



Macroalgal mat species diversity, composition, and seasonality at four coastal sites across the English Channel/La Manche region

Annesia L. Lamb, Daniel J. Franklin, Sinéad Morris, James R. Sokolnicki, Ronan Sulpice, Antoine Fort, Masami Inabi, Sophie Richier, Anthony Le Bris, Stéphanie Lemesle, Anne-Marie Rusig, Isabelle Mussio, Andrew van der Schatte Olivier, Zoe Morrall & Gordon Watson

To cite this article: Annesia L. Lamb, Daniel J. Franklin, Sinéad Morris, James R. Sokolnicki, Ronan Sulpice, Antoine Fort, Masami Inabi, Sophie Richier, Anthony Le Bris, Stéphanie Lemesle, Anne-Marie Rusig, Isabelle Mussio, Andrew van der Schatte Olivier, Zoe Morrall & Gordon Watson (02 Jun 2025): Macroalgal mat species diversity, composition, and seasonality at four coastal sites across the English Channel/La Manche region, European Journal of Phycology, DOI: [10.1080/09670262.2025.2500007](https://doi.org/10.1080/09670262.2025.2500007)

To link to this article: <https://doi.org/10.1080/09670262.2025.2500007>



© 2025 The Author(s). Published by Informa UK Limited, trading as Taylor & Francis Group.



[View supplementary material](#)



Published online: 02 Jun 2025.



[Submit your article to this journal](#)



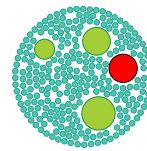
Article views: 196



[View related articles](#)



[View Crossmark data](#)



Macroalgal mat species diversity, composition, and seasonality at four coastal sites across the English Channel/La Manche region

Annesia L. Lamb ^a, Daniel J. Franklin ^a, Sinéad Morris ^a, James R. Sokolnicki^a, Ronan Sulpice ^{b,c}, Antoine Fort ^{c,d}, Masami Inabi ^c, Sophie Richier^e, Anthony Le Bris^e, Stéphanie Lemesle^f, Anne-Marie Rusig^{f,g}, Isabelle Mussio^{f,g}, Andrew van der Schatte Olivier ^h, Zoe Morrall^h and Gordon Watson ^h

^aDepartment of Life and Environmental Sciences, Faculty of Science and Technology, Bournemouth University, Poole BH12 5BB, UK; ^bPlant Systems Biology Lab, School of Chemical and Biological Sciences, Ryan Institute & Maree Centre, University of Galway, Galway, Ireland; ^cPristine Coasts Ltd, Galway, Ireland; ^dDepartment of Bioveterinary and Microbial Sciences, Technological University of the Shannon, Midlands, Limerick, Ireland; ^eCentre d'Etude et de Valorisation des Algues (CEVA), Pleubian, France; ^fLaboratoire de Biologie des Organismes et Ecosystèmes Aquatiques (UMR 8067 BOREA), Muséum National d'Histoire Naturelle, CNRS, IRD, Sorbonne Université, Université des Antilles, Université Caen-Normandie, Caen F-14032, France; ^gCentre de Recherche en Environnement Côtier - Station Marine - Université de Caen-Normandie, BP49, 54, rue du Docteur Charcot, Luc-sur-Mer BP49, 54, rue du Docteur Charcot, France; ^hInstitute of Marine Sciences, School of the Environment and Life Sciences, University of Portsmouth, Portsmouth PO4 9LY, UK

ABSTRACT

Seaweed mats are a consequence of eutrophication in coastal waters and can have negative ecological impacts. Consequently, many European environmental assessment frameworks (e.g. the Water Framework Directive, Marine Strategy Framework Directive) monitor seaweed mat biomass. *Ulva*, commonly referred to as sea lettuce, is often assumed to be the dominant taxon, but mats can contain multiple *Ulva* species, and other taxa, and within-mat diversity is often poorly known. Understanding the composition of seaweed mats has implications for nutrient removal from coastal waters because seaweeds uptake and store nutrients differently between species, time of year and location. The use of traditional molecular methods to identify seaweed species cannot easily be applied to mats. In contrast, with the development of Next Generation Sequencing and Cleaved Amplified Polymorphic Sequences assay, a bulk sampling approach for monitoring the seaweed species within mats can be applied. Here, we applied this bulk sampling approach to monitor seaweed species at four sites: three estuarine sites containing mudflats and one exposed sandy site across the English Channel/La Manche region that historically and currently have occurrences of seaweed mats. We assessed variability between sites with respect to biomass, entrainment, species composition and seasonality. The highest mat abundance was found at Holes Bay, Poole, UK and entrainment or burial of seaweed within the sediment was found at two sites, Holes Bay and the Ledano Estuary, France, correlating with similar sediment types and high seaweed biomass. Foliose *Ulva lacunculata* dominated at Holes Bay, while Langstone Harbour, Portsmouth, UK had many tubular and filamentous green species and one brown filamentous species. At the two French sites we identified foliose *Ulva* species. This study demonstrates the high seaweed species diversity and biomass that can be found within macroalgal mats, information that will be important in the refinement and development of model-based nutrient removal estimates as part of nutrient mitigation and management strategies.

HIGHLIGHTS

- We demonstrate a novel approach to the assessment of seaweed mat diversity.
- High mat-forming potential and dominance of *Ulva lacunculata* was measured at Holes Bay and *Ulva* species diversity characterized at all locations.
- Mat biomass and entrainment varied significantly with environmental conditions and between locations within close proximity to each other.
- We highlight the importance of consistent monitoring of seaweed species, biomass, per cent cover and entrainment to enhance coastal marine management efforts.

ARTICLE HISTORY Received 31 October 2024; Revised 17 April 2025; Accepted 22 April 2025

KEYWORDS Diversity; ecosystems; estuaries; macroalgal mats; nutrients; *Ulva*

Introduction

High nutrients in coastal estuaries tend to favour seaweed (macroalgae) growth, which may lead to accumulations and the formation of mats (Valiela *et al.*, 1997; Teichberg *et al.*, 2010). Seaweeds occurring in heavily nutrient-impacted estuaries tend to be

annual, dominating perennial seaweeds attached to substrate, and as growth continues, detachment occurs (Littler & Littler, 1981; Valiela *et al.*, 1997; Kletou *et al.*, 2018). Green seaweeds (Chlorophyta) such as the genera *Chaetomorpha*, *Cladophora*, and *Ulva* tend to bloom in excess during the summer when light and temperature are favourable (Lüning,

CONTACT Daniel J. Franklin dfranklin@bournemouth.ac.uk

© 2025 The Author(s). Published by Informa UK Limited, trading as Taylor & Francis Group.

This is an Open Access article distributed under the terms of the Creative Commons Attribution-NonCommercial-NoDerivatives License (<http://creativecommons.org/licenses/by-nc-nd/4.0/>), which permits non-commercial re-use, distribution, and reproduction in any medium, provided the original work is properly cited, and is not altered, transformed, or built upon in any way. The terms on which this article has been published allow the posting of the Accepted Manuscript in a repository by the author(s) or with their consent.

1993; Valiela *et al.*, 1997; Smetacek & Zingone, 2013; Wang *et al.*, 2015; Bermejo *et al.*, 2019). These genera are thought of as the dominant opportunistic seaweeds in the mats that occur in temperate estuaries and can be found detached from the substrate or entrained (buried) in muddy, intertidal sediment. Loose seaweed can be mobile, leading to high variability in accumulation and entrainment in the sediment, usually defined as >3 cm depth (Witt, 2022), which is thought to be an important overwintering mechanism in some species, enhancing the likelihood of blooms occurring in the spring and summer months (Gonzalez *et al.*, 2013; Robertson & Savage, 2018).

Seaweed mats can cause seagrass, salt marsh, and benthic invertebrate declines as well as decreased water quality (Valiela *et al.*, 1997; McGlathery *et al.*, 2001; Thornton, 2016). Mat domination can blanket other ecologically important communities, inhibiting light, causing changes in oxygen concentrations in the water and sediment, and can enhance potentially harmful sulphide concentrations (Gamenick *et al.*, 1996; Raffaelli *et al.*, 1998). Nutrient requirements in seaweeds are well known experimentally and can be helpful to identify nutrient-loading reduction targets with the idea that reductions in nutrient loads will reduce macroalgal production (Atkinson & Smith, 1983; Fujita *et al.*, 1989; Hernández *et al.*, 2008). The Water Framework Directive (WFD, 2000/60/EC) and the Marine Strategy Framework Directive (European Commission, 2008; MSFD, 2008/56/EC) are part of European Union legislation that requires governing agencies to monitor ecological and water quality parameters within estuaries and transitional waters (Witt, 2022) and are mirrored globally in other environmental management frameworks. The primary purpose of the WFD and MSFD are to monitor the ecology of a water body to determine where action is needed to enhance the function of the ecosystem and to promote good ecological status. Seaweed mats are monitored (with some national variations into what types are assessed) as a metric of the WFD framework as mats can cause harm to an ecosystem if at high biomass concentrations. However, for consideration of water body status (e.g. good, poor) other parameters are considered such as per cent biomass cover of affected area (AA) as a proportion of the available intertidal habitat (AIH) or area of biomass in the system, and nutrient concentrations in the water column and tributaries. The measurement of these parameters allows for a whole system approach to assessing impacts of seaweeds on the ecosystem (WFD, 2000; Scanlan *et al.*, 2007; Perrot *et al.*, 2014). In many European coastal water bodies, seaweed species compositions are not monitored routinely, and therefore an important understanding of nutrient storage between

species and the mats is not assessed for possible bioremediation methods. Recent Korean monitoring efforts, e.g. Han *et al.* (2023) based on a previously defined ecological index (Orfanidis *et al.*, 2011), assess informative characteristics of seaweed mats that aid understanding of the mat community, ecosystem status and potential usages. These characteristics are based on morphology and species identification, growth rates, phenotype adaptability and lifespan (Orfanidis *et al.*, 2011).

