Supplementary Table S3), the different characteristics of the sampling sites were also accounted for by including biounits, water depth categories, and sediment grain sizes (Supplementary Table S1) in the models. For this purpose, the only sample collected from the Glenelg biounit (DB01, 689 m to the Discovery Bay - Glenelg border) was assigned to Discovery Bay and another two samples from the Bellarine-Mornington biounit were incorporated into Surf Coast biounit. The 'mgcv' R package (Wood, 2011) was used in RStudio v2022.02.3 + 492 to test for a significant relationship (at $\alpha = 0.05$) between the ecological responses and the environmental variables and to visualize the results. The formulae and performance metrics of the final models and all potential models run are provided in Supplementary S5 and S6. A suite of performance metrics, including the Akaike Information Criterion (AIC), maximum likelihood (REML), explained deviance, and the predictive accuracy, was compared to select the best model (Bedrick and Tsai, 1994; Becker et al., 2020).

2.7.3. Scaling up predictions of transport and deposition of macroalgal biomass and total organic carbon in near-shore sediments

To extrapolate beyond our sampling sites to predict the potential transport and deposition of macroalgal biomass (as taxonomic richness) and TOC preserved in the sediments along the entire south-western coast of Victoria, the GAMs that performed best for taxonomic richness and TOC (while relative read abundance models were inadequate; see Section 3.1 below) were used. For the prediction of taxonomic richness, two different prediction maps obtained through the models using two link functions (log and square root) were compared, and the one that produced the lowest AIC with the highest deviance explained and the predictive accuracy and generated a more accurate prediction map was selected. Data layers that are in vector format (e.g., biounits, InfraArea, GrainSize, and Depth; Supplementary Table S3) were first converted to raster using 'Polygon to Raster' tool, then the mean and SD values of each raster (for the scales required by the final models) were extracted using 'Focal Statistics' tools. All the data processing was performed in ArcGIS 10.7.1. These rasters were then imported into *R*, prior to running the 'predict' function to derive the predicted taxonomic richness and TOC of each cell of the raster. Finally, the spatial prediction raster for each response variable was generated using 'rgdal' R package in RStudio. The rasters obtained were further processed in ArcGIS to produce the final maps predicting the taxonomic richness and organic carbon present in near-shore sediments throughout the south-western coast of Victoria.

3. Results

3.1. Macroalgal diversity in near-shore sediments

Sequencing of the 18S rRNA PCR library yielded a total of 7,807,406 DNA sequence reads (average per sample = 74,509 reads) and 11,915 unique haplotype sequences (ASVs). Subsequent analyses identified macroalgal DNA products in sediments collected from 111 of the 112 sites, with all major macroalgal lineages being commonly observed; Phaeophyceae (FOO 94.64 %), Rhodophyta (FOO 95.54 %), and Chlorophyta (FOO 91.07 %) (Fig. 2b). Confident taxonomic assignments were achieved for 68 macroalgal taxa from a total of 1424 ASVs, including 15 taxa assigned to Phaeophyceae (417 ASVs; 3.5 %), 38 taxa assigned to Rhodophyta (571 ASVs; 4.8 %), and 15 assigned to Chlorophyta (436 ASVs; 3.7 %) (Fig. 2a, Supplementary Fig. S2). Of these, 16 taxa were confidently identified to species level, 10 to genus level, 19 to sub-family or family, 11 to order, 9 to sub-class or class levels, and 3 phylum level. Given the universal nature of the 18S rRNA PCR assay, 2588 ASVs (21.7 %) representing 56 microalgal taxa (Chlorophyta), 3318 ASVs (27.8 %) representing 82 angiosperms (including 9 mangrove and 2 seagrass taxa), 513 ASVs (4.3 %) representing unknown eukaryotes, and 1512 unassigned ASVs (12.7 %) were also recorded (Fig. 2b, Supplementary Fig. S1).

