Article

Identifying and protecting macroalgae detritus sinks toward climate change mitigation

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Open Research: Experimental data produced during this study is publicly archived and accessible in Queirós, A. M. and C. Pascoe (2020). Mesocoms investigation of seaweed fragment degradation and skinking rates. Zenodo. doi:10.5281/zenodo.4309608.

All field eDNA sequence data is publicly available for download at the NCBI SRA database, using the BioProject number PRJNA472452 (Eukaryote diversity assessment of sediments of the Western English Channel).

Code for models FVCOM and PyLag used here has been previously published.

Abstract

Harnessing natural solutions to mitigate climate change requires an understanding of carbon fixation, flux and sequestration across ocean habitats. Recent studies suggest that exported seaweed particulate organic carbon is stored within soft sediment systems. However, very little is known about how seaweed detritus disperses from coastlines, or where it may enter seabed carbon stores, where it could become the target of conservation efforts. Here, focusing on regionally dominant seaweed species, we surveyed environmental DNA (eDNA) of natural coastal sediments, and studied their connectivity to seaweed habitats using a particle tracking model parameterized to reproduce seaweed detritus dispersal behavior based on laboratory observation of seaweed fragment degradation and sinking. Experiments showed

seaweed detritus density changing over time, differently across species. This, in turn, modified distances travelled by released fragments until they reached the seabed for the first time, during model simulations. Dispersal pathways connected detritus from the shore to the open ocean but, importantly, also to coastal sediments, and this was reflected by field eDNA evidence. Dispersion pathways were also affected by hydrodynamic conditions, varying in space and time. Both the properties and timing of released detritus, individual to each macroalgal population, and short-term near-seabed and medium-term water-column transport pathways, are thus seemingly important in determining the connectivity between seaweed habitats and potential sedimentary sinks. Studies such as this one, supported by further field verification of sedimentary carbon sequestration rates and source partitioning, are still needed to help quantify the role of seaweed in the ocean carbon cycle. Such studies will provide vital evidence to inform on the potential need to develop blue carbon conservation mechanisms, beyond wetlands.

Keywords: blue carbon, climate change, conservation, lagrangian, mitigation, seaweed.

Introduction

The short time-frame required to limit global greenhouse gas emissions to avoid planet-altering climate change has injected momentum into efforts to expand the contribution of ocean-based solutions within Nationally Determined Contributions to the Paris Agreement(Gallo, Victor, and Levin 2017; Hoegh-Guldberg et al. 2019). “Blue carbon” describes natural carbon sequestration in the ocean. Historically, the term has referred to vegetated coastal habitats including mangroves, seagrass beds and salt marshes, where carbon is fixed as part of a stable living biomass store, and organic matter trapped within sediments provides long-term storage. Blue carbon activities are thus management activities that protect these habitats (and associated carbon stores) from disturbance, supporting climate change

Article

mitigation through the resulting regulation of CO_2 (and potentially other greenhouse gas) emissions(Mcleod et al. 2011; Herr, Pidgeon, and Laffoley 2012). However, recent work has highlighted that vegetated coastal habitats represent a small fraction of coastal and marine ecosystems that contribute to blue carbon(Krause-Jensen et al. 2018; Queirós et al. 2019; Raven 2018). In contrast, seaweed-dominated habitats are distributed across almost a third of global coastlines and are amongst the most productive vegetated habitats globally(Smith 1981; Feehan, Filbee-Dexter, and Wernberg 2021). This production is not yet considered within global carbon budgets, as seaweed are typically not represented within global ocean biogeochemistry models (Friedlingstein et al. 2020). This indicates that there is currently a potential blind spot in our global assessment of the ocean as a potential carbon sink. Seaweed habitats are also not typically considered within blue carbon activities because they are overwhelmingly found on rocky shorelines and reefs, where there is limited potential for *in-situ* storage of the organic carbon they produce(Krause-Jensen et al. 2018).

For kelp (a dominant seaweed group), it has been estimated >80 % of annual production is exported from source habitats(Krause-Jensen and Duarte 2016), with export rates in some systems exceeding 95%(Smale et al. *in press*). A recent global study argued that this exported production, estimated at 323 Tg C/yr[10], may be globally available across the ocean water column(Ortega et al. 2019). The fate of this exported carbon is very poorly understood, but the inclusion of seaweed in blue carbon activities requires the verification that its carbon is sequestered in the long-term, in a way that is amenable to management(Sutton-Grier and Howard 2018). So although such a blue carbon scheme already exists (e.g. Yokohama Bay seaweed farming (Kuwae et al. 2022)) very few studies have heretofore measured the contribution of seaweed carbon to sedimentary carbon stores in the wild. One study provided evidence that 4-9% of the annual production of wild seaweed is sequestered as particulate organic carbon (POC) in coastal non-vegetated sediments (i.e. soft-sediment beds), that is,

outside of those typically considered within the blue carbon umbrella(Queirós et al. 2019). Other studies have not yet measured seaweed POC sedimentary sequestration rates, but have used environmental DNA (eDNA) alone to suggest that this may be taking place both inside and outside of vegetated habitats(Ortega et al. 2019; Ortega, Geraldi, and Duarte 2020). Another measured farmed seaweed contribution to the ocean's recalcitrant dissolved organic carbon pool(Li et al. 2022). These novel findings lend weight to the notion that seaweed may be an important component of blue carbon that is amenable to management, once habitats serving as sinks for this exported production can be identified(Polis, Anderson, and Holt 1997; Smale et al. 2018; Hunt 1925; Queirós et al. 2019). However, large questions still remain regarding how general the findings from these studies(Queirós et al. 2019; Ortega et al. 2019; Ortega, Geraldi, and Duarte 2020) may be, and therefore about the role of seaweed carbon within the context of long-term carbon sequestration(Sutton-Grier and Howard 2018). In particular, large uncertainties remain around: the fate of seaweed POC that is released as macroalgal detritus; what fraction of this remains in, and is potentially sequestered within, the coastal ocean (cf. exported to the open ocean and deep sea areas); as well as around the ability to identify and quantify the transport pathways that connect carbon source to sink habitats(Queirós et al. 2019; Smale et al. 2018). Without this knowledge, we cannot manage donor and sink habitats jointly, conserve them, or restore them. Improved management of seaweed-derived carbon, as well as growing investment in seaweed farming, are seen as vital approaches to curbing global carbon emissions[2]. However, regardless of the high productivity of seaweed habitats, understanding connectivity and identifying their associated sink habitats is a pre-requisite for conserving and promoting sequestration of their carbon(Bianchi et al. 2018; Li et al. 2022).

To this end, improved understanding of a number of additional processes operating at the sediment-water interface; a significant expansion of existing field-based data; and the

development and application of appropriately parameterized dispersal models that may enable the identification of detritus sink locations are needed, among other innovations(Queirós et al. 2019; Krause-Jensen and Duarte 2016; Krause-Jensen et al. 2018). Here, we contribute to the delivery of these aims, by investigating the following questions: i) how widely distributed is seaweed detritus in coastal sediments?; ii) how does seaweed detritus degradation impact transport dynamics and fate?; and iii) what transport pathways connect seaweed habitats to putative carbon sink habitats in the coastal ocean, and how dynamic are these? A two-year study combined novel field observations of environmental DNA, as well as, to our knowledge, the first application of Lagrangian particle tracking modeling using parameter values estimated via lab-based observations of seaweed detritus degradation and sinking velocity. We focused on the coastal ocean, where the largest fraction of seaweed detritus is expected to remain(Krause-Jensen and Duarte 2016), and where the majority of the world's MPAs are already located(UNEP-WCMC and IUCN 2020) with conservation mechanisms more easily implemented.