Ecosystem primary production prediction models typically use a one-size-fits-all approach to coastal green seaweeds calling them *Ulva* sp., *Ulva lactuca* Linnaeus (sea lettuce) or simply macroalgae (Trancoso *et al.*, 2005; Aldridge & Trimmer, 2009; Lavaud *et al.*, 2020). *Ulva* species can be very difficult to identify due to high morphological variability in response to changes in environmental conditions (Wang *et al.*, 2015; Gao *et al.*, 2016). Seaweed mats can consist of several species and diversity can be cryptic, especially with *Ulva* (Hofmann *et al.*, 2010; Melton & Lopez-Bautista, 2021). *Ulva* tends to dominate mat biomass because of their ability to exploit high nutrient regimes (Taylor *et al.*, 2001; Bermejo *et al.*, 2019, 2022). Seaweeds, including *Ulva* species, uptake and store nutrients in different amounts seasonally (Wu *et al.*, 2018; Jansen *et al.*, 2022). Variability is explained, in part, by different seasonal growth rates, but likely also by changes in biomass composition due to variations in environmental conditions. *Ulva* species exhibit intraspecific and interspecific variation in growth rates (Fort *et al.*, 2019), thus the present ecosystem primary production prediction models would benefit from better parameterization via use of species-specific information.

The management simplification in labelling green seaweeds arises due to the difficulty in identifying *Ulva* and other greens based on morphology alone. A rapid cost-effective assessment method for determining seaweed mat composition is needed for managers of coastal systems. Metagenomics via Next Generation Sequencing (NGS) and the Cleaved Amplified Polymorphic Sequences (CAPS) assay are two novel methods for identifying seaweeds using bulk samples (Fort *et al.*, 2018, 2020). Traditional Sanger sequencing for DNA Barcoding has limitations in that only one specimen can be analysed at once, and as a result, if several species are present on site, numerous samples will need to be analysed to get a proper quantitative and qualitative view of the species present (O'Kelly *et al.*, 2010; Kirkendale *et al.*, 2013). With NGS, bulk samples can be collected and species can be detected through a bioinformatic pipeline (Anyansi *et al.*, 2020). Alternatively, the CAPS is a sequencing-free assay (Fort *et al.*, 2021), which can identify *Ulva* species based on their unique band patterns following digestion of the ITS1 barcode

with restriction enzymes. The CAPS assay is currently only designed for foliose *Ulva* species identification due to genetic library development, and therefore, has limitations in identifying tubular species.

The aims of this study were to quantify seaweed biomass in both free-floating and entrained specimens within seaweed mats at three coastal estuaries and one exposed site across the Channel/La Manche region. The purpose was to assess feasibility for bioremediation and nutrient removal and compare biomass thresholds characterized in other systems to aid in determining the ecosystem status of our sites. We aimed to better understand mat composition by collecting bulk samples to identify seaweed species within the mats using NGS to understand cryptic diversity mainly in the green seaweed *Ulva*, leading to understanding of nutrient content and potential storage throughout the seasons.

Materials and methods

Sampling locations and site designations

Sampling occurred at four locations from Jan 2021–Dec 2022 across the Channel region, two in the UK (Holes Bay in Poole Harbour and Langstone Harbour), and two in France (the Ledano Estuary and

La Baie des Veys). Poole Harbour is designated as a Site of Special Scientific Interest (SSSI), Ramsar (designated under the Convention of Wetlands of International Importance as Waterfowl Habitat), and a Special Protection Area (SPA). Holes Bay ($50^{\circ}43'20''\text{N}$, $001^{\circ}59'44''\text{W}$) is an enclosed bay of Poole Harbour located in the northeast of the harbour that has silt mudflats and salt marsh environments (Fig. 1a). Langstone Harbour ($50^{\circ}48'41''\text{N}$, $001^{\circ}01'07''\text{W}$) is also classified as a SSSI and has marshes, seagrass meadows, rocky to silt mudflats (Fig. 1b). The Ledano Estuary ($48^{\circ}48'02''\text{N}$, $003^{\circ}05'40''\text{W}$) is composed of clay and silt mudflats with adjacent salt marsh environments and is in a transition water body (FRGT03) identified as a priority in the Master plan for Water Development and Management (SDAGE) of the WFD (Fig. 1c). Lastly, La Baie des Veys ($49^{\circ}21'52''\text{N}$, $001^{\circ}07'31''\text{W}$) is the most exposed of the sites with fine sand to silt sediments and with oyster cultivation nearby (Fig. 1d). This site is also located within a coastal zone closely monitored for green algal mats deposition as part of the WFD.

Seaweed sample collection and analysis for monthly biomass

To understand the changes in seaweed biomass at all four sites we monitored biomass monthly for two

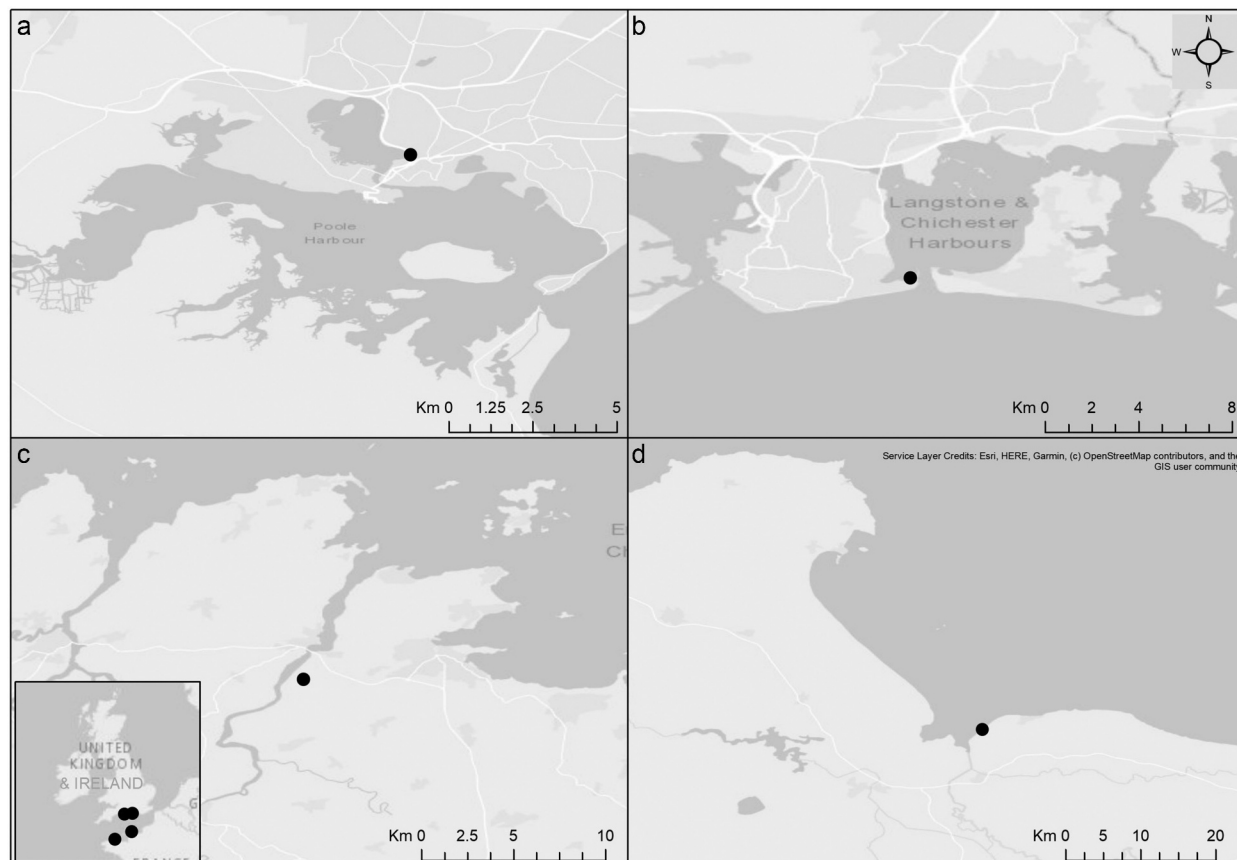


Fig. 1. Sample locations (black dots) within the four estuaries presented in this study. The four estuaries are located on the north and south positions in the channel. (a) Holes Bay and Poole Harbour, UK, (b) Langstone Harbour, UK, (c) Ledano Estuary, France, (d) La Baie des Veys, France.