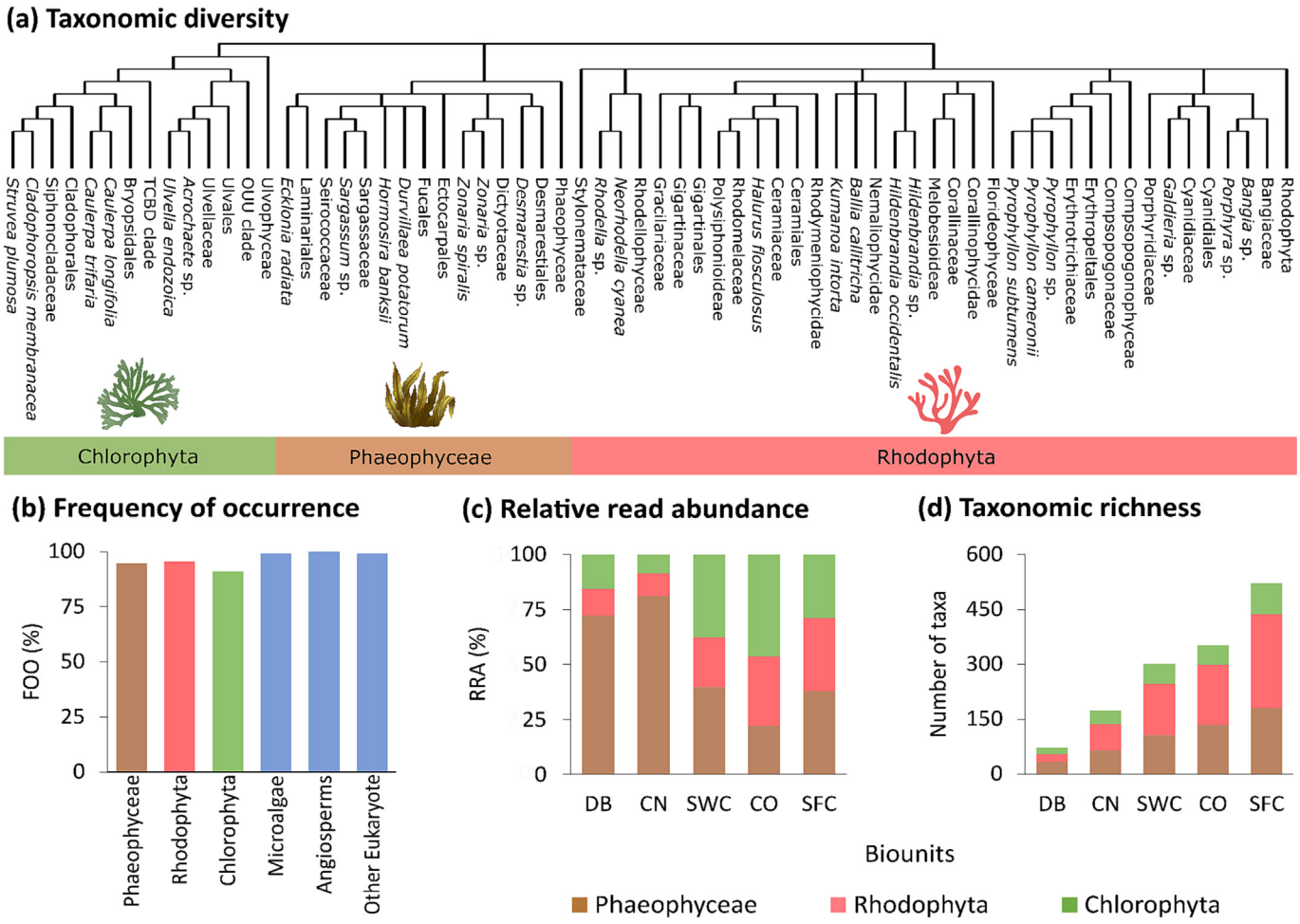

Fig. 2. Macroalgal eDNA derived community structure from sediments sampled along the south-western and south-central coast of Victoria. (a) Total diversity of macroalgal taxa identified across all 112 sediment samples (identified to lowest possible taxonomic rank), (b) Overall frequency of occurrence (FOO) for each major macroalgal group compared to other taxonomic groups recorded from all sedimentary eDNA samples, (c) Relative read abundance (RRA) for each major macroalgal group across biounits, (d) taxonomic richness for each major macroalgal group across biounits (Discovery Bay (DB), Cape Nelson (CN), Shipwreck Coast (SWC), Cape Otway (CO), Surf Coast (SFC)). Seaweed icons are courtesy of www.vectorstock.com/royalty-free-vectors and www.pngaaa.com.

Statistical analysis revealed that the effects of biounit on macroalgal composition were not consistent across depth gradients (PERMANOVA *biounit* × *depth* interaction: $P(perm) = 0.014$; Supplementary Table S4), which is at least in part due to differences in dispersion among some biounit and depth combinations (PERMDISP *biounit* × *depth* interaction: $P(perm) = 0.001$, although 31 out of 45 pairwise comparisons of the interaction term were not significant ($P(MC) > 0.05$); Supplementary Table S5). In shallow (<30 m) sediments, macroalgal composition of the SF biounit differed significantly from that of the western biounits DB and SW ($P(MC) < 0.05$), while all remaining pairwise comparisons did not differ significantly ($P(MC) > 0.05$; Supplementary Table S4). In deeper (≥30 m) sediments, macroalgal composition of CO was significantly different to the biounits of DB and CN ($P(MC) < 0.05$), while all remaining pairwise comparisons did not differ significantly ($P(MC) > 0.05$; Supplementary Table S4). Analyses revealed no significant effect of sediment grain size on the composition of the macroalgal taxa detected in sediments (PERMANOVA *GrainDesc*: $P(perm) = 0.387$; Supplementary Table S4).

In general, the DB and CN biounits had noticeably higher RRA of Phaeophyceae (72.2 % and 81.0 %, respectively) compared to the other three biounits, where RRAs across Phaeophyceae, Rhodophyta and Chlorophyta occurred in relatively similar proportions (Fig. 2c, Supplementary Fig. S3). Data interrogation also indicated that taxonomic richness varied with longitude, with the total number of taxa for all three major macroalgal groups (Phaeophyceae, Rhodophyta and Chlorophyta) increasing from west to the east (Fig. 2d). Overall, phaeophycean taxa were most speciose and dominant in the DB biounit, while the highest taxonomic diversity across all other biounits was within the Rhodophyta (Fig. 2d).

3.2. Key contributors to macroalgal eDNA detections

The FOO and RRA of all taxa confidently assigned were summarized to order level to identify the taxa most frequently detected and abundant in sediments across biounits and depths (Fig. 3a & b). Overall, two macroalgal orders, Fucales (Phaeophyceae) and Bryopsidales (Chlorophyta), were found to be the most common taxa detected in sediments across all biounits and water depths (FOO, 67–100 %) (Fig. 3a, Supplementary Fig. S2). Erythropeltales and Glaucosphaerales were the most commonly detected rhodophyte taxa (FOO, 83–100 % and 71–85 %, respectively) across four out of five biounits (CN, SWC, CO, and SFC) at depths ≥ 30 m, while Erythropeltales was the most frequently detected rhodophyte taxon (FOO, 63–88 %) within three biounits (CN, CO, and SFC) at depths < 30 m (Fig. 3a, Supplementary Fig. S2b & S2c). Consistent with their frequency of occurrences, the relative abundances of Fucales (RRA, 11–79 %), Bryopsidales (RRA, 3–73 %), and Erythropeltales (RRA, 5–32 %) were greater than all other macroalgal taxa across all biounits and depths (Fig. 3b). In contrast, while Glaucosphaerales were frequently recorded across biounits, they had low overall relative abundances relative to other taxa (RRA, 0.5–8 %) (Fig. 3b). Overall, most macroalgal orders were found to have greater FOOs and RRAs at depths ≥ 30 m across all biounits compared to depths < 30 m, except for Fucales and Bryopsidales which had

