

Mapping the Distribution of an Intertidal Invasive Red Macroalga at a National Scale Using Satellite Remote Sensing.

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Abstract :

Invasive species have been ranked among the greatest causes of biodiversity loss, specifically the loss of already threatened or endangered species, with coastal and estuarine systems often bearing the brunt of initial introductions and subsequent invasions. This is likely due to high levels of global transport, alongside other anthropogenic activities within these systems. Macroalgae species make up a large proportion (40 %) of Invasive Alien Species in the European marine environment. Yet, monitoring of these macroalgal species is lacking: how they spread, change seasonally and affect local ecosystems is poorly understood. This lack of spatio-temporal information is prevalent even for species widespread across multiple countries and coastlines, such as the intertidal red macroalga *Gracilaria vermiculophylla* (formerly *Agarophyton vermiculophyllum*). Here we present the methods and results of using open-access Copernicus Sentinel-2 satellite imagery to map this invasive red macroalga across the Atlantic Coast of France for the summer of 2024. We initially improved training data of a published intertidal habitat classifier and validated the results using independently sourced data. By doing so, we achieved high levels of classification accuracy at predicting this red macroalga (93.2% global accuracy and 0.82 F1 score). We found that, while there were no evident latitudinal patterns, *G. vermiculophylla* was most prevalent within transitional (i.e. estuarine) intertidal areas when compared to more open coastal areas, where some hotspots were still identified. Furthermore, while it has been suggested that the initial invasion of *G. vermiculophylla* was mediated through aquaculture activities, the presence of aquaculture showed no clear relationship to the proportion of the red macroalga covering the intertidal area. Moreover, seasonal dynamics of extent for this red macroalga revealed difference between two sites, Belon Estuary in Brittany and Bonne Anse in the Gironde Estuary, known to have consistent *G. vermiculophylla* cover. This work provides an open-access map of *G. vermiculophylla* across the whole Atlantic Coast of France, as well as illustrating a framework that could be employed to allow rapid monitoring of invasive macroalgae. Monitoring and understanding spatio-temporal dynamics is an essential step in managing both invasive species and the ecosystems that they influence.

Keywords : Intertidal Zone, Invasive Macroalgae, National Mapping, Remote Sensing

42 **1. Introduction**

43 **1.1 Marine Invasive Species**

44 Globally, coastal and estuarine areas have been the marine zones most altered by human activities, with a
45 variety of pressures and activities ranging from elevated shipping traffic, coastal construction, aquaculture
46 and wetland reclamation (Green et al., 2021; Murray et al., 2019). The increased anthropogenic activity in
47 these areas elevates the risk of non-native species invasions by providing spread vectors and ecological
48 niches for potentially invasive species (Katsanevakis et al., 2023). Therefore, initial invasions are often
49 located in coastal and estuarine areas, which behave as stepping stones for further spread. Across Europe,
50 over 700 Invasive Alien Species (IAS) had been introduced to the marine environment by 2020, 40 %
51 being macroalgal species (Van Der Loos et al., 2024; Williams and Smith, 2007; Zenetos et al., 2022).
52 While many invasions occur due to accidental release, like the case of *Rugulopteryx okamora* in the
53 Strait of Gibraltar (Altamirano-Jeschke et al., 2016), some invasions can be traced to intentional
54 introductions like *Magallana gigas* (formerly *Crassostrea gigas*) (Troost, 2010). The Pacific oyster (*M.*
55 *gigas*) was introduced to the Atlantic coastline of Europe after the collapse of the Portuguese oyster
56 population (*Magallana angulata* formerly *Crassostrea angulata*) in the seventies. However, the oyster
57 introduction may have also led to the invasion of European coastlines by other unintended stow-aways,
58 such as the intertidal red macroalga *Gracilaria vermiculophylla*.