Methods

Sedimentary eDNA sampling and processing

To address our first research question, we sampled marine soft-sediments at two inshore coastal areas in Plymouth Sound UK (one *Zostera marina* seagrass meadow and one non-vegetated) and one offshore site, circa 48 m deep and 13 km S-SW off Plymouth, which hosts the benthic site of the long-term monitoring Station L4 (50º 13’ 22.7’’N 4º 11’23.0’’W , https://www.westernchannelobservatory.org.uk/)(Queirós et al. 2019). We analysed sedimentary eDNA sampled from all three areas collected during one common time point, whilst the offshore area was further sampled on another 6 occasions over a 13 month period (Fig. 1; Queirós et al. 2019). Offshore sampling took place as previously described (Queirós

Article

et al. 2019), via deployment of a multi-corer (which penetrates between 30-50 cm into sediments depending on sediment type), sediment slicing, and the collection of small volumes of sediment from the preserved sediment water interface (0-2cm), which were frozen in liquid nitrogen on collection and until retrieval to Plymouth Marine Laboratory, where they were stored at -80°C until processing(Queirós et al. 2019). 3-4 eDNA samples were collected at the offshore site at each sampling event, corresponding to one per multi-corer core (Queirós et al. 2019). The seabed at the site is characterised as sandy mud (Queirós, Stephens, et al. 2015); its sediment surface is covered by a bottom water layer of varying thickness (cms) comprised of detritus, fine sediment and living organisms, that is flushed and re-settled tidally (the "fluff layer", Queirós et al. 2019); and the site is influenced by outflow from the Tamar estuary(Smyth et al. 2015). Inshore sediment samples were collected by scuba divers in April 2016, just before the last offshore sampling campaign (Queirós et al. 2019). Triplicate core samples were collected from a shallower area (~2 m depth below chart datum) dense with seagrass shoots (*Zostera marina* (Linnaeus)), and from a deeper unvegetated area (~8 m depth below chart datum) in Firestone Bay, Plymouth, SW UK (Fig 1). Firestone Bay is characterized by patches of soft sediment, interspersed within semi-stable boulders and bedrock harboring dense macroalgal assemblages (De Leij et al. 2017). Seagrass shoot density in the sampled area was circa ~60 m^{-2} at the shallower site, whereas the deeper sampling area was characterized by fine sediments supporting abundant infauna. Firestone Bay is also influenced by tidal currents and riverine input from the nearby Tamar Estuary; however, its waters are considered well-mixed and fully marine (Smyth et al. 2015). Divers collected surficial sediment cores using sterile piston corers made from cut-off 60 mL polyethylene syringes (2.9 cm diameter). Syringes were inserted vertically 8 cm into the sediment, capped, and returned to the laboratory where they were frozen at -80°C until later analysis. Care was taken not to disturb the sediment layer before sampling and to retain

Article

151 sediments on retrieval of syringes. Three replicate core samples were collected haphazardly
152 within each area, from locations positioned at least 3 m apart from one another. From each
153 syringe core, samples were extracted from the surficial 2 cm sediment for eDNA analysis, as
154 done for offshore samples, with inshore and offshore samples compared in subsequent
155 analyses.
156 eDNA was extracted from all sediment samples using the MoBIO Powersoil DNA©
157 extraction kit following the manufacturer's guidelines. The V9 region of the 18S rRNA gene
158 was amplified using the primer pair Euk1391F (GTACACACCGCCCGTC) and EukBr
159 (TGATCCTTCTGCAGGTTCACCTAC) (Amaral-Zettler et al. 2009), and sequenced using
160 MiSeq by commercial contract (Mr DNA, Molecular Research LP, USA). Distinct
161 Operational Taxonomic Units' (OTU) sequences were then allocated to taxa at the lowest
162 possible taxonomic resolution using the Basic Local Alignment Search Tool (BLAST) of the
163 National Centre for Biotechnology Information (NCBI, U.S. National Library of Medicine),
164 and then individually quality controlled. All sequences, including those from the offshore site
165 preliminarily analyzed in (Queirós et al. 2019), were re-analyzed in October 2020 to capture
166 the most up-to-date DNA sequence library data. Only sequences which closely matched
167 Chlorophyta, Rhodophyta and Ochrophyta seaweeds were included in our analyses. The
168 resulting eDNA presence-absence data for individual seaweed taxa (lowest level possible) in
169 sediments was analyzed in PRIMER 7.0 (PRIMER-E Ltd, Plymouth, UK). Bray-Curtis
170 similarity of presence-absence taxa data was estimated and visualized using Non-metric
171 Multi-Dimensional Scaling (nMDS) plots. Two way-PERMANOVA (Anderson 2014) was
172 then used to test for differences in the taxonomic composition of the sedimentary eDNA pool
173 between sites (inshore and offshore) and over time (offshore site only), using 999
174 permutations. Pair-wise comparisons between any identified groups were assessed using
175 permutational pseudo-t-tests.

Article

Laboratory estimation of macroalgae detritus degradation and sinking rates

To address our second research question, we investigated how the physical properties of degrading seaweed fragments that affect their transport in the wild change over time, upon release from source, and specifically, fragment buoyancy. Four species of macroalgae widely abundant in the shores surrounding Plymouth Sound, and known to contribute to particulate detritus identified at the offshore area sediments(Queirós et al. 2019), were sampled in September 2017 at low water, by hand, from the shore at Rame Head, Plymouth Sound (50°180 41.9″ N 4°130 15.9″ W) via snorkeling. The species sampled were: *Himanthalia elongata* (Linnaeus; Phaeophyceae), *Laminaria digitata* (Hudson; Phaeophyceae), *Saccharina latissima* (Linnaeus; Phaeophyceae), and *Palmaria palmata* (Linnaeus; Floridophyceae). Individuals were immediately returned to the laboratory and held in aerated seawater in the dark, overnight. Unfiltered seawater had been collected at the offshore sampling site on board the RV Quest in the week prior to experiments, and kept in the dark in the PML mesocosm laboratory to avoid autotroph growth, being allowed to adjust to laboratory controlled temperature conditions. On the following day, fragments from central areas of blades of all species and from receptacles (hereafter "straps") of *H. elongata* (devoid of epibionts) were excised from four individuals of each species. Three fragments were cut perpendicularly to the length of the blades and straps from four individuals across the four species (12 total per species), with lengths 2 cm, 5 cm and 10 cm, respectively. All fragment dimensions were recorded along with fresh weights. Sinking velocities were then estimated in a stationary 35 cm seawater column in the laboratory, using the same seawater sampled at the start of the experiments which had been allowed to settle overnight in a large glass tank. Each fragment was placed parallel to, and on top of, the water surface, and time to reach the bottom of the assessment tank recorded. Sinking velocity was estimated by dividing water column height by time of sinking. The fragments were then distributed across 16 x 8 L

seawater aquaria, housing one fragment from each species sampled. Seawater in aquaria was agitated by aquarium pumps of the same make and model across all aquaria, the inlets of which had been covered by a 63 µm mesh to prevent uptake of detritus. All aquaria were held in a seawater bath to minimise temperature differences between aquaria. Bath water was chilled to 16 ^{o}C using an aquarium chiller and agitated via aquaria pumps. This baseline temperature was chosen as it reflects the mean temperature experienced by seabed organisms in Plymouth Sound at this time of year(Queirós, Fernandes, et al. 2015). LED blocks (Biolumen, UK) were fitted to a frame positioned at the top of the seawater bath, and the whole setup covered by PVC sheets to reduce evaporation. LED blocks were programmed to mimic the photoperiod of the collection site at the time of experiments. During incubations, seawater temperature in aquaria was 18.01 +/- 2.44 ^{o}C (mean +/- SD), pH was 8.26 +/- 0.13, and salinity was 34.09 +/- 0.80 psu. The incubations lasted 35 days, at end of which sinking velocity measurements were repeated. Sinking velocities were analyzed using stepwise linear regression model fitting, based on Akaike's Information Criterion in R(R Core Team 2020) (package "MASS"). We tested for three main effects (experimental day, species and fragment length) as well as their first and second order interactions. Linear model assumptions were verified via graphical analyses of residuals and normal QQ plots, with extreme values with high leverage removed. Residuals were moderately right skewed and so were $\log_{10}$ transformed to meet the normality of residuals assumption of the linear model.