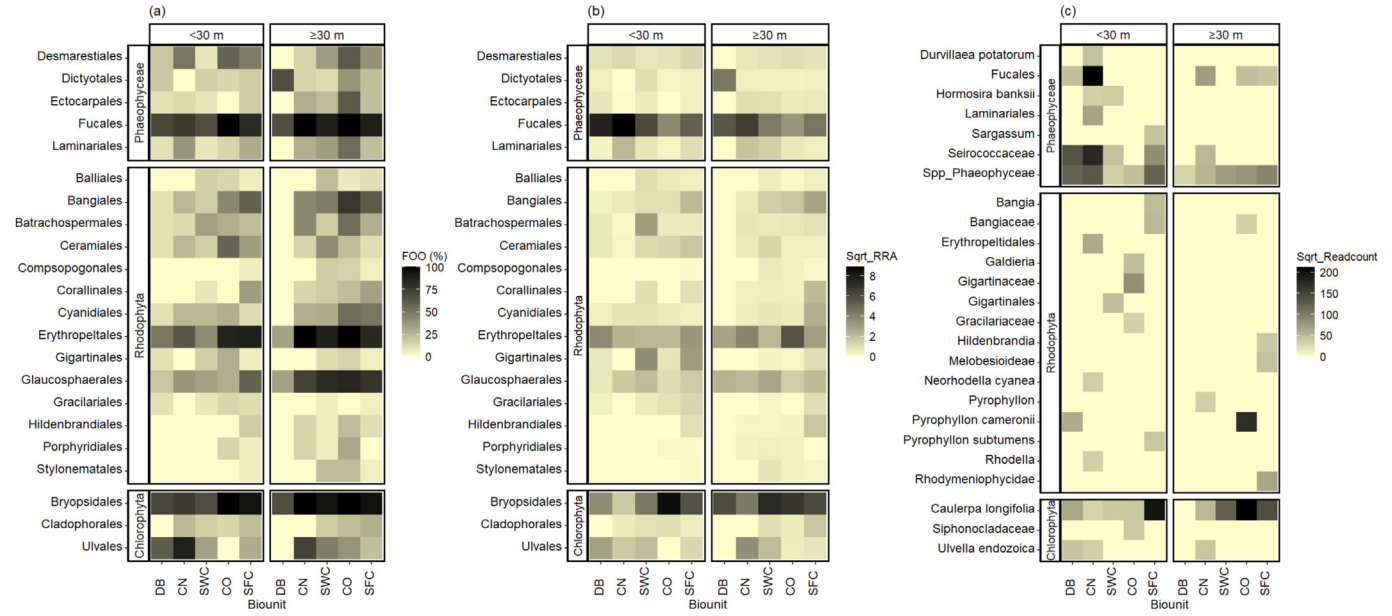

Fig. 3. Most common and abundant macroalgal taxa found across biounits and depths. (a) Frequency of occurrence (FOO) and (b) relative read abundance (RRA), for identified macroalgal taxa summarized to order level. (c) Most abundant taxa (identified to lowest taxonomic rank) meeting a minimum read count threshold of >1000 reads observed across biounits and depth. Values of RRA and read count were square-rooted for plotting purposes providing greater heatmap clarity.

a higher RRA at depths < 30 m for some biounits (Fig. 3a & b, Supplementary Fig. S2b & S2c). Assessments of read-count data for taxa based lowest assigned taxonomic rank and a minimum threshold of >1000 reads identified seven phaeophycean taxa as being among the most abundant taxa across all biounits at depths < 30 m, including *Durvillaea potatorum*, *Hormosira banksii*, *Sargassum*, and species belonging to the family Seirococcaceae, orders Fucales and Laminariales, and class Phaeophyceae that could not be identified to lower taxonomic levels (Fig. 3c). Of these taxa, only three (Seirococcaceae, Fucales and Phaeophyceae) were also abundant at depths ≥ 30 m (Fig. 3c). Although less abundant relative to phaeophycean taxa, an additional 15 rhodophyte and 3 chlorophyte taxa were also common and abundant across biounits and depths gradients (Fig. 3c).

3.3. Multiscale environmental drivers of transport and deposition of macroalgae and carbon in near-shore environments

The influence of different environmental drivers on macroalgal taxonomic richness, relative abundance, and TOC measured in near-shore sediment samples was tested using GAMs at two levels of resolution: *fine* (identification to the lowest possible taxonomic level) and *coarse* (higher-taxonomic assignment as Phaeophyceae, Rhodophyta or Chlorophyta). Overall, a suite of important oceanographic parameters that are likely to be the key environmental drivers of macroalgal carbon transport and deposition within near-shore sediments was identified. At the fine resolution, eight models were tested for each ecological response (i.e., richness, abundance, and TOC) consisting of four models for each of the full- and SV-models (including single and multiple scales of buffer area surrounding each sampling site; Supplementary Table S6). Sufficient performance metrics were obtained from a suite of different models tested for the taxonomic richness and TOC, while all models tested for the abundance did not produce adequate performance metrics (Supplementary Table S6).

The best GAM obtained for taxonomic richness was the multiscale full model (Supplementary Table S6). This model demonstrated that seven (of eight tested) oceanographic parameters (including water depth; 5-km and 30-km means of yearly-average wave orbital velocities; 5-km and 30-km means of easterly and northerly (respectively) current directions; 15-km SD of easterly current direction, and 5-km infralittoral area) were significantly correlated (P < 0.001–0.01) with the differences in taxonomic richness occurring across the study area (Supplementary Table S7). The smoothed components were plotted (Fig. 4) to visualize the partial effects of each parameter on the taxonomic richness. Although the mean sediment grain size included in this model did not contribute significantly to the smoothed effect (Fig. 4c), retaining it in the model increased the model performance and generated the highest metrics compared to the remaining models tested. In addition, the partial effects of three out of five biounits (including SWC, CO, and SFC) examined also contributed significant effects (P < 0.001–0.01) to the model performance (Supplementary Table S7). These results showed that the number of taxa identified in the sediment samples collected from these three biounits was significantly different from each other and the other two biounits. This suggests the richness of macroalgal taxa in sediment samples was significantly influenced by longitudinal effects. Overall, the seven environmental variables defined by the best-fit model for taxonomic richness explained 56.3 % of the deviance in the data with 58 % predictive accuracy (Supplementary Table S6).

From all TOC models tested, the multiscale SV-model generated the best performance indicators (Supplementary Table S6). This model showed that six environmental drivers (water depth, mean of sediment grain size, 30-km SD of easterly current, 30-km and 15-km infralittoral area, and 5-km mean of maximum current speed) demonstrated significant partial effects (P < 0.001 for the first four and P < 0.05 for the latter two, respectively) on the TOC present in sediments across the study location (Fig. 5, Supplementary Table S8). Even though 15-km mean of bathymetry was not significantly correlated with TOC (Fig. 5e), it was retained in the model to obtain optimal performance metrics of the multiscale SV-model with 72.4 % deviance explained and 49 % accuracy of prediction (Supplementary Tables S6 and S8). The biounits were not significant predictors of the TOC measured in the sediments of sampling sites (Supplementary Table S8).

At the coarse resolution (higher-taxonomic assignment: Phaeophyceae, Rhodophyta or Chlorophyta), the abundance model did not perform well for each macroalgal group at any spatial scale (Supplementary Table S9), consistent with the fine-resolution models of abundance. Meanwhile, the taxonomic richness models tested indicated better results than the abundance model yet did not produce adequate performance metrics (Supplementary Table S9). The 5-km-scale model (model with the best metrics; Supplementary Table S9, Fig. S2) for the Phaeophyceae, for example, explained 51 % of the deviance in the data, though R^2 and predictive accuracy were low (only 0.38 and 49 %, respectively, Supplementary Table S9).