years 2021–2022. At each site a 100 m transect was mapped in ArcGIS, dividing the transect into 10 m × 10 m plots. At the site during low tide, loose and entrained seaweed biomass samples were collected inside the plots with a 0.25 m² gridded quadrat and sampled 10 times each month. Per cent cover was also measured at each quadrat as mentioned above. Samples were collected in sealable plastic bags, put in a cool box on ice and transported to the laboratory. The biomass was washed to remove sediment and macrofauna within the samples. Tap water was used for an initial wash in a plastic bucket to remove most of the sediment. The biomass was placed in a nylon mesh bag and rinsed with tap water until the water stream was clear (1–5 minutes). The biomass was squeezed until no liquid remained. Biomass was put into tin trays, weighed to obtain a wet weight, and dried at 60°C for 4–5 days until the weights were constant to obtain a dry weight. Weights were multiplied to obtain grams of dry weight macroalgae biomass m⁻² (g DW m⁻²).

We performed normality and variance tests on all groups within the 2021–2022 seaweed biomass dataset. Biomass data was square root transformed due to the dataset having zero values. The Shapiro–Wilk normality hypothesis was rejected, and heterogeneity of variance was not rejected at all sites (Shapiro & Wilk, 1965). A Kruskal–Wallis ANOVA rank sum test was used to determine if there was variance between the months at each of the four sites (Kruskal & Wallis, 1952). Paired rank sum analysis between sites was performed with square root transformed monthly mean biomass data using the Friedman ANOVA (Friedman, 1937). A post-hoc rank sum Dunn's test was performed to understand the significance of variances in both tests (Dunn, 1964). Statistical tests were performed in the OriginPro version 2024 (Northampton, Massachusetts, USA) platform.

Genetic seaweed sample collection and preparation

At each site nine samples were collected (with selection based on seaweed tissue condition, i.e. green, non-degraded without excessive tissue degradation) seasonally (March, June, September, December 2021) with a 0.25 m² gridded quadrat to capture per cent cover of the seaweed. Three samples were collected at a low per cent cover (0–33%), medium per cent cover (34–66%), and high per cent cover (67–100%). Each quadrat was placed on the sediment along with a sample tag, an image and coordinates were taken at 1 m height above the quadrat. Using a knife, a square was cut around the quadrat to avoid collecting seaweed outside of the quadrat. All loose seaweed was collected inside the quadrat and put into a plastic bag and sealed. Each sample bag was placed in a cool box on ice until brought to the laboratory. In the laboratory samples were stored at 4°C until washing

(no more than 2 days). The seaweed was washed in a plastic bucket using 4–5 tap water rinses to remove sediment and infauna. Once washed the seaweed was squeezed and patted dry with paper towels, split in half, placed in plastic bags, and put in the –80°C freezer. Frozen samples were freeze-dried for a minimum of 48 hours in a Heto Power Dry PL3000 (Jouan Nordic, Denmark). Once freeze-dried samples were put into plastic bags with silica gel bead packets and shipped to Pristine Coasts (Galway, Ireland) for genetic analysis.

In 2021, we collected individual seaweed specimens at Holes Bay during the genetic seaweed sampling collection periods and at the same location. These individuals were preserved as pressings onto acid-free paper with species identification based on morphological characteristics and loosely on the NGS and CAPS assay findings in this study. Metadata for these individual specimen pressings are available in Supplementary table S3.

DNA extractions

Freeze-dried bulk biomass samples were first ground into a fine powder using a ball mill (QIAGEN TissueLyser II). Then, DNA was extracted in quadruplicate (i.e. 4 independent extractions from the same bulk sample) using either the magnetic beads protocol described in Fort *et al.* (2018) or using a custom CTABSILEX method (Vilanova *et al.*, 2020). The CTABSILEX method allows for DNA extraction using a higher amount of starting material, increasing DNA yields. For this protocol, ~15 mg DW of ground seaweed material was incubated in 800 µL CTAB buffer (2% CTAB, 1.4 M NaCl, 20 mM EDTA, 100 mM TrisHCL pH 8 & 2% PVP40) for 30 minutes at 65°C. Then, after adding 60 µl of 10% SDS, the mixture was vortexed and centrifuged at 11 000 g for 15 minutes at room temperature. The aqueous phase (~700 µl) was recovered and mixed with 420 µl of binding buffer (2.5 M NaCl, 20% PEG 8000), 630 µl of 100% ethanol and 20 µl of silica matrix. After 5 minutes of incubation with gentle shaking, the mixture was centrifuged for 6 seconds to pellet the silica matrix (which contains the nucleic acids). The pellet was washed twice with 70% ethanol and resuspended in 150 µl of sterile water and incubated at 65°C for 10 minutes to release the nucleic acids into the supernatant. Finally, the supernatant was separated from the silica matrix via centrifugation for 10 minutes at 11 000 g. After DNA extractions, the replicates (four per sample) were pooled into a single tube and concentrated via ethanol precipitation. Depending on the quality of the resulting DNA, species identification was performed using metagenomics or the CAPS assay described in Fort *et al.* (2021).

Metagenomic analysis of bulk seaweed samples for species identification

DNA samples were sent to the Beijing Genomic Institute (Hong Kong) or Novogene (Cambridge, UK) for NGS using DNBSeg or Illumina, respectively. Both techniques yielded 150 bp paired-end libraries with >5 Gb raw data per sample. Taxonomic labelling of the NGS reads was performed using the kraken2/bracken pipeline for metagenomic analysis (Wood *et al.*, 2019). A kraken2 database was used for taxonomic classification, which contained all published nuclear ITS1, *rbcl*, *tufA* and *COX1* sequences of algae in the NCBI (55 580 sequences) barcode database. For *Ulva* species, we used type specimen sequences, where available, to populate the database (the full list of *Ulva* sequences in the library is available in Supplementary table S1). A limitation of this methodology is that it requires accurate species annotation in the databases used. Given the large discrepancies in the application of names already observed and described for *Ulva* species, we anticipate that similar issues will be present in other families and genera. The assignment and quantification of reads to seaweed species was performed using kraken2 on the barcode database, using a confidence threshold of 0.25 and in paired-end mode. After read classification, bracken (Lu *et al.*, 2017) was used for estimating the relative proportions of each species in the samples, with a threshold of >20 reads classified at the species level to be included in the results.

Bulk sample analysis using CAPS assay

For samples failing quality control for NGS – largely due to the significant DNA degradation from samples collected in mudflat/sandflat environments, we used a PCR-based CAPS assay designed for the identification of foliose *Ulva* species in bulk samples (Fort *et al.*, 2021). For this, the ITS1 barcode was amplified via PCR using CAPS ITS1F (5'TCGTTGAACCCTCCCGTTTA3') and CAPS ITS1R (5'CGATGACTCACGGAATTCTGC3') primers, and the PCR amplicons were subsequently digested with two enzymes mixtures. Enzyme mix 1 contains the restriction enzymes BfaI, PspOMI, BamHI, HpaI and T7 endonuclease, while enzyme mix 2 contains CviQI, BtsCI and T7. Following digestion, the band patterns were separated and visualized on a 2% agarose gel. The restriction patterns observed are specific to the *Ulva* species present, and the band intensities allow for an estimation of the approximative relative proportions of the different species. However, precise relative proportions between each species within the bulk sample cannot be ascertained using this method, and we present the data here in qualitative terms (i.e. if three species are detected within a sample, each is given a 33.3% proportion in that sample). Importantly, we do not expect that all *Ulva* species can be identified using the enzymatic cocktail

described above, and further work will be needed to test more species than are currently included in the assay.