1.2 Gracilaria History

While *G. vermiculophylla*'s native range covers large areas of Japan and Korea, it has spread across the North Atlantic Ocean along both American and European coastlines, primarily driven by aquaculture and maritime activities (Krueger-Hadfield et al., 2017; Rueness, 2005; Van Der Loos et al., 2024; Weinberger et al., 2008). Since its first record in Europe in 1996, from the Belon Estuary in Western France, it has been recorded across much of the European Atlantic coast (Abreu et al., 2011; Nyberg, 2007; Rueness, 2005; Sotka et al., 2018; Weinberger et al., 2008). Its physiological plasticity, with high tolerance to large temperature, salinity, nutrient and disturbance ranges, allows it to inhabit a range of different intertidal habitats from rocky to muddy substrates, and from mesohaline waters of western Europe to the brackish waters of the Baltic Sea (Abreu et al., 2011; Nyberg, 2007; Rueness, 2005; Sotka et al., 2018; Surget et al., 2017; Weinberger et al., 2008). Once established this macroalga, unlike most native red macroalgae, forms dense monospecific expanses across large areas of the intertidal zone, especially mudflats, where it partially buries its thallus in the loose sediment to maintain its location (Surget, 2017). These monospecific expanses, often devoid of native macroalgae, have been argued to provide a beneficial influence on biodiversity by stabilising previously mobile sediments and providing habitat and food for small invertebrates and fish (Davoult et al., 2017; Nyberg et al., 2009). However, for this species, the full extent and ecosystem impact across the intertidal zone have been understudied, with little to no emphasis on its spatial or temporal dynamics (But see: Ross and Snyder (2024) and Bermejo et al. (2020)).

1.3 Monitoring Intertidal Invasions

Due to the practical difficulties of traditional *in situ* methods of studying intertidal soft-bottom environments, often characterised by large expanses of hard to access, potentially dangerous habitats that get flooded by the sea twice a day, the monitoring of intertidal vegetation has increasingly been supplemented by remote sensing techniques. Optical sensors attached to Uncrewed Aerial Vehicles (UAVs), such as drones, have been used to monitor individual sites, where their small pixel size can

provide extremely high resolution imagery over multiple kilometres squared from a single day (Oiry et al., 2024; Roca et al., 2022a; Román et al., 2024; Singh et al., 2024). Despite a lower spatial resolution, satellite remote sensing can usefully complement UAV remote sensing when trying to assess the spatial and temporal dynamics of an invasive macroalga as it provides systematically acquired and archived observations, making it possible to study the temporal dynamics of intertidal vegetation over a wide range of time scales (Zoffoli et al., 2021). Recent work aiming to map intertidal seagrass has led to the development of a modelling framework that categorises intertidal vegetation classes using the 10 m resolution imagery provided by Copernicus's Sentinel-2 mission (Davies et al., 2024a, 2024b). The Intertidal Classification of Europe: Categorising Reflectance of Emerged Areas of Marine vegetation using Sentinel-2 (ICE CREAMS) model provides a potential framework for mapping intertidal vegetation at national to international scales with a 10 m spatial resolution over time periods ranging from weeks to potentially decades, given current plans of Sentinel-2 continuity. To date, no operational algorithm exists for the consistent and scalable mapping of red macroalgae on soft-bottom substrates across national extents.

1.4 Objectives

The uniquely large spatial extents covered by *Gracilaria vermiculophylla* within the phylum of Rhodophyta occurring in intertidal mudflats of France allows for the detection at the spatial resolution of Sentinel-2 (i.e. 100 m² pixel size, Figure 1 c). By improving the ICE CREAMS model to detect red macroalgae from the Florideophyceae class ('red macroalgae' henceforth), we aimed to create a national scale map of the invasive intertidal algae across France, the country where it was first reported in Europe. This map allows us to explore potential associations with water body types (Coastal or Estuarine) and whether the potential original driver for its invasion, oyster aquaculture, continues to be associated with high levels of the algae. Furthermore, the ICE CREAMS model alongside archived data of Sentinel-2

106 allows us to explore the temporal dynamics of *G. vermiculophylla* in soft-bottom intertidal areas known
 107 to contain continual expanses of this macroalga.