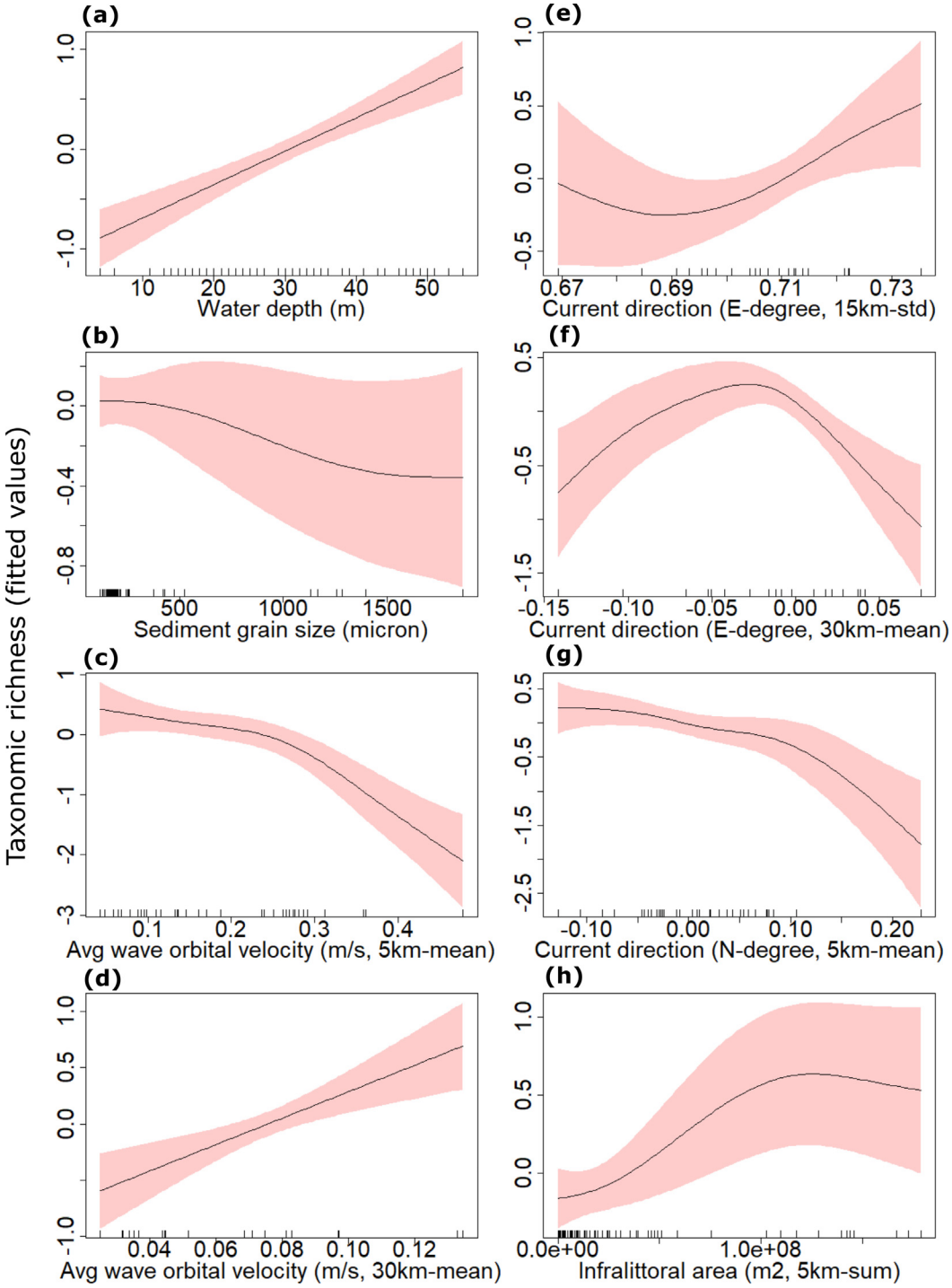

Fig. 4. Macroalgal taxonomic richness model described partial effects of environmental drivers on the number of macroalgal taxa identified in near-shore sediments along south-western coast of Victoria. Fitted values of taxonomic richness plotted against a) water depth and b) average sediment grain size at each site, c) average wave orbital velocity at the 5-km scale, d) average wave orbital velocity at the 30-km scale, e) standard deviation of the easterly current direction at the 15-km scale f) standard deviation of the easterly current direction at the 30-km scale, g) standard deviation of the northerly current direction at the 5-km scale, and h) average infralittoral area at the 5-km scale. The best-performing model generated for the taxonomic richness was the multiscale full-model (Supplementary Tables S6 & S7).

Overall, the coarse resolution cannot be sufficiently modelled for either taxonomic richness or abundance.

3.4. Scaling up predictions of transport and deposition of macroalgal biomass and carbon in near-shore sediments

The extrapolation of the spatial distribution of both the potential taxonomic richness of macroalgae deposited in sediments (detected by eDNA) and the TOC, was restricted to those biounits with sufficient data available; excluding GL and BM that consisted of only one and two sample sites, respectively (Fig. 6). The scaling up of the models predicted with accuracies of 49–58 % (Supplementary Table S6). The predictive map of macroalgal taxonomic richness in the sediments spanning south-western and south-central Victoria (Fig. 6a) were consistent with the continuous distribution of macroalgal habitats throughout the study area (Fig. 6c). The predicted macroalgal richness deposited in the near-shore sediments gradually