Modelling the transport and dispersal of macroalgal detritus in Plymouth Sound

To address our third research question, we used experimental data to parameterize a transport model to reflect the buoyancy of seaweed fragments in the water column. The modelling of macroalgal detritus transport (and thus dispersal) was achieved via a two-step process. First, a fine-scale hydrodynamic model for the area was configured and run; and variables describing the simulated flow field saved to file every hour. An offline particle tracking

Article

model was then used to compute trajectories of initially buoyant detrital particles, based on the outputs of the hydrodynamic model. For this study, we used the Finite Volume Community Ocean Model (FVCOM(Chen, Liu, and Beardsley 2003)), configured for the Plymouth Sound and surrounding coastal area (~ 49.7° – 50.6° N and ~ 4.8° – 3.8° W, Figure S1). FVCOM is a prognostic, unstructured-grid, finite-volume, free-surface, 3D primitive equation coastal ocean circulation model(Chen, Liu, and Beardsley 2003). Vertical turbulent mixing was modelled with the General Ocean Turbulence Model (GOTM) using a κ-ω formulation(Umlauf and Burchard 2005) whilst horizontal mixing was parameterised using the Smagorinsky scheme(Smagorinsky 1963) with a coefficient of 0.1. The unstructured horizontal grid allows variable resolution across the domain to reflect the complexity of the flow and scale of bathymetric features. The resolution of the model is ~600 m at Station L4, becoming finer towards the Plymouth Sound (~85 m), with highest resolution around the upper River Tamar channel (~40 m). The vertical grid is comprised of 24 equally spaced layers in terrain following (sigma) coordinates, allowing water column structure in shallower areas to be resolved in fine detail.

Atmospheric boundary data, including heat fluxes and surface stresses, were generated by downscaling the National Oceanic and Atmospheric Administration's (NOAA) Global Forecast System model, using a 3 level nested configuration of the Weather Research and Forecasting (WRF(Skamarock et al. 2008)) model, yielding a final resolution of 3 km. River input data was taken from the National River Flow Archive (http://nrfa.ceh.ac.uk/data/station). We used river gauge data for 11 rivers within the domain with temperature modelled using a regression model against WRF surface temperatures. Lateral boundary conditions were taken from the Atlantic Margin Model retrieved via the CMEMS service(North West Shelf Monitoring and Forecasting Center 2020), adjusted to the internal tidal solution. FVCOM was run for May 2016, matching the period when eDNA was

Article

sampled at all three field sampling sites. The model simulation was extensively validated against underway ship tracks for this period and against tidal gauge and Acoustic Doppler Current Profiler measurements for a longer period run using the same setup (see Appendix S1). The model was shown to reproduce well the Tamar river plume and salinity structure between the coast and L4 (please refer to the section on model validation in Appendix S1). Particle tracking simulations were then performed using the offline particle tracking model PyLag v0.6(Uncles et al. 2020) (https:// https://github.com/pmlmodelling/pylag). Particles were released from two circular release zones with a radius of 10 m and centered on (-4.22° E, 50.31 ° N) and (-4.14° E, 50.36° N). The two sites are in shallow, near coast waters off Rame Head and within Plymouth Sound respectively, matching shore communities sampled during our laboratory investigation into seaweed degradation and eDNA sampling carried out in this study (Figure 1). All particles were released at the surface, simulating initially buoyant seaweed detritus. To compute the time it takes initially buoyant particles to reach the bed once they start sinking through a turbulent water column, a set of simulations were also performed using input data from the General Ocean Turbulence Model configured for L4 (see Appendix S1).

To compute particle trajectories, the particle tracking model solves the equation:

$$\frac{\partial}{\partial t}\boldsymbol{X}_{\mathrm{i}}(t,\boldsymbol{r}_{\mathrm{i}}) = \boldsymbol{U}_{\mathrm{i}}(t,\boldsymbol{X}_{\mathrm{i}}) \quad (1),$$

where $\boldsymbol{r}_{\mathrm{i}} = \boldsymbol{X}_{\mathrm{i}}(t = t_0)$ is the position vector of particle i at time $t = t_0$, $\boldsymbol{U}_{\mathrm{i}}$ is the particle's velocity vector, and $\boldsymbol{U}_{\mathrm{i}} = [\boldsymbol{u}(t,\boldsymbol{x})]_{\boldsymbol{x}=\boldsymbol{X}_{\mathrm{i}}}$ in the case of passive transport, where $\boldsymbol{u}$ is the fluid velocity vector. The particle velocity vector is broken down into resolved and unresolved components, which are incorporated into a Random Displacement Model of the form:

$$dX_{\mathrm{j}} = \left[u_{\mathrm{j}} + \frac{\partial D_{\mathrm{jk}}}{\partial x_{\mathrm{k}}}\right]dt + (2D_{\mathrm{jk}})^{1/2}dW_{\mathrm{k}} \quad (2).$$

Article

Here, $dX_j = d\boldsymbol{X}$ is the incremental change in a particle's position and D_{jk} is the diffusion tensor. dW_k is an incremental Wiener process that builds stochasticity into the model. Equation (2) is integrated numerically to compute particle trajectories. Velocity and eddy diffusion terms are linearly interpolated in both space and time to particle positions. To simulate the movement of buoyant particles, a restoring function was used to keep detrital particles at the surface over the course of the simulations. Changes in detrital particle buoyancy over time were not modelled explicitly but are interpreted based on our experimental study. Lastly, the contribution of Stoke's drift was not included explicitly; however, a discussion of its likely impact is included in the discussion section. Further details of the run configuration options used with the particle tracking model are provided in the Appendix S1. Details on model configuration with FVCOM inputs can be found in PyLag's documentation (https://pylag.readthedocs.io/en/latest/).

To assess the impact of time varying environmental conditions on seaweed detritus transport, two sets of simulations were run. The first set cover a 14 day period starting on 1st May 2016. The period starts with neap tides and a fresh breeze blowing from the south-west and west. After a few days, the wind weakens and switches to come mainly from the east (Appendix S1: Figure S7c). The second set of simulations cover a 14 day period starting on 16th May 2016. Again, the period starts with neap tides. However, it is characterized by fresh to strong breezes that predominantly come from the south-west and west (Appendix S1: Figure S7d). In each simulation, 10,000 particles are released from each site at 14 consecutive high waters. Particle simulations were run forward for a total of 14 days each, with particle positions saved to file every 15 minutes. Connectivity between the release sites and the offshore L4 benthic sampling site (Fig. 1) was calculated by computing the time of flight to a square of side 2 km centered on L4 benthic (-4.18° E, 50.22° N).

Results

Article

Macroalgal eDNA in sediments

We identified macroalgal eDNA in all areas and all samples (Plymouth Marine Laboratory 2018, Fig. 1). In total, we identified 836 unique operational taxonomic units (OTUs), attributable to 176 species within 34 orders of seaweed (Fig.1c). A higher proportion of OTUs attributed to red seaweed species was always detected at the offshore site Station L4, whilst the inshore sites (Firestone Bay deep and shallow, "FBD" and FBS", respectively) had a comparatively higher proportion of brown macroalgal taxa, including kelp (Fig.1a). The taxonomic composition of seaweed occurring in the sedimentary eDNA pool varied significantly between sites (Fig. 1b; Pseudo-$F_{27,2} = 2.44$, $p_{perm}<0.01$), and between sampling dates (Pseudo-$F_{27,6} = 1.56$, $p_{perm}<0.05$). The latter was primarily due to a changing seaweed composition of the sedimentary eDNA pool at the offshore site, over time, as previously observed(Queirós et al. 2019), and there was no difference in the eDNA pools at the Firestone Bay sites (Fig.1b; t (FBD/FBS) = 1.72, $p_{perm}>0.05$). The offshore site Station L4 is where the highest number of OTUs was recorded throughout.