Results

Seaweed biomass

Free-floating or loose seaweed dry weight biomass and per cent cover sampled monthly in 2021 and 2022 displayed differences between and within sites. Holes Bay had significantly higher dry weight biomass than the other three sites ($p \leq 0.001$), whereas the comparisons between Langstone, Ledano Estuary and La Baie des Veys sites had no differences in biomass during the sampling period. However, per cent cover comparisons between sites showed that Holes Bay was significantly higher than the other three sites ($p \leq 0.01$; Supplementary table S4), and Langstone Harbour had higher seaweed per cent cover than Ledano Estuary and La Baie des Veys ($p \leq 0.02$). Within each site loose seaweed biomass showed differences between the time samples were collected, showing a seasonality pattern at some sites (Fig. 2a–d). At Holes Bay, monthly biomass was on average 201 g DW m⁻² with high standard error within months (Fig. 2a). There were no significant differences during the summer months of 2021 and 2022 with February 2021 variance differing from the 2021 summer months ($p \leq 0.01$) and March and December 2022 variance differing from the 2022 summer months ($p \leq 0.04$). The biomass peaked in August 2021 and again in February (Fig. 2a). Per cent cover was at or near 100% most of the year. Seaweed biomass was absent in Langstone Harbour during the winter months and peaked at 80.54 g DW m⁻² in August 2021 and 54.32 g DW m⁻² in October 2022. Upon analysis of peak months, we found they were not significantly different nor were there significant differences between months. Mean biomass was ~12 g DW m⁻² (Fig. 2b). Per cent cover similarly followed a seasonal pattern with a peak in July and August 2021 and July, September and October 2022. Similarly, the Ledano Estuary followed a seasonal biomass pattern, abundance peaking from Aug–Oct 2021 with a peak in August at 211 g DW m⁻² and 140 in September 2022 then declining in winter (Fig. 2c). The summer months varied significantly from the winter and part of the spring months ($p \leq 0.01$). The biomass and per cent cover displayed seasonal patterns with high biomass and per cent cover in the summer months. Biomass at La Baie de Veys did not follow seasonal patterns as the other sites in 2021 and 2022 with biomass reaching an average of 359 g DW m⁻² in January 2021 (Fig. 2d). However, the per cent cover was lower than the other sites. In 2022 biomass peaked at 57 g DW m⁻² but was not significantly different than the other collection points through the year.

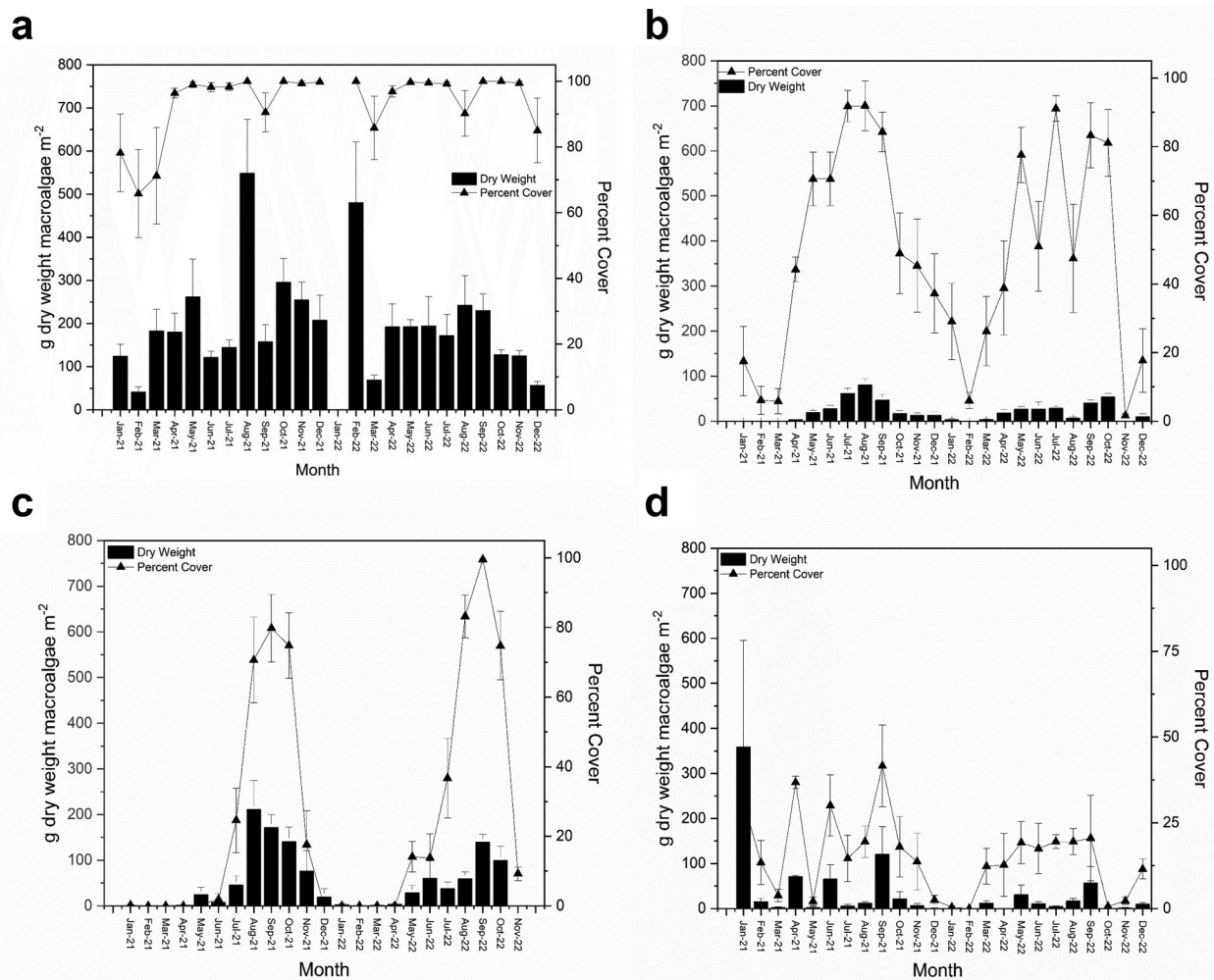


Fig. 2. Loose seaweed (macroalgae) dry weight biomass (bars) and per cent cover (triangles) monitored monthly at UK sites (a) Holes Bay and (b) Langstone Harbour, and at French sites (c) Ledano Estuary and (d) La Baie de Veys during the 2021–2022 field seasons. Error bars are standard error.

Entrained seaweed biomass was not present at all sites. No entrained seaweed was found at Langstone Harbour and La Baie de Veys at any time during the year. In contrast, entrained seaweed was found at Ledano Estuary and Holes Bay, with a significantly higher entrained dry weight biomass at Ledano Estuary than at Holes Bay ($p \leq 0.001$). Ledano Estuary entrained seaweed biomass followed a seasonal pattern similar to the loose seaweed at this site with entrained biomass at the peak in August 2021 at 144 g DW m^{-2} and higher in June 2022 at 274 g DW m^{-2} (Fig. 3b). Summer/autumn months were significantly different than the winter months ($p \leq 0.01$). Holes Bay had entrained seaweed at various times during the year, with no seasonal pattern (Fig. 3a). At Holes Bay, entrained per cent cover was below 30% on average all year except in May 2021 where entrained biomass and per cent cover peaked.

Seaweed identification

During the seasonal sampling period of 2021, we detected the presence of seaweed at all sites using

NGS and CAPS assay bulk sampling methods (Fig. 4; Supplementary figs S1–S3; Supplementary table S2). In Holes Bay we identified *Ulva lacunculata* (Kützinger) Wittrock as the dominant blade-like or foliose green seaweed species. A small per cent of tubular species belonging to the *Ulva linza/procera/prolifera* clade called the ‘*Ulva* sp. LPP clade’ was detected in June using both NGS and CAPS (Shimada *et al.*, 2008), as well as a small proportion of *Ulva compressa* Linnaeus (~3.5%). There were no differences in dominant species between months and per cent cover (Fig. 4a). This dominance of one *Ulva* species at Holes Bay was in clear contrast to the diversity of common green and brown mat species at Langstone Harbour, where the seaweeds cycled through a dominance of *Chaetomorpha* sp. in March to *Ulva* spp. in June to *Cladophora* sp. in September to a mixture of these species in December (Fig. 4b) with *Pylaiella littoralis* (Linnaeus) Kjellman, a commonly occurring brown seaweed, becoming dominant in December (Pye, 2000). At the Ledano Estuary there was significant

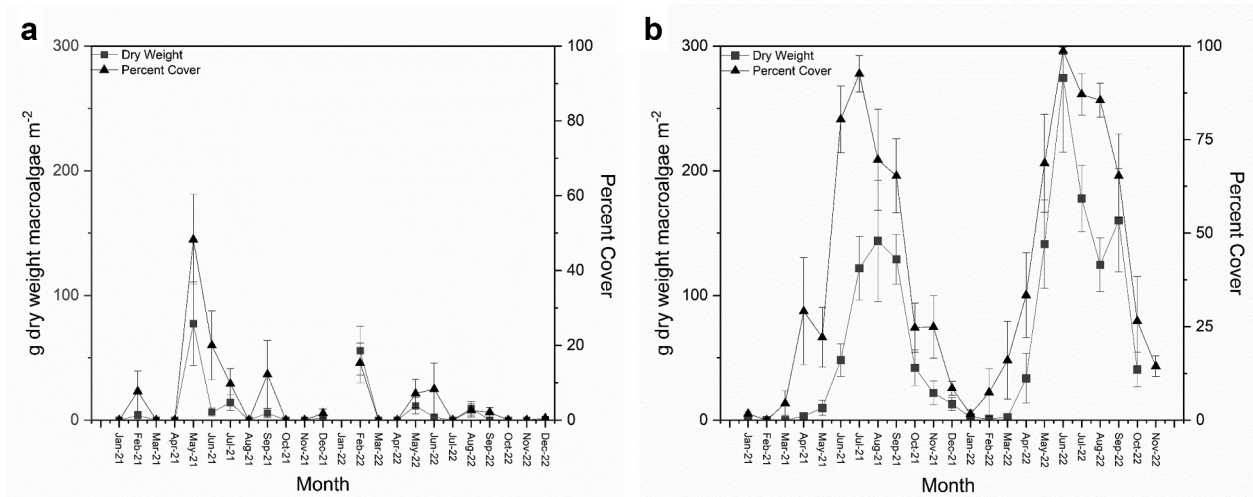


Fig. 3. Entrained seaweed (macroalgae) dry weight biomass (squares) and per cent cover (triangles) monitored monthly at (a) Holes Bay and (b) Ledano Estuary. Langstone Harbour and La Baie de Veys had no entrained macroalgae recorded during the 2021–2022 field seasons. Error bars are standard error.