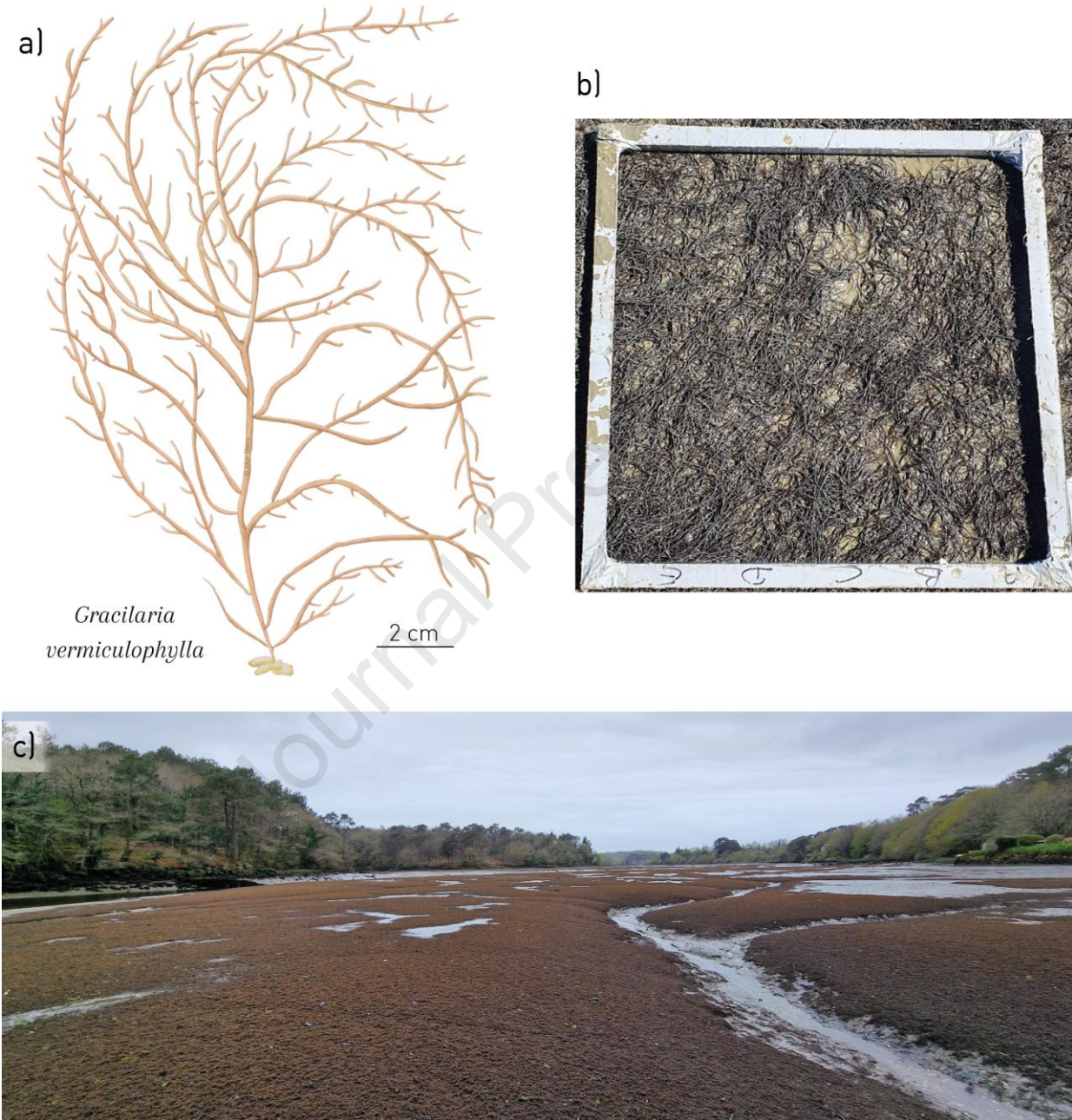


Figure 1: Scientific illustration of the general morphology of *Gracilaria vermiculophylla* (a, created by Mar Roca Mora), a high cover photo quadrat (b) and an example image of the

large spatial area of monospecific coverage by the red macroalga in the Belon estuary (c). All photos were taken by co-authors during fieldwork.