Macroalgal degradation and sinking velocities

Fragment sinking velocity changed over time, between species, and was size-dependent(Queirós and Pascoe 2020
) (Fig.2). All *H. elongata* fragments, of all sizes, completely degraded within 35 days. All fragments of the 2 cm size group of *S. latissima*, and half of those of this size from *L. digitata* and *P. palmata*, also completely degraded within 35 days. Fragments from *L. digitata* , *P. palmata* and *S. latissima* 5 and 10 cm in length remained viable to the end of the incubations, most with weights slightly increasing over time, as a potential result of fragment growth, as also found by others(Frontier et al. 2021). The fragments from these three species, of all sizes, were negatively buoyant at the start of the incubations, being resuspended by the action of the aquarium pumps and sinking again to the bottom of the aquaria. This was also

observed at the end of incubations. Conversely, *H. elongata* fragments were positively buoyant when fresh (as recorded by others(Jones and Demetropoulos 1968)) at the start of incubations, but became negatively buoyant after 6, 7 and 21 days, for fragments of 2, 5 and 10 cm, respectively. However, as *H. elongata* fragments degraded completely before the end of the 35 day incubations, no sinking velocities were estimated for this species. For the other three species, sinking velocity changed over time, between species, and with fragment size (Fig.2; log10 (sinking velocity) ~ date + species + fragment length + date x species + species x fragment length; R^2= 56.78%. $F_{50,8}$=10.53, p<0.01). Fragment length generally decreased sinking rates (β = -0.02 , p < 0.01), but the reverse was true for *P. palmata* (Fig. 2, β = 0.05 , p < 0.01). The pattern of velocities was different at the start and end of incubations, but changes differed among species, with a sharper decrease in velocity for *P.palmata* over time than for other species (Fig.2). Potential differences between species in how mechanical properties of fragments may have changed over time may thus have been important. The overall mean sinking velocity over these three species, over the tested fragment size, was estimated at 1.98 ± 0.78 $cm.s^{-1}$ (mean ± standard deviation).

Tracking trajectories of macroalgal detritus using Lagrangian particle tracking

Experimentally derived mean sinking seaweed fragment velocities were used to interpret the results from the particle tracking modelling. Based on these, 1D GOTM simulations (Fig. 3) indicate that initially negatively buoyant seaweed detritus (e.g. *L. digitata* , *P. palmata* and *S. latissima*) would sink and reach the seabed for the first time within one hour (Fig.3b), and thus very likely near their source seaweed community around the Plymouth shore. The effect of turbulent mixing in the water column results in a spread of sinking times, but this is generally small (of the order of minutes, Fig. 3b). However, for buoyant seaweed detritus (e.g. *H. elongata*), initial transport along the surface of the water column could allow them to quickly reach waters further along the shore, or offshore, before sinking to the seabed for the

first time (Fig. 4). Based on our experimentally-derived estimates for the time taken for *H. elongata* fragments to become negatively buoyant (i.e. 6-21 days), our Lagrangian modeling suggests that initial transport in the water column would take detritus 10-20 km along the coastline and offshore before sinking to the seabed for the first time (Fig. 4). However, the net direction of this transport and the proportion of detritus retained inshore before reaching the seabed was strongly dependent on the release site and environmental conditions experienced during that period. Specifically, in simulations starting in early May (Fig.4a, c), when winds were mainly from the south-west and west (Appendix S1: Figure S7), particles initially tracked east, inshore, from both sites. However, this motion was reversed after two days when the wind weakened and switched to come mainly from the east. Following this period, and with the switch from neap to spring tides, particles then tracked west near the coast. After a week, there was a clear accumulation in Whitsand Bay for particles released from both Plymouth Sound and Rame Head (Fig. 4a, c), and the particles continued to track west out of the domain. In contrast, particles released during neap tides later in May rapidly track east and south-east (Fig. 4b, d), moving out of the domain after a few days. In both sets of simulations, a fraction of the particles released inside Plymouth Sound became trapped, with some remaining within Firestone Bay (where the inshore sites we sampled are located) for several days. This trapping of particles may be partially explained though the simulation of particle beaching and resuspension events in the intertidal zone, slowing the passage of particles out of Plymouth Sound. For the particle releases in early May, from both release sites, very limited connectivity with Station L4 was observed (the offshore eDNA sampling site, Fig.4a, c). In contrast, for particles released in mid to late May when the wind was predominantly blowing from the south-west and west (Fig. 4b, d), stronger connectivity with the offshore L4 station was estimated. This was true for particles released from both sites. Indeed, during this period of strong winds from the south-west and west, and spring tides,

lead particles reached Station L4 in just 1-2 days, and by 6 days (the shortest amount of time taken for *H.elongata* fragments to become negatively buoyant during experiments) more than 10% of the particles had passed over the site in single releases (Fig.5a-b). Under these conditions, L4 became a potential sinking site for seaweed detritus released from both sites, whilst under tidal and wind patterns experienced earlier in the month, this was unlikely. The impact of the wind on particle transport is consistent with the findings of (Uncles et al. 2020) where the relative effect of the wind and the tide on sediment transport in the same area was investigated. Seaweed detritus staying buoyant for 21 days (the longest period observed for *H. elongata* fragments, during experiments) had moved outside of the modelled domain (not shown) under the conditions investigated.

Discussion

The presence of macroalgal detritus within sediments (indicated via eDNA sampling) was ubiquitous across our study region. Indeed, seaweed detritus was found within sediments located at the inshore and offshore sites, inside and outside vegetated habitats. Our modelling simulations, and our experimental assessments, suggested that, for some seaweed species, a portion of detritus which is negatively buoyant upon release may be accessible to the seabed very close to source. That from other species (such as *H. elongata*), being initially buoyant, may reach significant distances before reaching the seabed for the first time. These differences between species indicate that in the wild, where seaweed communities are composed of many species, detritus should be expected to exhibit different transport pathways (horizontally and vertically) across the water column, reflecting its source and physical properties. As detritus degrades over time, changing in size and buoyancy, so should sinking velocities be expected to change, with path complexity increasing over time, and driven also by local hydrodynamics. Here, we explored the effects of tides and wind patterns specifically on the connectivity between detritus source population and the seabed, but it is

399 likely that other sources of environmental variability will play a key part in determining the
400 exact transport pathways. This will, in turn, depend on the specific detritus production
401 ecology of each species population(Queirós et al. 2019). Studies such as this one, including
402 observational, experimental and modelling data can help understand net detritus transport
403 pathways, and in future, inform potential hotpots for seaweed detritus accumulation. What is
404 clear, is that sedimentary sinks for this detritus are likely located not just in the deep ocean,
405 but also in the coastal ocean.
406 eDNA from species producing initially negatively buoyant detritus was found in inshore as
407 well as offshore sediments. This indicates that at least part of this detritus that reaches the
408 seabed for the first time very close to source, will become resuspended and travel further
409 offshore in subsequent events of deposition and resuspension (i.e. "saltation"), just as we
410 observed during experiments, when the water housing seaweed fragments was agitated by
411 aquarium pumps (cf. stationary conditions during which sinking velocities were measured).
412 Seaweed detritus taxonomic composition in inshore environments thus likely reflects more
413 closely that of local species, with predominantly negatively buoyant detritus upon release,
414 whilst detritus reaching the seabed further offshore will likely originate from both groups of
415 species. This was corroborated by a lower taxonomic diversity and greater similarity of
416 seaweed eDNA found in inshore sediments than that found in offshore sediments, with the
417 later potentially reflecting the ecology and release dynamics of seaweed populations from a
418 comparatively larger source pool, as previously suggested(Queirós et al. 2019).
419 Furthermore, pathways leading to carbon sequestration into the seabed compartment will be
420 affected by the specific biogeochemical properties of each sedimentary site, varying in space
421 and time(Bianchi et al. 2018; Snelgrove et al. 2018; Queirós et al. 2019). Identifying the
422 location of the seabed sinks of seaweed particulate organic carbon (released as detritus)
423 could invaluably aid the design of management activities aiming to protect blue carbon

habitats from disturbance, and thus support climate change mitigation(Mcleod et al. 2011; Herr, Pidgeon, and Laffoley 2012). Given the findings presented in this study, the identification of those sites should thus require careful consideration of a number of processes. Specifically: local and regional-scaled hydrodynamic conditions; regional seaweed species composition and detritus release ecology; as well as the spatial and temporal dynamics of biogeochemical processes affecting seabed carbon fluxes at identified sedimentary sites. As all of these properties are strongly modified by climate change driven alteration of the marine ecosystems(Bianchi et al. 2021; Smale and Vance 2015; Ravaglioli et al. 2019) , protecting sedimentary sinks of seaweed particulate organic carbon will also require the identification of sites where carbon sequestration processes are climate-resilient or increasing over time(Queirós et al. 2021).