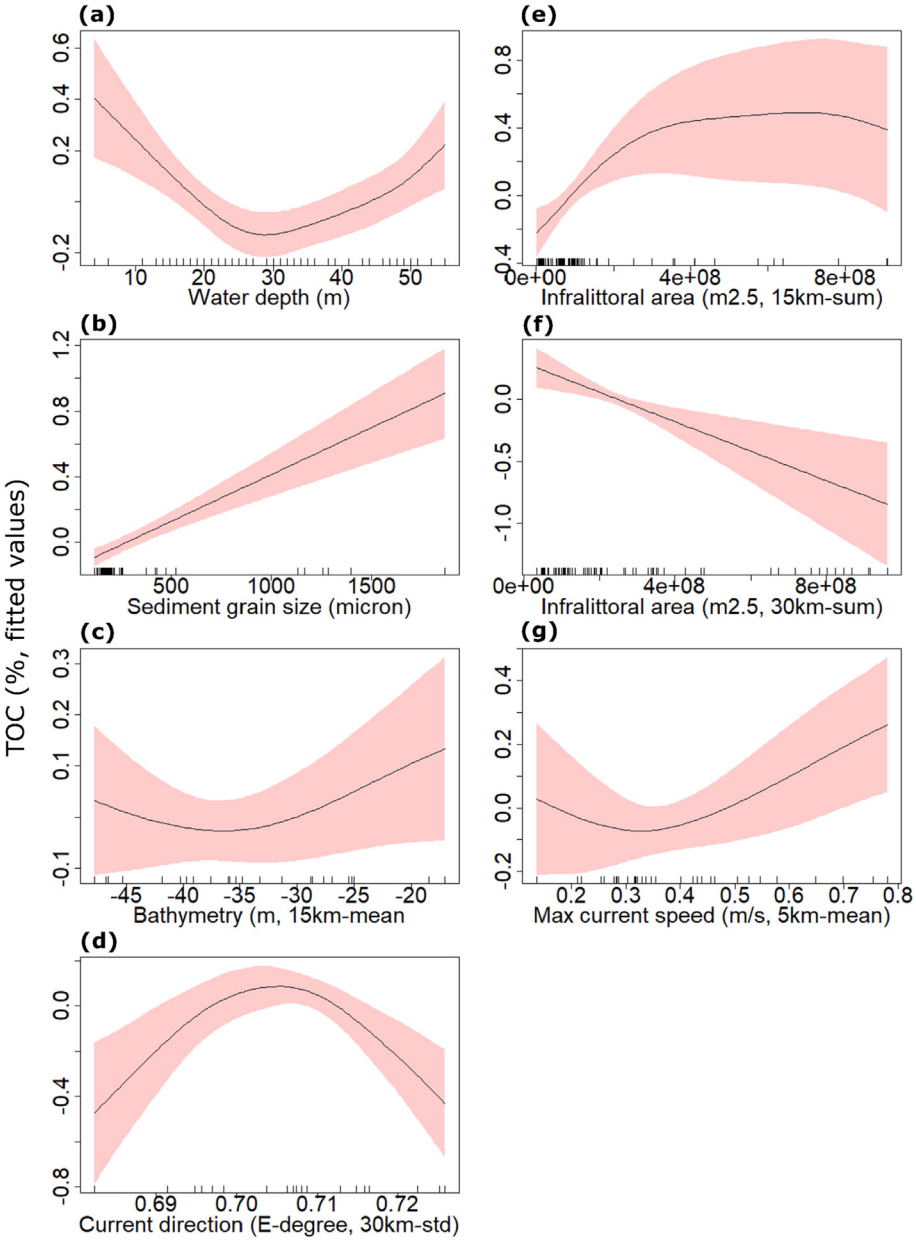

Fig. 5. TOC model demonstrated the partial smoothed effects of the environmental predictor variables on the signature of total organic carbon retained in near-shore sediments along south-western coast of Victoria. Fitted values of TOC plotted against a) water depth and b) average sediment grain size at each site, c) average bathymetry at the 15-km scale, d) standard deviation of the easterly current direction at the 30-km scale, e) average infralittoral area at the 15-km scale, f) average infralittoral area at the 30-km scale, and g) average maximum current speed at the 5-km scale. The best performing model obtained for the TOC was the multi scale SV-model (Supplementary Tables S6 & S8).

decreased with distance from shore and was predicted to be higher at some locations within the CN, SWC and CO biounits (Fig. 6a). Areas within the DB, SWC and SFC biounits, with no visible macroalgal habitats (Fig. 6c), were predicted to have lower macroalgal richness in local sediments (Fig. 6a). In contrast, the predicted concentration of TOC, in general, increased with the distance from shore (Fig. 6b), such that the areas with the highest TOC (Fig. 6b) have relatively low taxonomic richness (Fig. 6a). While the TOC concentration in our sediment samples ranged 0.57–2.42 %, the extrapolation of the model predicted that the near-shore of south-eastern Australia may store up to 4.28 % of TOC within about ~7 cm surficial sediment.

Patterns and drivers of dislodged macroalgal transport and deposition and the spatial distribution of potential carbon sinks in near-shore marine environments. An eDNA metabarcoding approach has demonstrated evidence of macroalgal genetic products in the near-shore marine sediments from south-eastern Australia. These findings suggest that macroalgal-derived carbon is frequently exported to near-shore marine environments in the region, and supports the notion that macroalgae act as carbon donors to areas beyond their natal habitats (Kennedy et al., 2010; Hill et al., 2015; Krause-Jensen and Duarte, 2016; Thormar et al., 2016; Ould, 2022; Yong et al., 2022). Furthermore, the detection of genetic products from a wide range of taxa, representing all major macroalgal taxonomic groups, suggests that macroalgal carbon donors in near-shore environments could be both speciose and diverse. In addition, this study reveals key environmental factors influencing spatial patterns of macroalgal transport and deposition, and TOC, across south-eastern Australia, and demonstrates how such information can be used to predict the occurrence of potential carbon sinks in near-shore marine environments. While previous studies have suggested dislodged macroalgal biomass is likely to be exported to deep-sea carbon sinks (>1000 m depth; Krause-Jensen and Duarte, 2016), this study