2. Materials and Methods

2.1 General Overview

To assess the occurrence and prevalence of the invasive intertidal red macroalga *Gracilaria vermiculophylla* at the scale of the Atlantic Coastline of France, an approach that combined a previously developed intertidal classification algorithm and a maximum vegetation composite of Sentinel-2 data was used (Figure 2). The Intertidal Classification of Europe: Categorising Reflectance of Emerged Areas of Marine vegetation using Sentinel-2 (ICE CREAMS v1.1) model, which has been previously used and validated to classify and quantify intertidal habitats across Europe (Davies et al., 2024a, 2024b), was updated and improved with the goal of effectively detecting intertidal red macroalgae colonising soft-bottom environment (ICE CREAMS v1.2, henceforth). The improvements to ICE CREAMS v1.2 were achieved by augmenting the quantity of training data by ~5000 pixels for the red macroalgae class. These new training data were derived from three multispectral UAV images, taken from two estuaries in Brittany, France (Aven and Belon) and one in Cantabria, Spain (Saja). To appraise the improved accuracy of ICE CREAMS at detecting red macroalgae, independently acquired validation data, in the form of 561 geo-referenced quadrats, were collected from across multiple other sites in Brittany, France, as well as a high-resolution drone image in Bonne Anse, an enclosed bay located in the northwestern part of the Gironde estuary, France. These data were used to assess the accuracy difference at identifying red macroalgae by ICE CREAMS v1.1 and v1.2. To assess the intertidal soft-bottom area along the French Atlantic coast covered by red macroalgae, a composite of Sentinel-2 imagery was created for soft-bottom intertidal areas, taking the maximum vegetated pixels captured from 1st July to 31st October of 2024, as

the time of year with the highest vegetation coinciding with the largest tidal ranges in France. The results of applying ICE CREAMS v1.2 to this composite provided a full intertidal red macroalgae estimate of the Atlantic coast of France. Finally, two sites known to harbour *G. vermiculophylla* were selected (Bonne Anse and Belon Estuary, France). These are two sites in France known to have consistently hosted large extents of *G. vermiculophylla* throughout the time frame of Sentinel-2 (i.e. 2016-present). Hence, all available cloud-free low-tide Sentinel-2 images from 2018 to 2024 were downloaded, processed and predicted on by ICE CREAMS V1.2. Given that no other species of soft-bottom intertidal red macroalgae in Europe is known to form extensive, anchored covers at the spatial scale of Sentinel-2 pixels, all pixels classified as red macroalgae were assumed to correspond to *G. vermiculophylla*, even though the methodology does not allow species-level discrimination. This assumption is supported by empirical observations across 47 sites from northern Brittany (France) to Galicia (Spain), where *G. vermiculophylla* was the only species forming large, anchored mats detectable at this scale (See Supporting Information). The results from these predictions allowed for an initial assessment of the temporal dynamics of *G. vermiculophylla* for these sites.