Protecting sedimentary sinks of seaweed blue carbon

The three lines of evidence explored here jointly suggest that particulate seaweed detritus may be broadly available for uptake in coastal sediments, where the largest proportion of macroalgal production is also expected to remain(Krause-Jensen and Duarte 2016). If this is also true in other coastal regions near macroalgae beds (potentially, 28% of shores globally(Feehan, Filbee-Dexter, and Wernberg 2021)), and given the high productivity of seaweed, then it is possible that macroalgae may drive a much larger blue carbon capability than that traditionally recognized by global carbon models or protected by blue carbon policies around the world, currently focused on wetlands(Sutton-Grier and Howard 2018) (Fig.6). Research in our study region contemporary to the present study demonstrated that the presence and taxonomic composition of seaweed eDNA in sediments reflected the ecology of seaweed detritus from the surrounding shores, which in turn was reflected in the proportion of seaweed carbon contributing to sedimentary carbon pools over the year(Queirós et al. 2019). The ubiquitous presence of seaweed eDNA within sediments in the broader region

studied here, both inshore and offshore, suggests that sequestration of seaweed organic carbon into sediments, whilst potentially peaking in specific periods of the year(Queirós et al. 2019), may remain within sediments beyond the seasonal cycle. And while long-term organic carbon sequestration is unlikely to occur in the most dynamic areas of the coastal ocean, the conditions necessary for net carbon sequestration are found across many coastal and ocean shelf soft-sediment habitats(Gattuso, Frankignoulle, and Wollast 1998; Widdicombe and Somerfield 2012) (e.g. fjords(Smeaton et al. 2017), muddy seabed). Furthermore, long travel periods across the water column, from the shore to the deep ocean, reduce the organic carbon loading of particulate detritus(Bianchi et al. 2018). These aspects challenge the often held view that organic carbon sequestration may be limited to the deep sea in the open ocean(Krause-Jensen and Duarte 2016), or to wetland habitats(Sutton-Grier and Howard 2018). Indeed, particulate organic carbon (POC) sequestration hotspots occur also elsewhere, wherever high net deposition of organic material, high burial rates, low bed shear and scarcity of biogeochemical oxidants (such as oxygen) are observed near and within the seabed(Krause-Jensen and Duarte 2016). What's more, it is known that POC sequestration hotspots are globally concentrated in soft sediments on the ocean's coastal margin, outside of vegetated habitats(Krause-Jensen and Duarte 2016). And as shown here, the pathways connecting seaweed particulate detritus to the seabed appear to be highly dynamic and to also include coastal sediment areas, inside and outside vegetated habitats. Together with the published evidence basis, our findings suggest that coastal and shelf macroalgal organic carbon sinks likely exist. Further field verification of carbon fluxes at sites identified using the methodologies employed here is now needed. Protecting those potential sinks, along with their sources, could therefore become a viable strategy to expand the proportion of global ocean falling under blue carbon activities in the near future (Fig.6)(Kuwae and Crooks 2021; Queirós et al. 2019).

Article

Recent research has suggested protection of vast areas of the ocean toward the conservation of blue carbon may be needed. But verification of realized carbon fluxes (and those of other greenhouse gases) and/or an estimation of avoided emissions are a necessary steps of blue carbon policy implementation(Needelman et al. 2018). As verification will be highly challenging in the deep sea, as will be the enforcement of protection of sites in areas beyond national jurisdiction (ABNJ), investing in the protection of those sites will likely bring uncertain climate change mitigation value. In turn, the ocean's coast and shelf are where the world's marine protected areas (MPAs) are already concentrated(UNEP-WCMC and IUCN 2020). Understanding the potential macroalgae carbon sequestration value of already designated sites within national waters, or seeking the conservation of additional coastal and shelf sites potentially identified in the future (as suggested here) as blue carbon activities, could thus present a comparatively more certain and easier route to enhance the ocean's role as a carbon sink. Supported by the type of science presented here, and with further field verification of carbon flows, the current ambition to extend the world's protected areas to 30% of the ocean by 2030(CBD 2010) could provide the correct impetus to deliver nature-based solution helping to mitigate climate-change(Austin et al. 2021). The pace of climate change justifies this action(IPCC 2019, 2021). However, field measurements of the ecosystem processes that drive carbon flows across ecosystems (seaweed particulate and dissolved organic carbon production, POC and DOC); net sedimentary uptake (dissolved inorganic production and POC uptake); carbon dating studies; and crucially, carbon source partitioning studies (e.g. bulk and compound specific stable isotope analyses)(Queirós et al. 2019) remain rare heretofore.

Verifying these processes with field measurements of flows at sources and sedimentary sinks could provide a necessary evidence basis to support a policy development boost toward the conservation of macroalgal carbon donor and sink habitats, including natural communities as

well as farmed seaweed(Kuwae and Crooks 2021) (Fig.6). Protecting and enhancing sources and sinks together, alongside a potentially booming global seaweed farming industry, could provide, in tandem, important outcomes for blue growth. Whilst protecting macroalgal carbon donor and sink habitats contributes to United Nations Sustainable Development Goals 13 and 14(United Nations 2015) ("SDG", limit climate change and protect life under water, respectively), an informed expansion of the seaweed industry could be harnessed in this way too, helping to deliver on those aims, as well as further supporting the delivery of SDG2 and 5 (alleviate poverty, gender equality, respectively)(United Nations 2015). For instance, in the Western Indian Ocean region, seaweed farming is a socially valuable activity because it is primarily undertaken by women, and their key livelihood(Msuya 2012).

The importance of capturing ecosystem connectivity within Marine Protected Areas and other effective area-based conservation measures' design has been previously recognized for other purposes(Carr et al. 2017). Capturing also the connectivity of macroalgae organic carbon donors and sinks within such mechanisms could potentially greatly expand the global ocean's blue carbon capability harnessed within conservation areas(Queirós et al. 2019). Further field verification of macroalgae detritus transport pathways elucidated via modelling shown here, and a close collaboration with practitioners, may help to guide the development of the next stage of blue carbon research. This should now seek to provide policy makers with needed, field-based carbon flow rate measurements (and of their variability) for spatially explicit carbon sources and sinks. Such evidence would allow for much needed, improved ocean carbon accounting, which should in turn be used to inform the design of future-proofed, and actionable, blue carbon conservation mechanisms.