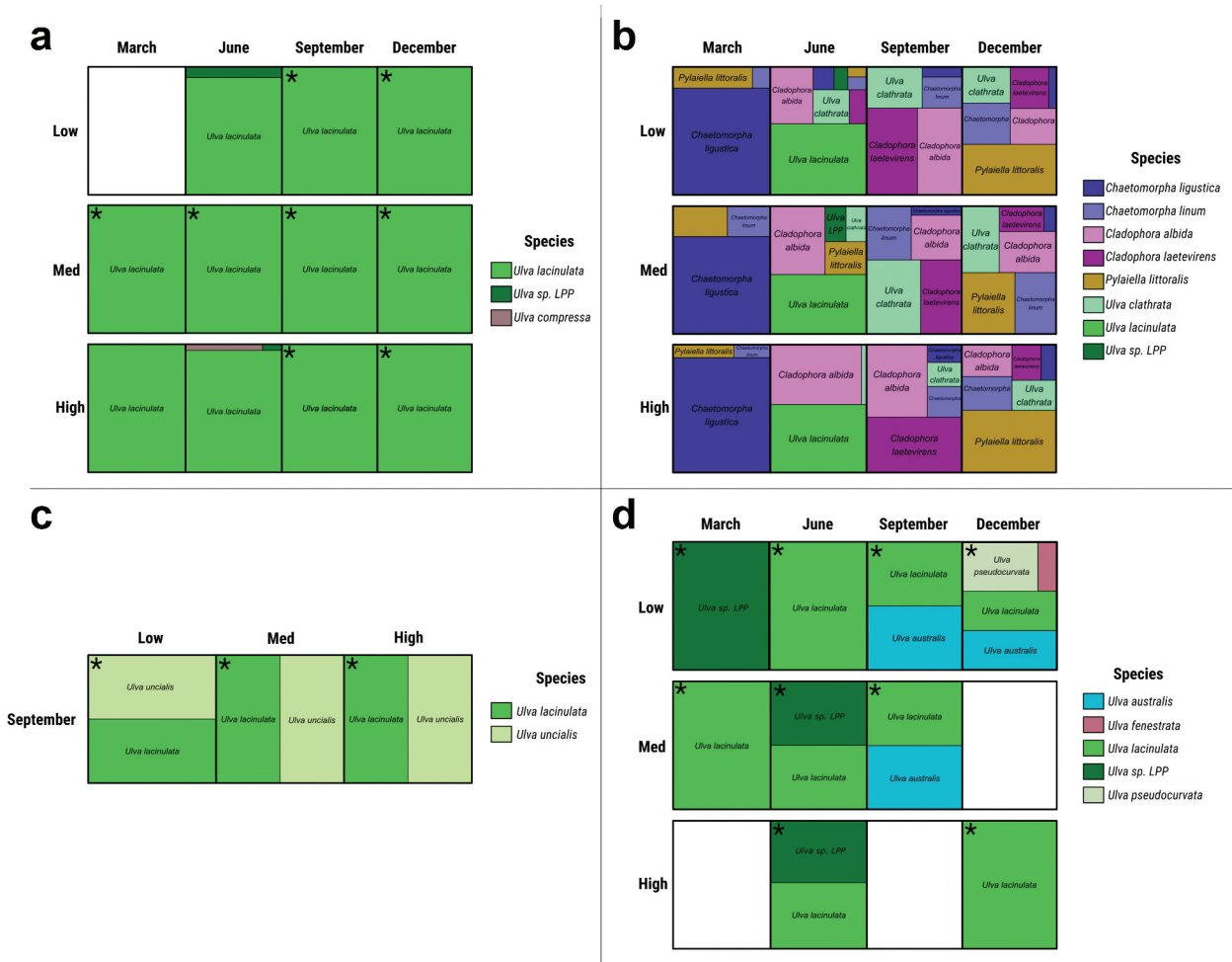


Fig. 4. Tree map of seasonal bulk samples at high, medium and low per cent seaweed cover collected in 2021. Relative abundance Next Generation Sequencing (NGS) or presence of species *Cleaved Amplified Polymorphic Sequences (CAPS) enzymatic assays from samples collected in 2021. (a) Holes Bay, (b) Langstone Harbour, (c) Ledano Estuary, (d) La Baie de Veys.

DNA degradation in the samples analysed. Only the CAPS assay was successful in September and genetic library limitations allowed us to only detect foliose *Ulva* species during this month, *Ulva lacunculata* and *Ulva 'uncialis'* (Kützing) Montagne (formerly and incorrectly called *U. rigida* C.Agardh), Bachoo *et al.* (2023). Both laminar *Ulva* species (Fig. 4c) were present, however this finding does not exclude the presence of tubular green seaweed that is not detected by the CAPS assay. The CAPS assay results from La Baie des Veys indicated a mixture of laminar *U. australis* Areschoug, *U. fenestrata* Postels & Ruprecht, *U. pseudocurvata* Koeman & C.Hoek (Maggs *et al.*, 2024), *U. lacunculata* and *U. sp. LPP* clade (Fig. 4d). These results do not exclude the presence of tubular *Ulva* species.

Discussion

Our four study sites, and the Channel region in general, have had elevated seaweed mat abundances above ecosystem consequence thresholds for decades (Pye, 2000; Smetacek & Zingone, 2013; Witt, 2022; Louis *et al.*, 2023) with *Ulva* the principal taxon involved. Globally, *Ulva* is most frequently responsible for the formation of nuisance macroalgal mats (Joniver *et al.*, 2021). Eutrophication, the ultimate cause of high seaweed mat abundance, occurs from point and non-point nutrient sources both of which have become the focus of local nutrient budgeting studies and increased management efforts in recent years. In Poole Harbour, for example, which tidally exchanges with our Holes Bay site, most macronutrients enter via riverine inputs (Witt, 2022) whilst Holes Bay itself receives substantial amounts of treated wastewater. The harmful ecological thresholds of seaweed mat accumulation are debated (Thornton *et al.*, 2020; Witt, 2022) and are clearly taxa specific. Frequently there is a focus on infauna effects, e.g. Green *et al.* (2014) performed an experimental study and review of *Ulva* mat effects and found 110–120 g DW m⁻² of mat had an ecological impact on the infauna as well as wider ecosystem consequences at around 200 g DW m⁻². Impacts are clearly local, variable, and can rapidly change depending on the morphology and movement of the mat biomass around the mudflat or estuary. Many other chemical, physical and biological factors are used to predict ecosystem decline and decreased water quality status (Water Framework Directive, 2000; Perrot *et al.*, 2014). The adaptation of the Ecological Evaluation Index (EEI-c) for estimation of habitat ecological status for transitional waters aims to incorporate these other predicting factors (Orfanidis *et al.*, 2011). A seaweed community monitoring index based on the EEI-c to monitor coastal habitats that are influenced by anthropogenic and climate changes

(Han *et al.*, 2023) has recently been designed in Asia. In Holes Bay, the seaweed mat measured over the two-year monitoring period was persistent over the year and was seen as healthy viable tissue over all seasons. The Holes Bay mat was above the 200 g DW m⁻² ecosystems consequences threshold for 8 of the 23 months assessed, and mat accumulation at this site was clearly much higher than at our other three monitoring sites where exceedances of the WFD threshold were rare. Holes Bay had very favourable conditions for mat accumulation, and the ecological impacts of the mat accumulations were therefore more pronounced at this site (Witt, 2022) relative to the other monitoring sites.