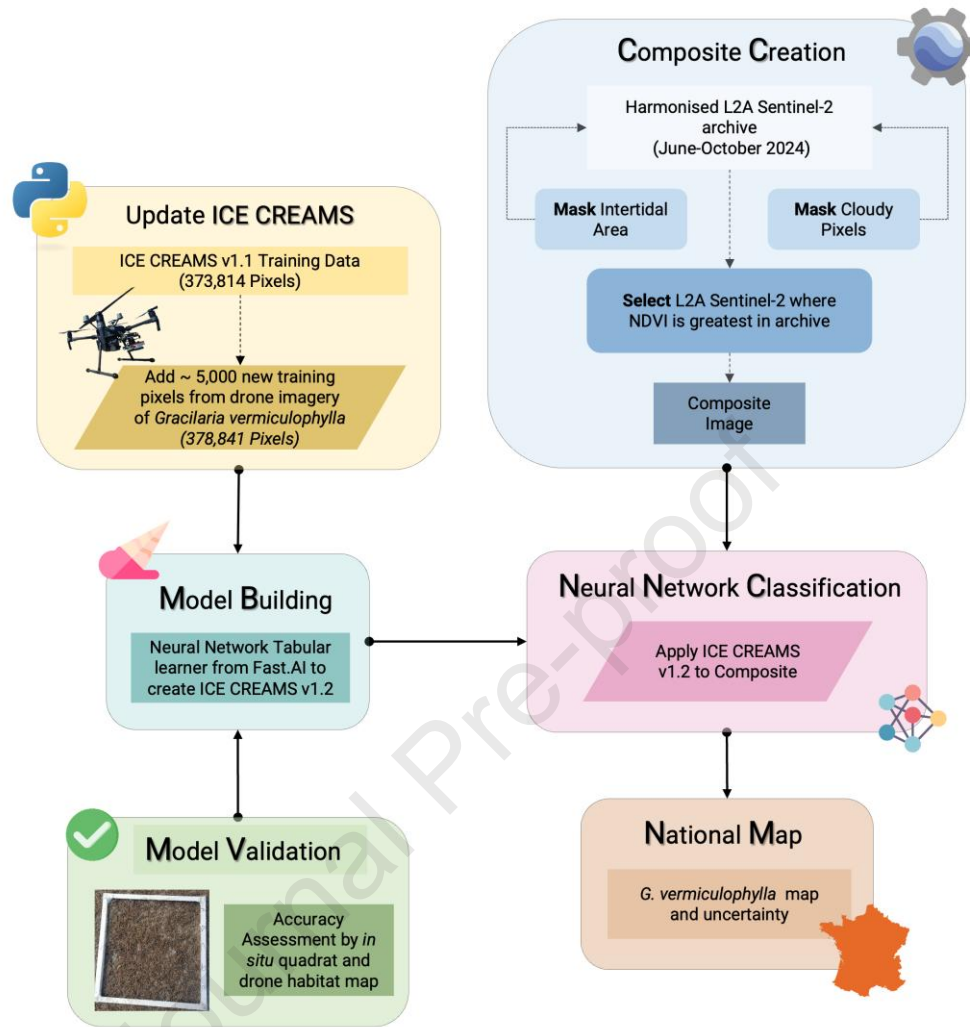


Figure 2: Flow chart of ICE CREAMS model update to detect *G. vermiculophylla*, composite image creation and application of updated ICE CREAMS to this composite.

2.2 Update ICE CREAMS and Model Building

2.2.1 ICE CREAMS v1.1

The ICE CREAMS model is a neural network tabular learner from the FastAI framework in Python v3 (Howard and Gugger, 2020; Van Rossum and Drake, 2009). ICE CREAMS v1.1 consisted of 373,814

labelled pixels consisting of 26 features (12 bottom-of-atmosphere reflectances, 12 standardised reflectances, Normalised Difference Vegetation Index (NDVI) and Normalised Difference Water Index (NDWI)), with labels covering 9 classes: Bare Sand, Bare Mud, Ulvophyceae (green macroalgae), Magnoliopsida (seagrass), Microphytobenthos (unicellular photosynthetic eukaryotes and cyanobacteria), Mixed-Rocks and Phaeophyceae (brown macroalgae), Rhodophyta (red macroalgae), Xanthophyceae (yellow-green macroalgae) and Water (Davies et al., 2024a, 2024b).

2.2.2 ICE CREAMS v1.2

ICE CREAMS v1.2 was created by retraining the model on a training data set with an increased total number of labelled pixels (378,841), while maintaining all other training parameters and model architectures from v1.1 (2 hidden layers, 26,761 trainable parameters and fine-tuned across 20 epochs using the ADaptive Moment estimation (ADAM) optimiser). These new labelled pixels were derived from multispectral UAV to provide both geographically and temporally explicit delineation of known intertidal habitats (Oiry et al., 2025, 2024). Three UAV flights were performed during low-tide and during favourable atmospheric conditions (i.e low cloud cover), meaning that the areas of red macroalgae were observed during vegetation emersion. These three flights were carried out in two sites in Brittany, France and one in Cantabria, Spain (Figure 3). From the high resolution UAV imagery, resampled 10 m red macroalgae dominant pixels were used.