The next frontiers in macroalgal blue carbon research supporting conservation

Article

A recent field data provided evidence that macroalgal detritus can travel a substantial distance from source locations[31]. The data presented here supports this view, suggesting that, in a given site, macroalgal beds contributing to a detritus pool available to sediments may be located both local and at far-afield locations. Differences in the sedimentary eDNA pools analysed here, varying over time and space, indicated potentially different dynamics of detrital connectivity and transport from sources to sediments. To our knowledge, this is the first study employing Lagrangian particle-tracking in this context. We illustrated the importance of environmental conditions, and their effects on hydrodynamic patterns, in establishing connectivity routes between seaweed communities exporting detritus to different areas of the seabed. However, longer model simulations, the inclusion of missing processes such as saltation, Stoke's drift, and the refinement of simulated particle properties to better reflect observed changes in seaweed detritus attributes over time, will be required to identify long-term, macroalgal detritus accumulation sites. Other processes still, about which we know very little, will further affect these transport pathways, including: the detritus release ecology of source species; the mechanical properties of the released detritus (e.g. autumn, wave-driven whole detachment cf. loss of small, degraded fragments over time); and the balance between fragment viability during transport and degradation(Queirós et al. 2019; Frontier et al. 2021). As recently found by others(Frontier et al. 2021), our experiments also suggest that macroalgal fragments may remain viable for long periods after export from their source. This, in turn, may extend transport time and support long travel distances for macroalgal fragments(Filbee-Dexter et al. 2018).

The use of eDNA as evidence of the presence of a macroalgal signature within sea-bed habitats is growing. It is unarguably an invaluable tool to track the transfer of macroalgal detritus from shore to seabed, and can offer a more detailed taxonomic discrimination of taxa present than other techniques. This provides important evidence that helps understand the

548 ecological processes underpinning macroalgal blue carbon(Ortega, Geraldi, and Duarte 2020;
549 Queirós et al. 2019). However, given the spatial and temporal contextual specificity of the
550 seabed processes that determine carbon sequestration rates(Queirós et al. 2019; Legge et al.
551 2020; Snelgrove et al. 2018), and the dynamic nature of transport pathways connecting
552 macroalgal beds to potential sedimentary carbon sinks sites, it seems ill-advised to expect that
553 any site specific relationship between sedimentary macroalgal eDNA and POC stores should
554 be expected to hold ubiquitously(Ortega et al. 2019; Anglès d'Auriac et al. 2021).
555 Linking macroalgal carbon sources and sinks is, at least in part, a biotracing problem, and
556 biotracing in natural ecosystems typically requires more than one technique to be employed,
557 given the uncertainties of each approach(Nielsen et al. 2018). For instance, using a
558 combination of Bayesian stable isotope mixing modelling and seabed process measurements,
559 a previous study established that macroalgal eDNA in sediments at our offshore site appeared
560 to reflect the seasonal ecology of both source populations and the seabed habitat(Queirós et
561 al. 2019). And as with any technique, it must be acknowledged that a suite of validation and
562 optimization experiments are also necessary to fully exploit the usefulness of eDNA in such
563 environmental studies, now and into the future. For instance, and as done here, sample
564 collection and preparation must be optimized (*e.g.* sediment volumes and choice of DNA
565 extraction methods specifically designed for difficult to lyse seaweed fragments). Secondly,
566 the choice and design of PCR primers should always be scrutinized. Because macroalgal blue
567 carbon science is in its infancy, in the present study, as in others(Ortega et al. 2019; Ortega,
568 Geraldi, and Duarte 2020), universal 18S rRNA PCR primers that amplify short (~260 bp)
569 DNA fragments have been used to enable the detection of as wide a range of macroalgal taxa
570 as possible, but these offer limited taxonomic resolution for some taxa. Advances in DNA
571 sequencing technology that enable sequencing of longer DNA fragments will provide more
572 detailed identification(Anglès d'Auriac et al. 2021). Together with the population of public

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DNA databases with sequences of as many taxa as possible, the accuracy of taxonomic identification via eDNA studies will also increase(Queirós et al. 2019). Thirdly, and crucially, the potential use of eDNA to assess the prevalence and diversity of macroalgae detritus within sediments requires robust understanding of the persistence of eDNA, and the factors controlling macroalgal detritus degradation and eDNA decomposition, both of which we are only beginning to investigate as a community. Combining eDNA analysis with other approaches, such as carbon sequestration rate measurements and carbon source partitioning via stable isotope techniques, is thus likely to provide a more robust evidence basis necessary to inform the potential need to develop macroalgal blue carbon activities. For these reasons we should not, and cannot, build better carbon accounting or improve global biogeochemical modelling based on eDNA data alone. Finally, the argument for conserving macroalgal carbon sequestration sites (Fig.6) requires us to think about long-term sequestration, and thus also about the sensitivity of these sites and carbon flows to climate change(Ravaglioli et al. 2019). Investing in blue carbon conservation without acknowledging these effects is thus unlikely to produce tangible climate change mitigation. This too requires further work.

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Figure captions

Figure 1: The composition of eDNA in sedimentary samples, from the three sampled sites: the inshore sites are Firestone Bay "shallow" ("FBS") and Firestone Bay "deep" ("FBD"); the offshore site is station L4. a) Pie charts give the mean relative seaweed sequence abundance per class and sampling site and time point (3-4 replicates, except for May 2016 at L4, when there was only 1 replicate). Pie chart shading reflects the proportion of sedimentary eDNA sequences retrieved from macroalgae classes: Compsopogonophyceae (light pink); Bangiophyceae (pink); Florideophyceae (red); Phaeophyceae (brown); and Ulvophyceae (green). b) similarity of sedimentary eDNA sequences for seaweed per site, with inshore sites separating from the offshore site. c) seaweed taxa diversity per time point and sampled area, showing that sedimentary eDNA at inshore sites corresponds to a lower number of seaweed taxa than that found offshore.

Figure 2: The sinking velocity of seaweed fragments, at the start (a) and end (b) of 35 day incubations.

Figure 3: 1D simulations of seaweed detritus settling out through a turbulent water column. Results are generated using the particle tracking model PyLag coupled to GOTM, using a configuration for Station L4 in the WEC (see Appendix S1). Diagram (a) illustrates the sinking of (green) seaweed fragments over time (t). Insert plot (b) shows the estimated fraction of particles remaining in the water column as a function of time, for a range of fixed particle sinking velocities. The average measured sinking velocity of blade/strap fragments in the laboratory was 0.019 ± 0.008 m.s^{-1}. In each case, 10,000 particles were released from the surface of the water column at midnight on 1st May 2021. The depth of the water column is 50 m.

Figure 4: Simulated spatial distribution of buoyant seaweed fragments released from Plymouth Sound (a, b) and Rame Head (c, d) under contrasting environmental conditions

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(please see Fig. 1 for release site location). In each case, 1000 particles are released at high water from the two sites, starting at 1215 on 1st May 2016 (a, c) and 0100 on 16th May 2016 (b, d). A further 1000 particles are released at each subsequent high water. Particle positions are plotted at 09:45 on the 8th May 2016 (a, c) and at 21:15 on 22nd May 2016 (b, d), corresponding to a time three hours after high water following the 14th release of particles (see also Fig. S7b). Station L4 is identified with a star.

Figure 5: Histograms showing the time taken ("time of flight") for buoyant particles to reach L4 station after release from Plymouth Sound (a) and Rame Head (b). Simulations were carried out during the second half of May 2016, during a period of strong southerly winds. Results are based on the full ensemble of runs (14 members, 10,000 particles released per member per release site). The 14 releases were performed at consecutive high waters starting at 01:00 on 16th May 2016. The time of transport is computed from the difference between the release time and the first time point at which the particle is observed in the box bounding the L4 benthic sampling site (SI Fig. S7a).

Figure 6: In habitats typically captured by blue carbon conservation schemes (saltmarsh, seagrass meadows and mangroves), CO_2 is fixed in the same area where organic carbon is sequestered (a), so that protected habitat patches deliver the whole blue carbon process ($C_{org\ source}$ and $C_{org\ sink}$). Protecting connected macroalgal-sediment blue carbon (b) requires the protection of highly productive macroalgal communities where CO_2 is fixed into the living biomass ($C_{org\ source}$) as well as the seabed hotspots of sequestration where exported macroalgal organic carbon sinks ($C_{org\ sink}$) after transport across the coastal ocean.