In addition to measuring surface accumulations of mat tissue, European monitoring efforts tend to measure seaweed entrainment as part of monthly seaweed surveys to determine ecosystem status (Water Framework Directive, 2000; Witt, 2022). The extent of mat entrainment will have a relationship with overlying mat biomass (this study; Witt, 2022) and sediment type/tidal regime. Entrainment is thought to be an important overwintering mechanism in certain species (e.g. Gonzalez *et al.*, 2013; Robertson & Savage, 2018) and therefore, seaweed species detection within the mat is important for making sense of entrainment dynamics. In our study, entrained seaweed (buried > 3 cm into the sediment) was found at two sites, Holes Bay, and the Ledano Estuary, associated with a silt and clay sediment type and high seaweed mat biomass which we identified to be dominated by *Ulva lacunculata*. In contrast, our La Baie des Veys site was sandy and therefore ecologically distinct from our other three (mudflat) sites. Biomass accumulation at La Baie des Veys occurs by true beaching after growth on adjacent rocky shores. Any overwintering is dependent on growth on the adjacent rocky shore as the possibilities for entrainment in the sandy sediment (Merceron *et al.*, 2007; Louis *et al.*, 2023) are limited. Our study further confirms the close relationship between mat accumulation and sediment entrainment in certain sediment conditions that likely contribute to overwintering potential and persistence at some channel sites.

Assessing seaweed mat biomass is not only important for understanding impacts on ecosystem status but also as a predictive measure for potential nutrient removal, especially nitrogen. Morrall *et al.* (2025) quantified the per cent nitrogen in the mat tissue we examined and concluded that seasonal nitrogen content in the seaweed tissue depended on several factors including water and sediment nutrient concentrations and inputs, and the species composition of the mat. Across our study sites, there was high variability in species composition between sites with Holes Bay dominated by a foliose *Ulva* whilst Langstone Harbour had multiple genera with

a typically filamentous or tubular morphology. The Ledano Estuary and La Baie des Veys showed conspecifics of the same genera, with only foliose *Ulva* species throughout the year. However, our diversity assessments on the French side of the Channel were limited to detection of foliose *Ulva* species using the CAPS assay (see methods). At the Ledano Estuary seaweed biomass is mostly tubular during the year and makes up most of the biomass (personal observations, CEVA). The high-density monospecific foliose mat in Holes Bay (*Ulva lacunculata*) is associated with a combination of a low tidal energy regime and high nutrient inputs, whereas Langstone Harbour's lower nutrient inputs (though both systems have had eutrophic water designations) and higher tidal energy regime likely contribute to an increased seaweed mat diversity with no clear overall dominance. The conditions in Holes Bay, and the extended period (>3 decades from this project's observations) for which these conditions have occurred, could have amplified the potential for selection of a mat-specialized *Ulva* strain as has recently been demonstrated (Fort *et al.*, 2020) and therefore how specialization to high nutrient conditions can become reinforced.

Past studies at or near our four sites have investigated green seaweed diversity. In Holes Bay, Thornton (2016) reported the dominance of *Ulva rigida* based on morphological identification, which has been reported recently to be genetically close to *U. lacunculata*, and has now been assigned to the same species (Hughey *et al.*, 2021) or as a close relative species named *U. sp. A* (Fort *et al.*, 2022), now referred to as *Ulva 'uncialis'*. In Langstone Harbour, the *Ulva* diversity reported in this study as *U. 'clathrata'* (Roth) C. Agardh and *U. lacunculata* is similar to the dominance of *Ulva* species shown in past studies, for example Pye (2000) showed tubular *Ulva* (formerly *Enteromorpha*) dominance across a north/south gradient in Langstone Harbour in 1994–1996. Also, Tan *et al.* (1999) performed a molecular identification study of *Ulva* in the harbour and found *U. scandinavica* Bliding which is synonymous with *U. lacunculata* (Hughey *et al.*, 2021). Tan *et al.* (1999) also identified *U. armoricana* Dion, de Reviere & Coat, *U. rotundata* Bliding, and *U. rigida* in Brittany, France. also synonyms of *Ulva lacunculata* (Hughey *et al.*, 2021). The areas surrounding La Baie des Veys has limited *Ulva* identification studies and therefore we are unable to compare our *U. australis*, *U. fenestrata*, *U. pseudocurvata* *U. sp. LPP* clade, *U. lacunculata* identification results with historical data from the same location. These recent *Ulva* species confirmations using DNA sequences highlight the importance of using bulk collection and NGS methods.

Confirmation of seaweed mat species at these four sites allows us to better understand potential specific growth rates, further develop macroalgal growth model predictions and predict the quantity of nitrogen removal possible with seaweed removal methods. Perrot *et al.* (2014) developed a coupled hydrodynamic and biological model for Brittany, France that incorporated many physiological parameters of *Ulva*, including maximal growth rates, optimal temperature and nutrient uptake rates in addition to the hydrodynamic parameters. They predicted that if river nitrates were reduced to 5 mg N l⁻¹ in mudflat environments, and to 15 mg N l⁻¹ in sandy environments then *Ulva* mat biomass would be reduced by half. This model can be further refined and tailored to other estuaries based on seaweed species composition. Seaweed identification and physiological laboratory experiments are essential to developing a marine water body management plan because each seaweed species has different physiological requirements for growth (Hurd *et al.*, 2014; Bermejo *et al.*, 2023). Aldridge and Trimmer (2009) described and implemented a model for tubular and foliose *Ulva* spp. which incorporated seaweed tissue stressors such as tidal regimes (height range/durations) and therefore included the time *Ulva* tissue was potentially desiccated. Nutrient exchange through diffusion/absorption of nitrate and ammonium, the two forms of dissolved inorganic nitrogen that influence growth, exchange through the seaweed's cell membrane when the mat is submerged, and so the time spent submerged is clearly a key driver of growth potential. Tidal regimes at the four sites are likely significant in explaining variations in mat accumulation. Holes Bay has a small tidal range (0.4–1.5 m) and a double high-water pattern whereas the other three sites have higher tidal ranges (~5.0–8.0 m) with a typical tidal curve. Foliose *Ulva* morphology corresponds to higher growth rates, superior nutrient acquisition and greater mat-forming potential (Bermejo *et al.*, 2023). Higher surface area to volume ratios contribute to fronds being better able to exploit nutrient-rich conditions compared with tubular types; Bermejo *et al.* (2023) found *U. lacunculata* had greater uptake and growth rates compared with that of *U. compressa* in the tubular morphology. *Ulva lacunculata* also responded with a high growth rate to increase in temperature while *U. compressa* did not. Therefore, our study adds further evidence of the greater capacity of *U. lacunculata* to dominate under eutrophic estuarine conditions.

Our work confirms the high mat-forming potential of *Ulva lacunculata* across the Channel region and illustrates how bulk genetic sampling methods can be used to gain a rapid overview of regional seaweed diversity. Accurate and extended identification of mat species, and their population dynamics, is beneficial

for the various mat exploitation strategies (human diet, livestock feed, biofuel, agricultural fertilizer, anaerobic digestion) currently being explored (Joniver *et al.*, 2021; Morris *et al.*, 2022) and which will contribute to improvements in coastal marine management regimes.

Acknowledgements

The authors would like to thank Alice Parker and Fatima Amat Trigo for assisting with collection and processing of samples used in this study.

Disclosure statement

No potential conflict of interest was reported by the author(s).

Funding

This study was co-financed by the European Regional Development Fund through the Interreg France (Channel Manche) England Programme via the Rapid Reduction of Nutrients in Transitional Waters (RaNTrans) project.

Supplementary Information

The following supplementary material is accessible via the Supplementary Content tab on the article's online page at <https://doi.org/10.1080/09670262.2025.2500007>

Supplementary table S1. *Ulva* species type specimen sequences used to populate the kraken2 database for determining species identification.

Supplementary table S2. Metadata for NGS and CAPS analysed specimens SRA bioproject PRJNA1014254 collected and described in this study.

Supplementary table S3. Metadata for individual specimens collected during the bulk sampling used for NGS for Holes Bay, UK. See 'Table S3 Metadata on Individual Specimen Pressings Holes Bay.xlsx'

Supplementary table S4. Summary of non-parametric test of analysis of variance using Kruskal-Wallis ANOVA and post-hoc Dunn's test statistics for within site monthly seaweed biomass data. Summary of non-parametric test of analysis of variance by ranks using Friedman ANOVA and post-hoc Dunn's test statistics for between site monthly seaweed biomass data. See 'Table S4 Biomass Statistics.xlsx'

Supplementary fig. S1 DNA band patterns resulting after enzyme digestion of September and December 2021 Holes Bay seaweed samples.

Supplementary fig. S2 DNA band patterns resulting after enzyme digestion of September 2021 Ledano Estuary seaweed samples.

Supplementary fig. S3 DNA band patterns resulting after enzyme digestion of La Baie des Veys A. March – September 2021 B. December 2021 seaweed samples.

Author contributions

Lamb: primary writer of the manuscript, project organization, sample collection and processing, data analysis and interpretation; D. Franklin: editor of the manuscript,

fieldwork, project planning and administration; J. Sokolnicki: sample collection, sample processing and Fig. 1 map generation; S. Morris: sample collection and processing; R. Sulpice: editor of the manuscript, data analysis; A. Fort: editor of the manuscript, data analysis and Fig. 4 generation; M. Inaba: processing of samples and data analysis for genetics; S. Richier: editor of the manuscript, sample collection and processing; A. Le Bris: sample collection and processing; A. van der Schatte Olivier: sample collection and processing; Z. Morrall: sample collection and processing; S. Lemesle: sample collection and processing; A. Rusig: sample collection and processing; I. Mussio: sample collection and processing; G. Watson: editor of the manuscript, project planning, conceptualization and administration, RaNTrans funding acquisition, RaNTrans project PI.