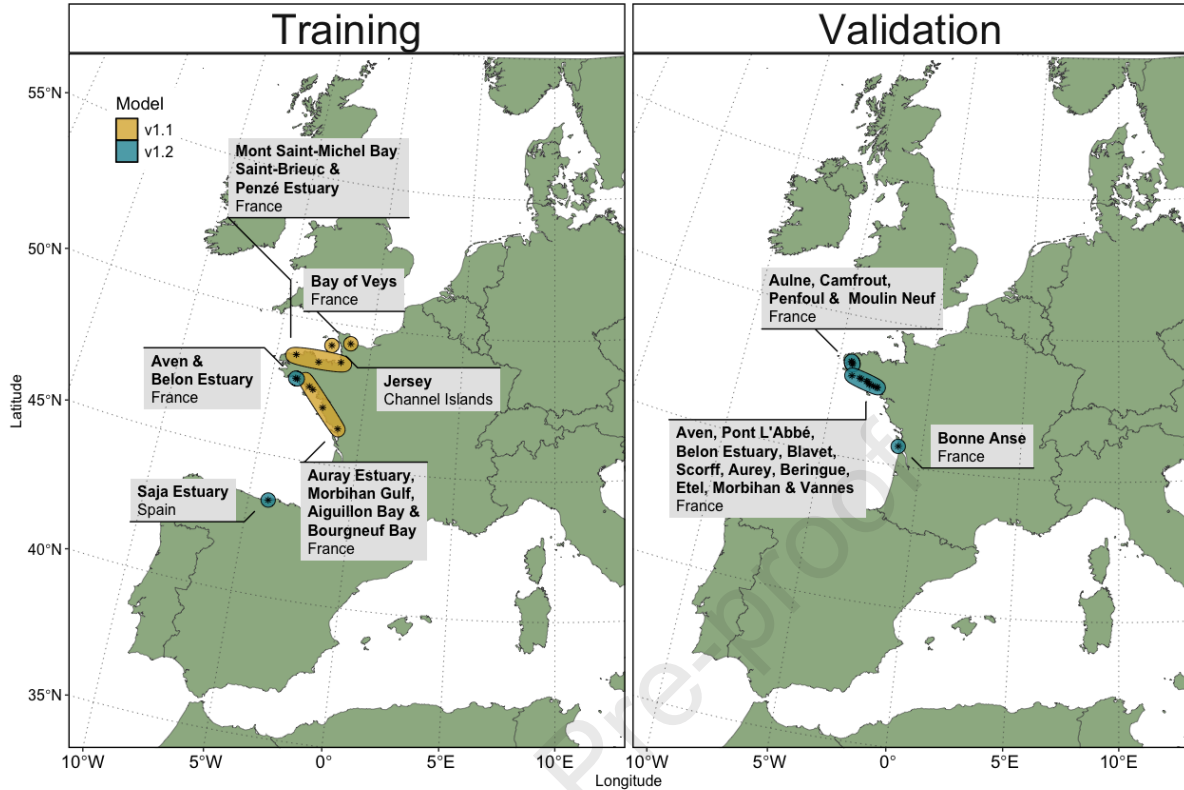


Figure 3: Training and Validation data collection sites for ICE CREAMS v1.1 and v1.2 across Europe. Coloured polygons show geographically nearby regions, while asterisks denote specific locations within those regions. Note that only validation for v1.2 is displayed.

2.2.3 Model Validation

To create an independent validation set of intertidal *G. vermiculophylla*, sites were gathered from previous research as well as new sites identified through remote sensing imagery inspection (17 in total). For new site prospection, intertidal zones matching the preferred biogeophysical characteristics for *G. vermiculophylla* across the Atlantic European coastline were inspected visually using historical satellite imagery. Potential *G. vermiculophylla* zones were then assessed for their practical accessibility and distribution. Geo-referenced quadrats were then taken across Brittany as well as a high resolution RGB drone image from Bonne Anse Bay (Figure 3). This resulted in 25,213 validation pixels: 5,021 of *G.*

vermiculophylla and 20,192 without *G. vermiculophylla*. Low-tide cloud free Sentinel-2 imagery was then predicted on by both ICE CREAMS v1.1 and v1.2 for the closest temporal match to the validation data (± 30 days). Comparisons of these predictions and the *in situ* validation data were used to assess model performance. Global model accuracy (G_a Equation 1) and F1 score ($F1$ Equation 2) were calculated for both ICE CREAMS v1.1 and v1.2 across all validation data as binary presence or absence of red macroalgae:

$$G_a = \frac{n_{TP} + n_{TN}}{n_{TP} + n_{TN} + n_{FP} + n_{FN}} \quad (1)$$

$$F1 = \frac{n_{TP}}{n_{TP} + 0.5 * (n_{FP} + n_{FN})} \quad (2)$$

where n_{TP} is the number of True Positives, n_{TN} the number of True Negatives, n_{FP} the number of False Positives and n_{FN} the number of False Negatives.