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Figures

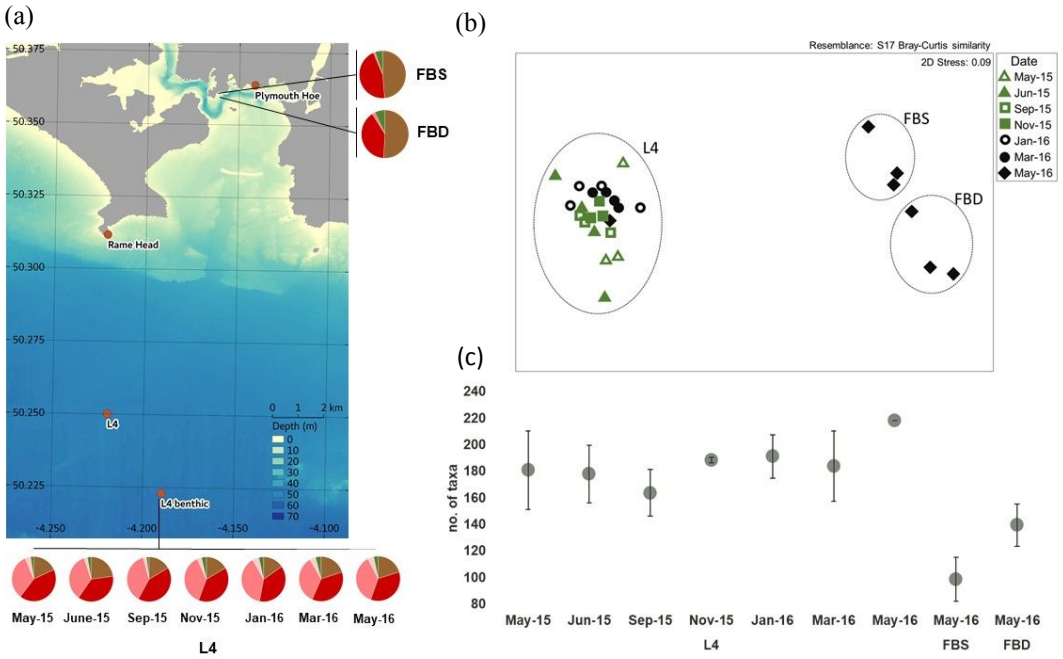

Figure 1

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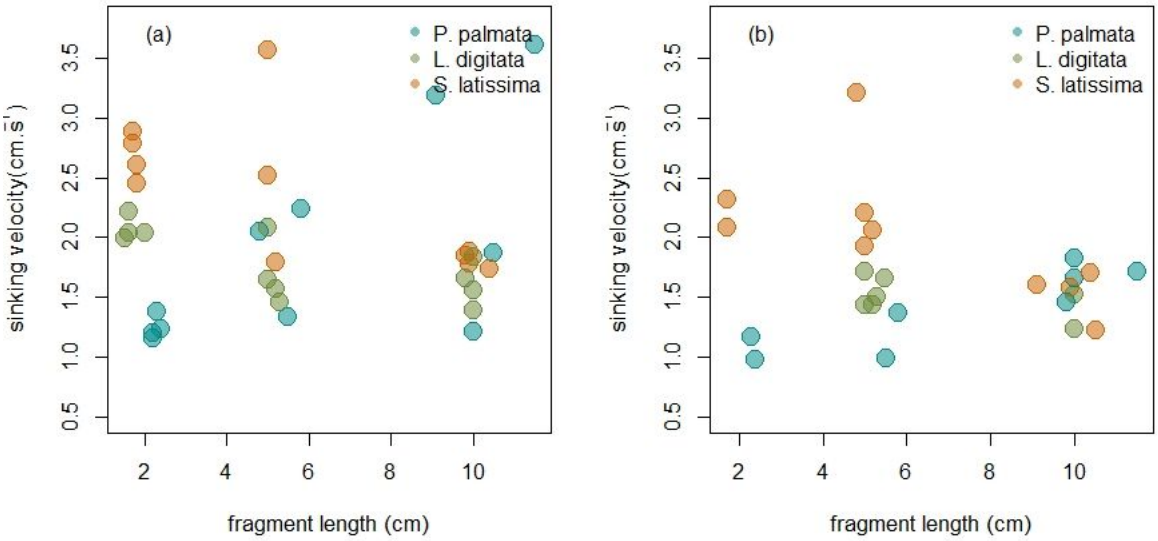

Figure 2

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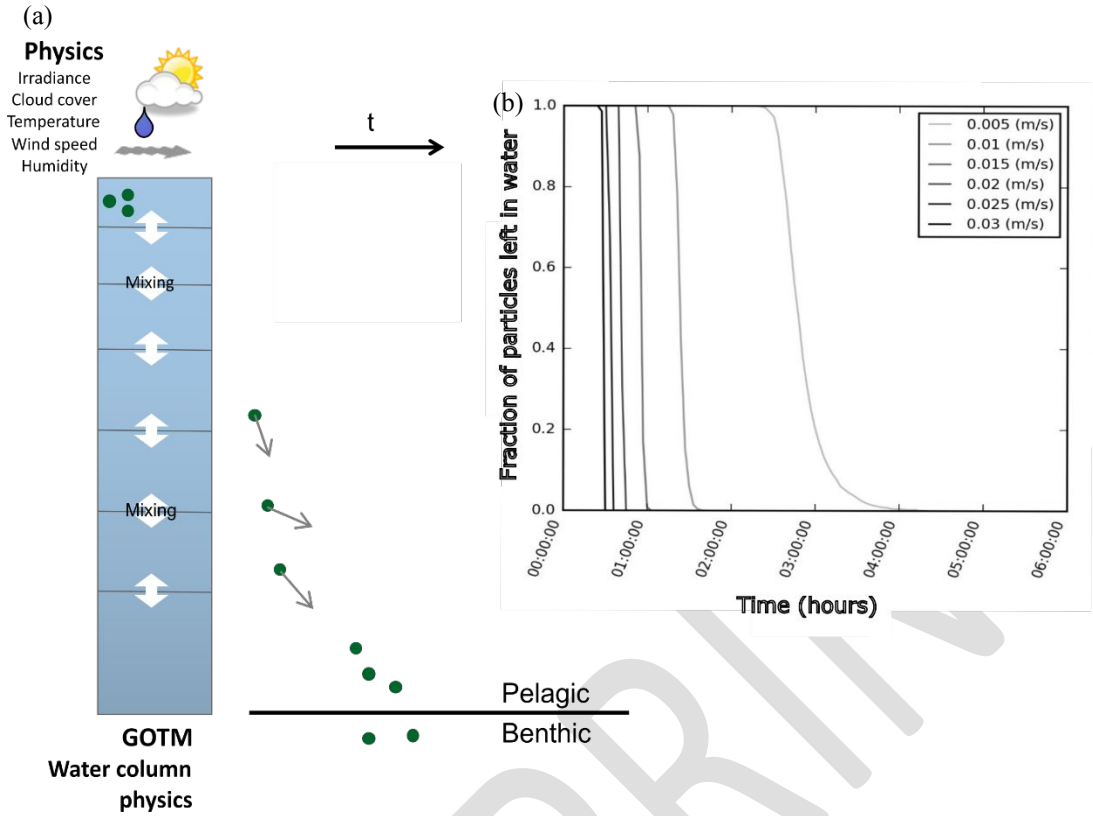