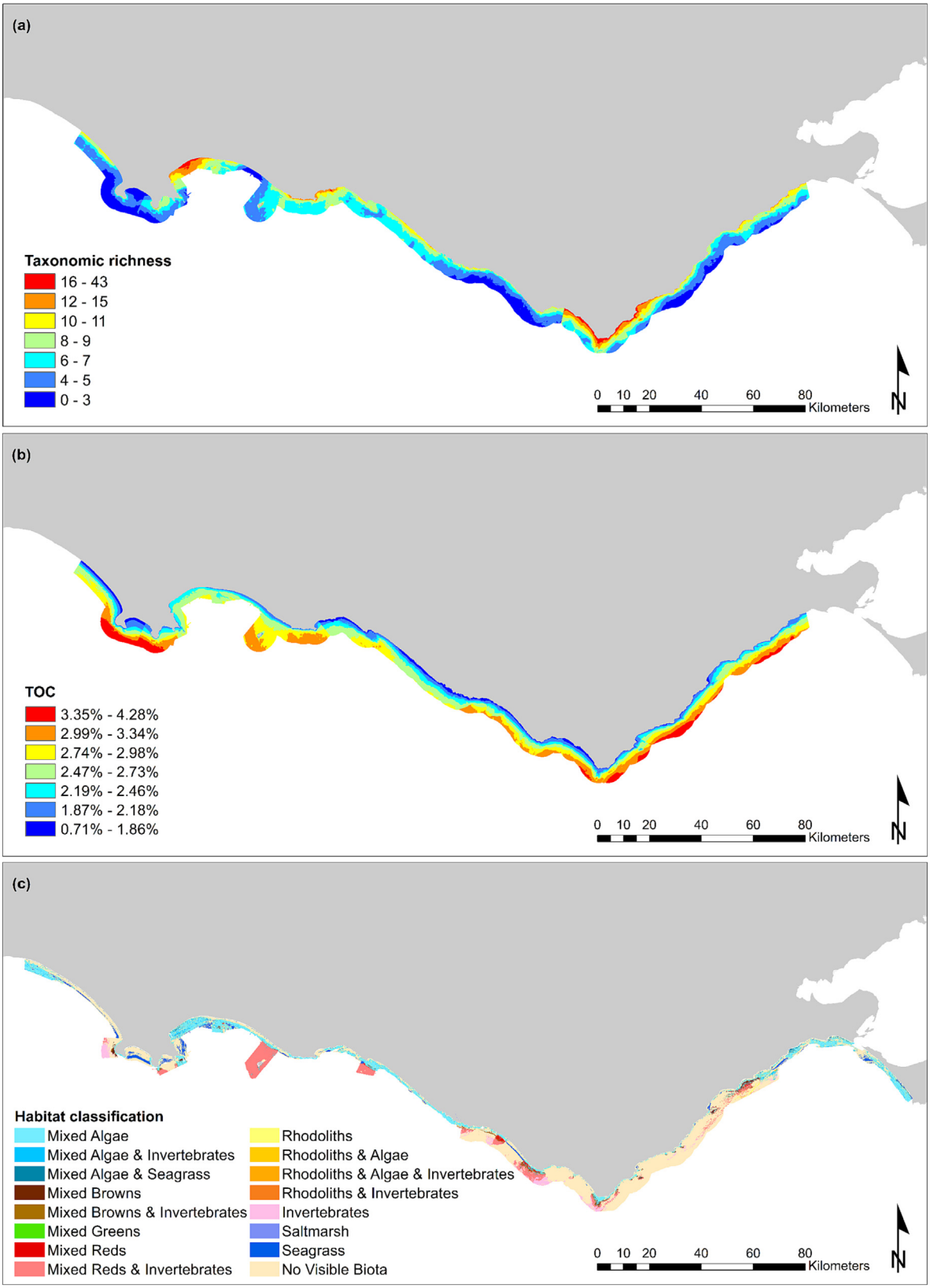

Fig. 6. Predicted distributions of a) macroalgal taxonomic richness and b) total organic carbon in near-shore coastal sediments from south-western and south-central Victoria, in relation to c) the known distribution of coastal habitats extracted from Seamap (Ierodiaconou et al., 2007, Lucieer et al., 2019) and excluding non-algal associated habitat classes.

indicates that near-shore environments are important sinks for macroalgal biomass and may be more important macroalgal carbon sinks than currently assumed.

4. Discussion

This study provides new insights into patterns and drivers of dislodged macroalgal transport and deposition and the spatial distribution of potential carbon sinks in near-shore marine environments. An eDNA metabarcoding approach has demonstrated evidence of macroalgal genetic products in the near-shore marine sediments from south-eastern Australia. These findings confirm that dislodged macroalge carbon is frequently exported to near-shore marine environments in the region, supporting the notion that near-shore environments are important and largely overlooked sinks for macroalgal carbon (Queirós et al., 2019; Ortega et al., 2020; Hamaguchi et al., 2022; Ørberg et al., 2022). Furthermore, the detection of genetic products from a wide range of taxa, representing all major macroalgal taxonomic groups, suggests that macroalgal carbon donors in near-shore environments could be both speciose and diverse. In addition, this study reveals key environmental factors influencing spatial patterns of macroalgal transport and deposition, and TOC, across south-eastern Australia, and demonstrates how such information can be used to predict the occurrence of potential carbon sinks in near-shore marine environments. Further research is now needed to confirm whether macroalgal carbon detected in surficial sediments (≤7 cm) can be sequestered to sediments for extended time scales, making important contributions to blue carbon stocks in and beyond the study area.

4.1. Drivers of macroalgal carbon transport and deposition in the near-shore environment

Understanding physical environmental factors influencing the transport and deposition of macroalgal biomass is critical for predicting the spatial distribution of carbon sinks across the world's oceans (Dolliver and O'Connor, 2022). Modelling performed here suggests that a suite of environmental factors interact to affect the transport and deposition of macroalgal biomass beyond reef habitats and into near-shore soft sediments. Specifically, our best models suggest complex interactions between macroalgal transport and deposition and factors including water depth, multiscale wave orbital-velocity, current speed and its direction, and the extent of surrounding macroalgal-dominated area. Indeed, water motion associated with ocean currents and wave energy is recognised as a fundamental abiotic factor affecting macroalgal biomass detachment and dispersion (Hurd, 2000; Wernberg et al., 2019). In particular, wave exposure and severe storm events are commonly attributed to significant losses of intertidal and subtidal macroalgal canopies (Kennelly, 1987; Underwood, 1999; Dierssen et al., 2009; Krumhansl and Scheibling, 2012; Carnell and Keough, 2020), with detached macroalgal often contributing to offshore sedimentary habitats (Filbee-Dexter and Scheibling, 2012). Additionally, macroalgal communities typically differ across depth gradients and between that infralittoral vs circalittoral reef zones (Pedersén and Snoeijs, 2001; Krause-Jensen et al., 2007; Valdivia et al., 2015). In addition to those predictors, sediment grain size also appears to influence carbon retention in marine sediments (Bergamaschi et al., 1997; Dahl et al., 2016). Our models indicated that grain size was positively correlated with the TOC in sediment, contrary to some studies that have demonstrated a negative relationship (Burdige, 2007; Serrano et al., 2016). However, evidence suggests the relationship between sediment size with TOC is not always linear (Serpetti et al., 2012) and can vary geographically (Pace et al., 2021). Hence, grain size alone cannot explain carbon retention in marine sediments. Nevertheless, this study demonstrates how this information can be used to model spatial patterns of macroalgal deposition and sedimentary TOC when high resolution oceanographic- and geomorphological-data layers are available.

The models generated in this study will help to inform future surveys aimed at confirming the potential for long-term sequestration of macroalgal carbon and the distribution of blue-carbon sinks in south-eastern Australia. Similar studies will be needed in other parts of the world to test the generality of our findings and to prioritise further investments. However, having access to high-resolution, oceanographic-data layers is essential to identifying factors influencing spatial patterns of macroalgal deposition and TOC in marine sediments and to model the distribution of macroalgal deposition hotspots and potential carbon sinks. Fortunately, there have been efforts across south-eastern Australia to model high-resolution hydrodynamics across the near-shore environment, hindcasted over long (>20 years) time-scales (Young et al., 2020). Additionally, several efforts in the region have resulted in high-resolution bathymetry data from both LiDAR and multibeam echosounder data, which provide depth and substrate information. While necessary, such data layers are often deficient or not always publicly available for large parts of the world's near-shore coastal environments (Trice et al., 2021). Consequently, global investment to improve the resolution and availability of high-resolution, oceanographic- and habitat-data layers should be prioritised to advance blue-carbon research in the future.