ORCID

Annesia L. Lamb  <http://orcid.org/0000-0002-0509-9586>
 Sinéad Morris  <http://orcid.org/0000-0001-7371-0001>
 Ronan Sulpice  <http://orcid.org/0000-0002-6113-9570>
 Antoine Fort  <http://orcid.org/0000-0002-2210-7234>
 Masami Inabi  <http://orcid.org/0000-0001-7618-4748>
 Andrew van der Schatte Olivier  <http://orcid.org/0000-0002-2534-0568>
 Gordon Watson  <http://orcid.org/0000-0001-8274-7658>

References

- MSFD 2008/56/EC. Directive 2008/56/EC of the European Parliament and of the Council of 17 June 2008 establishing a framework for community action in the field of marine environmental policy (Marine Strategy Framework Directive). EUR-Lex - 32008L0056 - EN - EUR-Lex (europa.eu)
- Aldridge, J.N. & Trimmer, M. (2009). Modelling the distribution and growth of 'problem' green seaweed in the Medway estuary, UK. *Hydrobiologia*, **629**: 107-122.
- Anyansi, C., Straub, T.J., Manson, A.L., Earl, A.M. & Abeel, T. (2020). Computational methods for strain-level microbial detection in colony and metagenome sequencing data. *Frontiers in Microbiology*, **11**: 1925.
- Atkinson, M.J. & Smith, S.V. (1983). C: N: P ratios of benthic marine plants. *Limnology and Oceanography*, **28**: 568-574.
- Bachoo, T., Bolton, J.J., Macey, B.M., Kandjengo, L. & Reddy, M.M. (2023). Resolving the identity of commercially cultivated *Ulva* (Ulvaceae, Chlorophyta) in integrated seaweed-abalone aquaculture farms in South Africa. *Journal of Phycology*, **59**: 1272-1283.
- Bermejo, R., Galindo-Ponce, M., Golden, N., Linderhoff, C., Heesch, S., Hernández, I. & Morrison, L. (2023). Two bloom-forming species of *Ulva* (Chlorophyta) show different responses to seawater temperature and no antagonistic interaction. *Journal of Phycology*, **59**: 167-178.
- Bermejo, R., Golden, N., Schrofner, E., Knöller, K., Fenton, O., Serrao, E. & Morrison, L. (2022). Biomass and nutrient dynamics of major green tides in Ireland: implications for biomonitoring. *Marine Pollution Bulletin*, **175**: 113318.
- Bermejo, R., Heesch, S., Mac Monagail, M., O'Donnell, M., Daly, E., Wilkes, R.J. & Morrison, L. (2019). Spatial and

- temporal variability of biomass and composition of green tides in Ireland. *Harmful Algae*, **81**: 94–105.
- Dunn, O.J. (1964). Multiple comparisons using rank sums. *Technometrics*, **6**: 241–252.
- European Commission. (2008). Directive 2008/56/EC of the European Parliament and of the Council Establishing a Framework for Community Action in the Field of Marine Environmental Policy (*Marine Strategy Framework Directive*). Brussels: Official Journal of the European Union, **L164**: 19–40.
- Fort, A., Guiry, M.D. & Sulpice, R. (2018). Magnetic beads, a particularly effective novel method for extraction of NGS-ready DNA from macroalgae. *Algal Research*, **32**: 308–313.
- Fort, A., Lebrault, M., Allaire, M., Esteves-Ferreira, A., McHale, M., Lopez, F., Fariñas-Franco, J.M., Alseekh, S., Fernie, A.R. & Sulpice, R. (2019). Extensive variations in diurnal growth patterns and metabolism among *Ulva* spp. strains. *Plant Physiology*, **180**: 109–123.
- Fort, A., Linderhof, C., Coca-Tagarro, I., Inaba, M., McHale, M., Cascella, K., Potin, P., Guiry, M.D. & Sulpice, R. (2021). A sequencing-free assay for foliose *Ulva* species identification, hybrid detection and bulk biomass characterisation. *Algal Research*, **55**: 102280.
- Fort, A., Mannion, C., Fariñas-Franco, J.M. & Sulpice, R. (2020). Green tides select for fast expanding *Ulva* strains. *Science of the Total Environment*, **698**: 134337.
- Fort, A., McHale, M., Cascella, K., Potin, P., Perrineau, M. M., Kerrison, P.D., da Costa, E., Calado, R., Do Rosario Domingues, M., Costa Azevedo, I., Sousa-Pinto, I., Gachon, C., van der Werf, A., de Visser, W., Beniers, J. E., Jansen, H., Guiry, M.D. & Sulpice, R. (2022). Exhaustive reanalysis of barcode sequences from public repositories highlights ongoing misidentifications and impacts taxa diversity and distribution. *Molecular Ecology Resources*, **22**: 86–101.
- Friedman, M. (1937). The use of ranks to avoid the assumption of normality implicit in the analysis of variance. *Journal of the American Statistical Association*, **32**: 675–701.
- Fujita, R.M., Wheeler, P.A. & Edwards, R.L. (1989). Assessment of macroalgal nitrogen limitation in a seasonal upwelling region. *Marine Ecology Progress Series*, **53**: 293–303.
- Gamenick, I., Jahn, A., Vopel, K. & Giere, O. (1996). Hypoxia and sulphide as structuring factors in a macrozoobenthic community on the Baltic Sea shore: colonisation studies and tolerance experiments. *Marine Ecology Progress Series*, **144**: 73–85.
- Gao, G., Zhong, Z., Zhou, X. & Xu, J. (2016). Changes in morphological plasticity of *Ulva prolifera* under different environmental conditions: a laboratory experiment. *Harmful Algae*, **59**: 51–58.
- Gonzalez, D.J., Smyth, A.R., Piehler, M.F. & McGlathery, K.J. (2013). Mats of the non-native macroalga, *Gracilaria vermiculophylla*, alter net denitrification rates and nutrient fluxes on intertidal mudflats. *Limnology and Oceanography*, **58**: 2101–2108.
- Green, L., Sutula, M. & Fong, P. (2014). How much is too much? Identifying benchmarks of adverse effects of macroalgae on the macrofauna in intertidal flats. *Ecological Applications*, **24**: 300–314.
- Han, S.J., Jang, J.G., Kim, H.J., Seo, T.H. & Park, J.M. (2023). Ecological evaluation of marine macroalgal communities on five islands of Korea in the Yellow Sea. *Acta Oceanologica Sinica*, **42**: 9–56.
- Hernández, I., Pérez-Pastor, A., Mateo, J.J., Megina, C. & Vergara, J.J. (2008). Growth dynamics of *Ulva rotundata* (Chlorophyta) in a fish farm: implications for biomitigation at a large scale. *Journal of Phycology*, **44**: 1080–1089.
- Hofmann, L.C., Nettleton, J.C., Neefus, C.D. & Mathieson, A.C. (2010). Cryptic diversity of *Ulva* (Ulvales, Chlorophyta) in the Great Bay Estuarine System (Atlantic USA): introduced and indigenous distromatic species. *European Journal of Phycology*, **45**: 230–239.
- Hughey, J.R., Gabrielson, P.W., Maggs, C.A. & Mineur, F. (2021). Genomic analysis of the lectotype specimens of European *Ulva rigida* and *Ulva lacinulata* (Ulvaceae, Chlorophyta) reveals the ongoing misapplication of names. *European Journal of Phycology*, **57**: 143–153.
- Hurd, C.L., Harrison, P.J., Bischof, K. & Lobban, C.S. (2014). *Seaweed Ecology and Physiology*. Cambridge, UK: Cambridge University Press.
- Jansen, H.M., Bernard, M.S., Nederlof, M.A., van der Meer, I.M. & van der Werf, A. (2022). Seasonal variation in productivity, chemical composition and nutrient uptake of *Ulva* spp. (Chlorophyta) strains. *Journal of Applied Phycology*, **34**: 1649–1660.
- Joniver, C.F., Photiades, A., Moore, P.J., Winters, A.L., Woolmer, A. & Adams, J.M. (2021). The global problem of nuisance macroalgal blooms and pathways to its use in the circular economy. *Algal Research*, **58**: 102407.
- Kirkendale, L., Saunders, G.W. & Winberg, P. (2013). A molecular survey of *Ulva* (Chlorophyta) in temperate Australia reveals enhanced levels of cosmopolitanism. *Journal of Phycology*, **49**: 69–81.
- Kletou, D., Savva, I., Tsiamis, K. & Hall-Spencer, J.M. (2018). Opportunistic seaweeds replace *Cystoseira* forests on an industrialised coast in Cyprus. *Mediterranean Marine Science*, **19**: 598–610.
- Kruskal, W.H. & Wallis, W.A. (1952). Use of ranks in one-criterion variance analysis. *Journal of the American Statistical Association*, **47**: 583–621.
- Lavaud, R., Filgueira, R., Nadeau, A., Steeves, L. & Guyondet, T. (2020). A dynamic energy budget model for the macroalga *Ulva lactuca*. *Ecological Modelling*, **418**: 108922.
- Littler, M.M. & Littler, D.S. (1981). Intertidal macrophyte communities from Pacific Baja California and the upper Gulf of California: relatively constant vs. environmentally fluctuating systems. *Marine Ecology Progress Series*, **4**: 145–158.
- Louis, J., Ballu, S., Rossi, N., Lasbleiz, M., Perrot, T., Daniel, C., Cellier, L., Hénaff, F. & Richier, S. (2023). Multi-year renewal of green tides: 18 years of algal mat monitoring (2003–2020) on French coastline (Brittany region). *Marine Pollution Bulletin*, **193**: 115–173.
- Lu, J., Breitwieser, F.P., Thielen, P. & Salzberg, S.L. (2017). Bracken: estimating species abundance in metagenomics data. *PeerJ Computer Science*, **3**: e104.
- Lüning, K. (1993). Environmental and internal control of seasonal growth in seaweeds. *Hydrobiologia*, **260**: 1–14.
- Maggs, C., Bunker, A., Bunker, F., Harries, D., Kelly, J., Mineur, F., Blomster, J., Díaz-Tapia, P., Gabrielson, P., Hughey, J. & Brodie, J. (2024). Updating the Ulvaceae in the green seaweeds of Britain and Ireland. *Botanica Marina*, **67**: 181–203.
- McGlathery, K.J. (2001). Macroalgal blooms contribute to the decline of seagrass in nutrient-enriched coastal waters. *Journal of Phycology*, **37**: 453–456.
- Melton, J.T., III & Lopez-Bautista, J.M. (2021). Diversity of the green macroalgal genus *Ulva* (Ulvophyceae,