Figure 3

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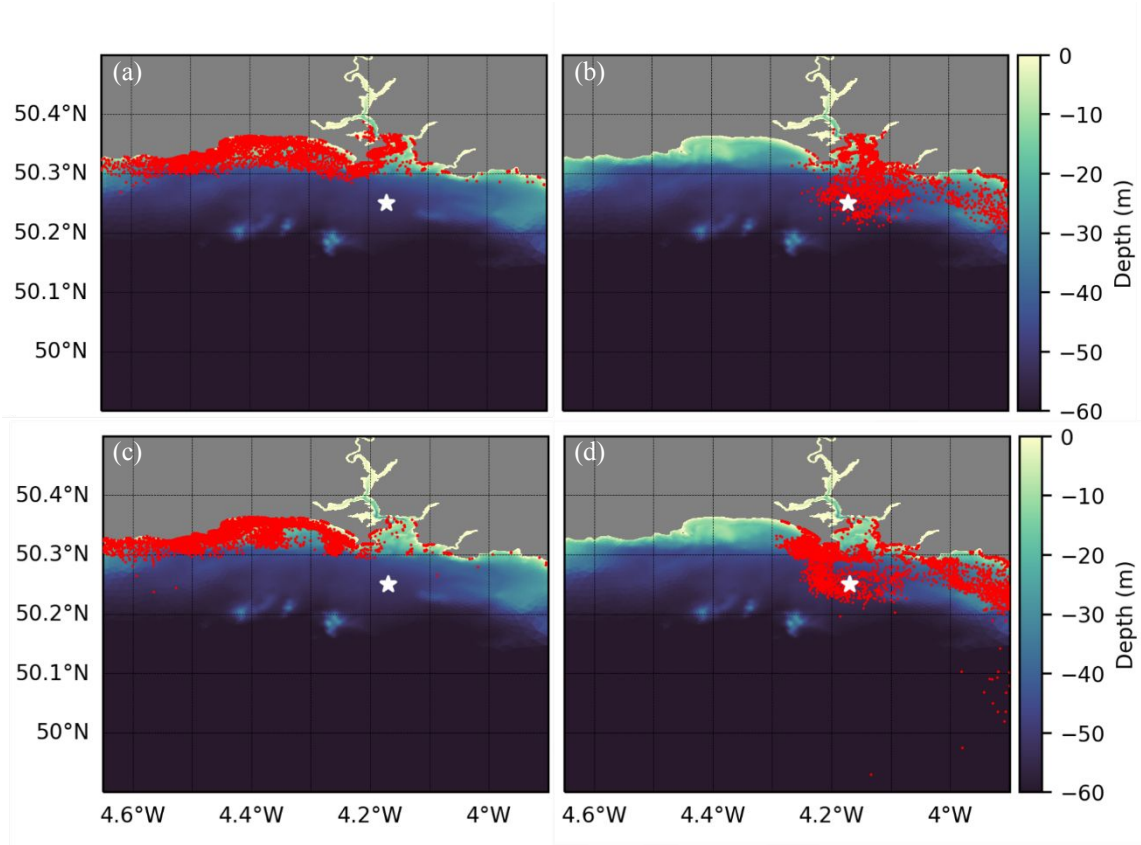

Figure 4

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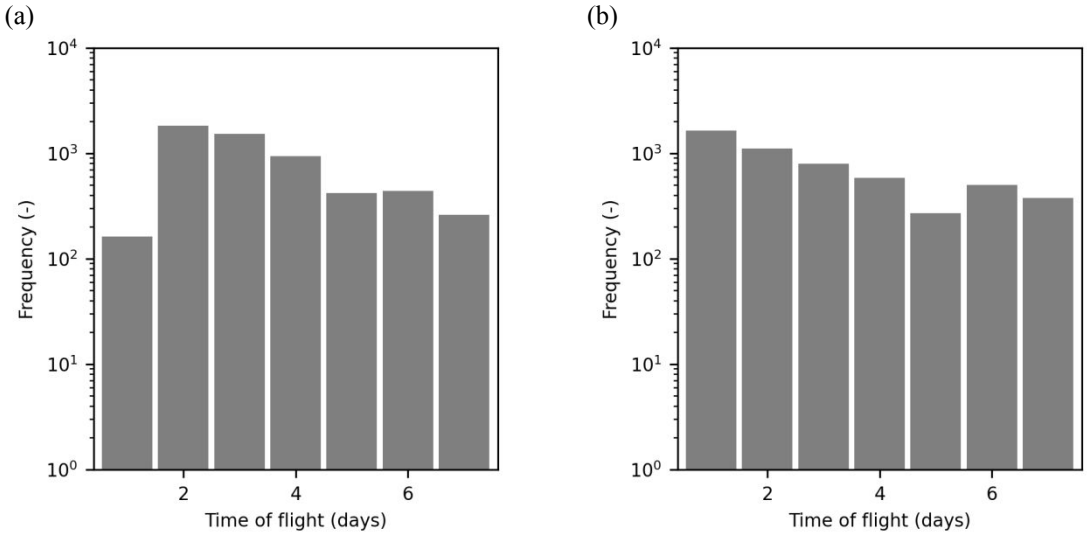

Figure 5

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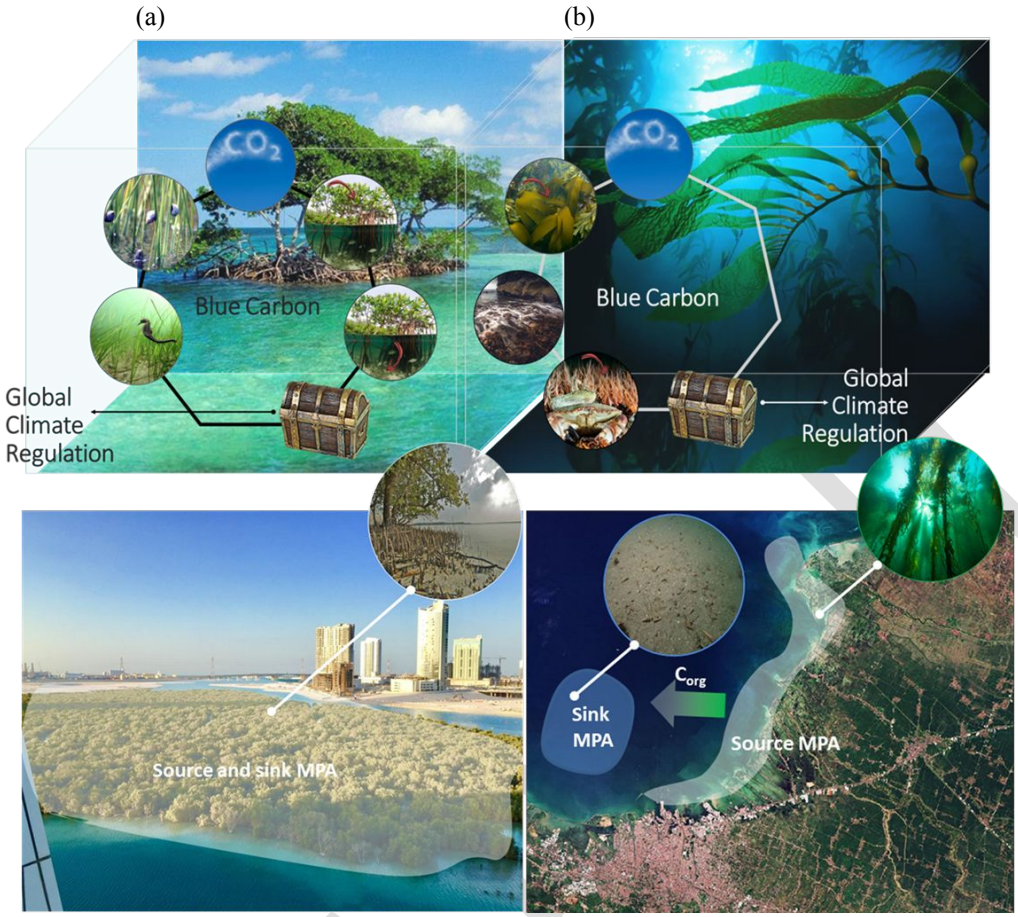

Figure 6