4.2. Key contributors to macroalgal carbon in near-shore sediments

The high diversity of macroalgal taxa detected in near-shore sediment samples from this study area may be correlated with the fact that the southern coast of Australia is recognised as a global hotspot of macroalgal diversity with at least 1150 described species (Phillips, 2001). While many of the recorded ASVs were taxonomically assigned to species and genus, a large number were assigned to family, order and higher taxonomic levels. This is likely to be an artefact of reference library limitations (Santamaria et al., 2012; Gold et al., 2021), highlighting the need for improved genomic resources for native macrophyte species from the region to help improve the taxonomic resolution of potential carbon donor species in future eDNA metabarcoding studies. Despite these limitations, several taxa were consistently recorded in high frequency and abundance in sediments across the region in both shallow (<30 m) and deep (≥30 m) water environments (Fig. 3a). These consist of taxa from the phaeophyceaen orders Fucales, including *Durvillaea potatorum, Hormosira banksii*, *Sargassum* sp., the family Seirococcaceae (most likely *Phyllospora comosa* and/or *Seirococcus axillaris* (Womersley, 1987)); and Laminariales (most likely *Ecklonia radiata* and *Macrocystis pyrifera*), and several ASVs of uncertain taxonomic status. Indeed, fucoid and laminarian species are dominant biological components of intertidal and shallow subtidal zones throughout the Great Southern Reef (GSR) of Australia (Bennett et al., 2016), accounting for a large proportion of living macroalgal biomass in the region (Hill et al., 2015). Consequently, it is not surprising that their prevalence in the sediments in this study was high. In contrast, low abundances of DNA products for most red algae were observed, despite the Rhodophyta making up ~77 % of macroalgal species in southern Australia (Womersley, 1994; Phillips, 2001); but very high frequencies of occurrence of Erythropeltales and Glaucosphaerales throughout the study area. Rhodophytes tend to be of smaller biomass compared to phaeophytes (McHugh, 2003) and many are common epiphytes, including on large fucoid and laminarian brown algae (Ducker et al., 1976; Nelson, 1993; Nelson et al., 2003), which may explain these patterns. Finally, only a few chlorophyte taxa in the orders Bryopsidales (including *Caulerpa longifolia* and *C. trifaria*) and Ulvales (e.g. *Ulvella endozoica*) were commonly detected among sediment samples, consistent with the low diversity of chlorophyte macroalgal taxa in marine environments relative to the Rhodophyta and Phaeophyceae (Womersley, n.d., Phillips, 2001), and distribution and abundance of these taxa (Womersley, 1984). Nevertheless, this study suggests that biomass from a wide range of macroalgae, representing all major taxonomic groups, have the potential for transport to and deposition in near-shore coastal sediments, potentially contributing to blue carbon deposits.

At this stage, no studies have empirically verified the potential long-term sequestration of macroalgal carbon within oceanic sediments. The potential for sequestration will depend largely on the relative macromolecular composition of refractory and labile carbon compounds (Wakeham and

Canuel, 2006). The structure and composition of cell walls will likely support the long-term storage of macroalgal carbon deposited in marine sediments, but may vary among taxa (Trevathan-Tackett et al., 2015). The cell walls of macroalgae vary in composition and complexity among and within taxonomic lineages, but are generally composed of a microfibrillar network (e.g. cellulose, mannans, xylans) embedded with an amorphous polysaccharide (often sulphated) matrix including alginates, fucoidan, galactans, ulvans (Lee, 2008). Most of these biomacromolecules are known to be resistant to decay and have been proposed to support the preservation of the associated carbon (Wakeham and Canuel, 2006; Bianchi and Canuel, 2011). Moreover, the polysaccharide matrices in cell walls, which are also taxon-specific and account for up to 76 % of the total dry weight (DW) of macroalgal biomass (Jönsson et al., 2020), are also highly recalcitrant (Trevathan-Tackett et al., 2015). In addition to cell-wall components, long-chain complex polysaccharides, which again vary among macroalgal lineages (Kraan, 2012), are also likely to be refractory since their role is associated with the long-term energy and carbon storage (Yu et al., 2002; Graiff et al., 2016). Moreover, although macroalgae have low lipid contents (commonly 1–6 % DW; Jung et al., 2013, Rioux and Turgeon, 2015, Santos et al., 2019), they are rich in long-chain polyunsaturated fatty acids (Dalsgaard et al., 2003; Schmid et al., 2014; Santos et al., 2019; Skrzypczyk et al., 2019), which are predicted to be recalcitrant in marine sediments (Bianchi and Canuel, 2011). Consequently, while labile-carbon compounds may be easily broken down through microbial degradation (Bianchi and Canuel, 2011), their recalcitrant contents could enable macroalgal carbon to be effectively sequestered in marine sediments (Wada et al., 2008; Li et al., 2022; Salmeán et al., 2022). However, the potential for long-term sequestration may vary between taxa and depositional environments and, hence, warrants further investigation.

4.3. Potential carbon stored in near-shore environments

Globally, marine sediments have been estimated to store approximately 2322 Pg C in the top 1 m (nearly double the capacity of terrestrial soils (1325 Pg C)), with 11.5 % of this carbon (256–276 Pg C) likely to be stored in the sediments of the continental shelf, incorporating near-shore environments (Atwood et al., 2020). Due to technical limitations of the grab sampler used in our study, our sampling was limited to surficial sediments, and the total volume of the sediment needed to calculate the dry bulk density of each sample (Howard et al., 2014) could not be measured; hence the total carbon stock within the study region could not be estimated. Consequently, only the potential carbon stored in the form of TOC (%) could be reported. It has been estimated that the TOC content in surficial sediments (<5 cm depth) of the seafloor globally ranges between <0.01 and ~20 % (median 0.62 %; Seiter et al., 2004, Seiter et al., 2005, Radke et al., 2017). This study found that the TOC in the top ~7 cm of near-shore sediments in the study region ranged from 0.57 to 2.42 %, with modelled extrapolations/projections estimating that sediments within this region may contain up to ~4.25 % TOC (ranged from 0.71 to 4.25 %). These estimates are high compared to global estimates (Seiter et al., 2005), suggesting near-shore sediments in this region could represent productive carbon sinks. However, it is important to acknowledge that TOC estimates are expected to be influenced by carbon contributions from a wide range of life forms including macroalgae, microalgae, vascular plants, microbes, and infauna (Romankevich, 1984; Canuel and Hardison, 2016), and further research is needed to quantify relative macroalgal contributions. Nevertheless, these findings have demonstrated that near-shore environments may represent significant, and largely overlooked, blue carbon sinks. In order to confirm these claims, studies aimed at measuring preservation of macroalgal carbon over extended time-scales and quantifying the contributions of macroalgal carbon relative to other potential carbon contributors will be important next steps.