- Chlorophyta) from the east and gulf coast of the United States based on molecular data. *Journal of Phycology*, **57**: 551–568.
- Merceron, M., Antoine, V., Auby, I. & Morand, P. (2007). In situ growth potential of the subtidal part of green tide forming *Ulva* spp. stocks. *Science of the Total Environment*, **384**: 293–305.
- Morrall, Z., Preston, J., Richier, S., Franklin, D.J., Lamb, A., van der Schatte Olivier, A., Scott Harris, E., Parry, D., Horton, G., Lemesle, S., Hellio, C., Fauchon, M. & Watson, G. (2025). Ecological impacts, efficacy and economic feasibility of algal mat removal from temperate intertidal mudflats under blue nitrogen trading schemes. *Marine Pollution Bulletin*, **214**: 117747. <https://doi.org/10.1016/j.marpolbul.2025.117747>
- Morris, S.E., Watson, G.J., Richier, S., Green, I.D., Lamb, A. L. & Franklin, D.J. (2022). The potential economic exploitation of macroalgal mats in Poole Harbour and other Channel estuarine systems. In *Harbour ecology: Environment and development in Poole Harbour* (Humphreys, J. & Hall, A., eds.), 245–257. London: Pelagic Publishing.
- O’Kelly, C.J., Kurihara, A., Shipley, T.C. & Sherwood, A.R. (2010). Molecular assessment of *Ulva* spp. (Ulvophyceae) in the Hawaiian Islands. *Journal of Phycology*, **46**: 728–735.
- Orfanidis, S., Panayotidis, P. & Uglund, K. (2011). Ecological Evaluation Index continuous formula (EEI-c) application: a step forward for functional groups, the formula and reference condition values. *Mediterranean Marine Science*, **12**: 199–232.
- Perrot, T., Rossi, N., Ménesguen, A. & Dumas, F. (2014). Modelling green macroalgal blooms on the coasts of Brittany, France to enhance water quality management. *Journal of Marine Systems*, **132**: 38–53.
- Pye, K. (2000). The effects of eutrophication on the marine benthic flora of Langstone Harbour, South Coast of England. PhD dissertation. University of Portsmouth.
- Raffaelli, D.G., Raven, J.A. & Poole, L.J. (1998). Ecological impact of green macroalgal blooms. *Oceanography and Marine Biology*, **36**: 97–125.
- Robertson, B.P. & Savage, C. (2018). Mud-entrained macroalgae utilise porewater and overlying water column nutrients to grow in a eutrophic intertidal estuary. *Biogeochemistry*, **139**: 53–68.
- Scanlan, C.M., Foden, J., Wells, E. & Best, M.A. (2007). The monitoring of opportunistic macroalgal blooms for the water framework directive. *Marine Pollution Bulletin*, **55**: 162–171.
- Shapiro, S.S. & Wilk, M.B. (1965). An analysis of variance test for normality (complete samples). *Biometrika*, **52**: 591–611.
- Shimada, S., Yokoyama, N., Arai, A. & Hiraoka, M. (2008). Phylogeography of the genus *Ulva* (Ulvophyceae, Chlorophyta), with special reference to the Japanese freshwater and brackish taxa. *Journal of Applied Phycology*, **20**: 979–989.
- Smetacek, V. & Zingone, A. (2013). Green and golden seaweed tides on the rise. *Nature*, **504**: 84–88.
- Tan, I.H., Blomster, J., Hansen, G., Leskinen, E., Maggs, C. A., Mann, D.G., Sluiman, H.J. & Stanhope, M.J. (1999). Molecular phylogenetic evidence for a reversible morphogenetic switch controlling the gross morphology of two common genera of green seaweeds, *Ulva* and *Enteromorpha*. *Molecular Biology and Evolution*, **16**: 1011–1018.
- Taylor, R., Fletcher, R.L. & Raven, J.A. (2001). Preliminary studies on the growth of selected ‘green tide’ algae in laboratory culture: effects of irradiance, temperature, salinity and nutrients on growth rate. *Botanica Marina*, **44**: 327–336.
- Teichberg, M., Fox, S.E., Olsen, Y.S., Valiela, I., Martinetto, P., Iribarne, O., Yuriko Muto, E., Petti, M. A., Corbisier, T.N., Soto-Jiménez, M., Páez-Osuna, F., Castro, P., Freitas, H.Z., Cardinaletti M, A. & Tagliapietra, D. (2010). Eutrophication and macroalgal blooms in temperate and tropical coastal waters: nutrient enrichment experiments with *Ulva* spp. *Global Change Biology*, **16**: 2624–2637.
- Thornton, A. (2016). The impact of green macroalgal mats on benthic invertebrates and overwintering wading birds. (PhD dissertation, Bournemouth University).
- Thornton, A., Herbert, R.J.H., Stillman, R.A. & Franklin, D. J. (2020). Macroalgal mats in a eutrophic estuarine marine protected area: Implications for benthic invertebrates and wading birds. In *Marine protected areas: science, policy and management* (Humphreys, J. & Clark, R., eds.), 703–727. Amsterdam: Elsevier.
- Trancoso, A.R., Saraiva, S., Fernandes, L., Pina, P., Leitão, P. & Neves, R. (2005). Modelling macroalgae using a 3D hydrodynamic-ecological model in a shallow, temperate estuary. *Ecological Modelling*, **187**: 232–246.
- Valiela, I., McClelland, J., Hauxwell, J., Behr, P.J., Hersh, D. & Foreman, K. (1997). Macroalgal blooms in shallow estuaries: controls and ecophysiological and ecosystem consequences. *Limnology and Oceanography*, **45**: 1105–1118.
- Vilanova, S., Alonso, D., Gramazio, P., Plazas, M., García-Fortea, E., Ferrante, P., Schmidt, M., Jose Diez, M., Usadel, B., Giuliano, G. & Prohens, J. (2020). SILEX: a fast and inexpensive high-quality DNA extraction method suitable for multiple sequencing platforms and recalcitrant plant species. *Plant Methods*, **16**: 1–11.
- Wang, Z., Xiao, J., Fan, S., Li, Y., Liu, X. & Liu, D. (2015). Who made the world’s largest green tide in China? -An integrated study on the initiation and early development of the green tide in Yellow Sea. *Limnology and Oceanography*, **60**: 1105–1117.
- WFD 2000/60/EC. Directive 2000/60/EC of the European Parliament and of the Council of 23 October 2000 establishing a framework for Community action in the field of water policy OJ L 327, 22.12.2000, pp. 1–73.
- Witt, S. (2022). Water Framework Directive ecological monitoring in Poole Harbour, 2007–2019. In *Harbour ecology: environment and development in Poole Harbour* (Humphreys, J. & Hall, A., eds.), 183–195. London: Pelagic Publishing.
- Wood, D.E., Lu, J. & Langmead, B. (2019). Improved metagenomic analysis with Kraken 2. *Genome Biology*, **20**: 1–13.
- Wu, H., Gao, G., Zhong, Z., Li, X. & Xu, J. (2018). Physiological acclimation of the green tidal alga *Ulva prolifera* to a fast-changing environment. *Marine Environmental Research*, **137**: 1–7.