As with every model, there are limitations in the application of the modelling approach and variables used in this study. Although we used knowledge of coastal processes to select explanatory variables to be included in the model, the variable selection was limited to those we could obtain maps of continuous data for the whole region of interest. Using variables such as the aerial coverage of reef extent within different depth zones, and eco-physical regions (biounits) as a proxy for macroalgal community variation, may not completely encapsulate the true diversity and limit the explanatory power of the models. It is likely that additional variables, such as biotic maps of macroalgae communities, would likely improve the variability explained. Finally, some of the variables available for this project were outside the time range of this study (e.g., hydrodynamic variables). Instead we used relative estimates of variation in wave energy and currents between sampling locations based on historical data, rather than capturing the temporally matched conditions that likely drove the current distribution of macroalgae offshore transport. Despite these limitations, this modelling approach could be applied in other regions as long as similar variables are available for associating with locally acquired sediment core data.

4.4. Implications for blue carbon research

Macroalgae are recognised as the most productive of all marine macrophytes, having the largest global coverage and biomass in rocky coastal ecosystems in temperate oceans (Duarte et al., 2005; Duarte, 2017). It has been suggested that macroalgae may be one of the predominant organic carbon sources in marine sediments spanning shallow- to deep-water environments contributing to blue carbon sinks in the deep sea, submarine canyons, anoxic basins, coastal vegetated habitats, and depositional areas of coastal ecosystems (De Leo et al., 2010; Krumhansl and Scheibling, 2012; Filbee-Dexter and Scheibling, 2014; Renaud et al., 2015; Krause-Jensen and Duarte, 2016). It has been also suggested that macroalgal carbon donations to ocean carbon sequestration could be substantial and in the order of 61–268 Tg C $year^{-1}$ with average burial in shelf estimated ~14 Tg C $year^{-1}$ (Krause-Jensen and Duarte, 2016). However, recent global predictions of the net primary productivity (NPP) of subtidal and intertidal seaweed habitats (656 and 1711 gC m − 2 year − 1, respectively; Pessarrodona et al., 2022) suggest that these values (based on a global mean NPP 420 gC m^{-2} yr^{-1}; Krause-Jensen and Duarte, 2016) are likely to be significantly underestimated. This study provides the empirical evidence for macroalgal biomass from a wide range of taxa being consistently exported to, and deposited in, near-shore sediments in south-eastern Australia. While these findings are novel and point to potentially important and underappreciated blue carbon contributors, validation steps are now needed. Specifically, further research, perhaps using eDNA assays in combination with novel biomarker systems, will help to test for evidence of macroalgal carbon in age-dated sediments and to quantify the relative contributions of macroalgal donors to sequestered carbon stocks in marine environments. Nevertheless, this study provides a significant advance in our understanding of the fate of dislodged macroalgal biomass in coastal environments, and a framework for informing future surveys aimed at validating long-term sequestration of macroalgal carbon and the spatial distribution of blue-carbon stocks.

This study adds to a growing body of literature pointing to the power of eDNA technologies for blue-carbon research, in particular for resolving the taxonomic status of potential carbon donor species from marine sediments. This study involved the application of a single universal PCR assay that has been widely used for the taxonomic discrimination of metazoan DNA products, and an emerging biomarker for coastal macrophytes from environmental samples (Reef et al., 2017; Ortega et al., 2020; Ørberg et al., 2022). While our study provided the necessary taxonomic resolution for differentiating between major macroalgal groups, and many lineages within these groups, the conserved nature of the 18S gene means that reliable species level discrimination is not always possible (Hamaguchi et al., 2022). Improvements will be gained in future studies using PCR assays targeting more variable gene markers and assays that are more specific to marine macrophytes (Zhang et al., 2018; Foster et al., 2021; Liu and Zhang, 2021; Hamaguchi et al., 2022). This will be particularly important in studies needing to differentiate between congeners and close relatives. Despite the unparalleled taxonomic resolution offered by eDNA approaches, further gains will be achieved through investments in the

improvement of reference library databases (Cristescu, 2014). Like many studies, we encountered a significant number of unassigned ASVs due to a lack of reference sequence data for some macroalgal taxa. With at least 1150 formally recognised macroalgal taxa from south-eastern Australia, significant investment will be needed to improve reference library databases, including greater coverage of underrepresented macroalgal taxa, to enhance the taxonomic resolution of future eDNA studies.

5. Conclusions

This study represents the most comprehensive investigation of macroalgal carbon contributions to near-shore coastal sediments, providing insights into the potential taxonomic breadth of macroalgal carbon donors, factors influencing spatial patterns of macroalgal transport and deposition, and the potential distribution of blue carbon sinks in marine environments. This study demonstrates how eDNA technologies, combined with replicated spatial sampling and oceanographic data, can be used to identify physical environmental factors influencing patterns of macroalgal transport and deposition, and to predict the distribution of potential blue carbon sinks in near-shore coastal environments. While further research is still needed to validate the potential for long-term macroalgal carbon sequestration in marine sediments, this study suggests that near-shore environments are important sinks for macroalgal biomass and could be significant, and largely overlooked, blue carbon sinks (Queirós et al., 2019; Ortega et al., 2020; Hamaguchi et al., 2022; Ørberg et al., 2022). These findings have important implications for informing blue carbon schemes and GHG inventories both in Australia and internationally.

CRediT authorship contribution statement

This project was conceived by E., A.B., P.I.M., and A.D.M. Acquisition of funding and resources were led by E., A.B, A.D.M., P.I.M., D.I. and D.K. Data generation, analysis and interpretation was led by E. and A.D.M. with contributions from O.J.H., Z.C., M.A.Y., and A.B. Sediment sampling was coordinated and performed by D.I., R.C.C., and D.K. Writing of the manuscript was led by E., A.D.M. and A.B. with critical revision from all authors.

Data availability

Data will be made available on request.

Declaration of competing interest

The authors declare no conflict of interest.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2023.164430.

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