2.3 Composite Creation

2.3.1 Spatial Masking

Composites were created by first spatially masking intertidal areas along the French Atlantic coast, using the intertidal flats product from Murray et al. (2019), modified with NDVI and NDWI time-series analysis of Sentinel-2 imagery for all pixels of 6-years of Sentinel-2 L2A imagery (2018-2023) that occurred within 900 m of the previous intertidal mask using cloud-computing hosted by Google Earth Engine (GEE) (Gorelick et al., 2017). Areas that were both commonly flooded (negative NDVI and positive NDWI), and exposed and dry (positive NDVI and negative NDWI) were selected (Davies et al., 2026). Solid structure (i.e. artificial structures or natural rock formations) and saltmarsh habitats were further spatially masked using time-series of Sentinel-1 Synthetic Aperture Radar (SAR) data from within GEE. Both co- and cross-polarisation (VV and VH) bands of SAR data were summarised from within the previous intertidal mask for the year of 2022. For each pixel and each band, the 90th percentile (VV_{90} and

VH_{90}) and Standard Deviation (VV_{σ} and VH_{σ}) were calculated and thresholds were derived for pixels of high structural complexity (high VV_{90} and VH_{90}) and high variation due to emersion and immersion during tidal cycles (high VV_{σ} and VH_{σ}).

2.3.2 Temporal Masking

Pixels that visually showed inaccurate spectra or included clouds were also removed following Davies et al. (2026). Cloudy pixels were also masked following a 2 step process. First, a 15% mean cloud-cover threshold for each clipped tile according to the designed coastal geometry assets was applied to reduce the cloud probability dataset ('COPERNICUS/S2_CLOUD_PROBABILITY') into per-pixel probabilities for each image (Roca et al., 2022b). Second, the Cloud Score + method (CS+: 'GOOGLE/CLOUD_SCORE_PLUS/V1/S2_HARMONIZED'), an integrated model in GEE that uses a maximum likelihood estimate of terrain illumination, was used to mask the remaining clouds and cloud shadows (Pasquarella et al., 2023). The cloud masking was performed using the CS+ Cumulative Distribution Function (CDF) of Quality Assessment (QA) band 'cs_cdf' at a 0.6 threshold.

2.3.3 Quality Mosaic

To generate the composite image, a quality mosaic containing all available bands of Sentinel-2 was created, that maximised the NDVI from all remaining pixels available between 1st July and 31 October 2024.

2.3.4 Neural Network Classification and National Map

The ICE CREAMS v1.2 model was then applied to this composite image and all red macroalgae pixels, their accompanying model probability score and date of acquisition were extracted.

2.4 Hotspots of Intertidal Red Macroalgae

Hotspots of red macroalgae were made by calculating the weighted kernel density of all red macroalgae locations using the ‘spatialEco’ package in R (Evans and Murphy, 2023; R Core Team, 2023). Predicted probabilities were used as weights, with a ground resolution of 500 m and a kernel bandwidth of 2000 m. All above zero density values were then converted to polygons, and all polygons within 2 kilometres of another were grouped, and the median density was aggregated per hotspot.

2.5 Water Body Characteristics

2.5.1 Transitional vs Coastal

All raw red macroalgae predictions were spatially grouped into water bodies defined by the Office Français de la Biodiversité (OFB), which can be defined as either Coastal or Transitional. A total of 116 coastal (73) and estuarine (43) areas were analyzed along the French western coastline, ranging from 51 °N at the Belgian border to 43 °N at the Spanish border. For each water body the total intertidal area was calculated, as well as the proportion of that area predicted to be covered by red macroalgae. Only water bodies that contained soft-bottom intertidal area were assessed. The uncertainty (τ Equation 3) was calculated for each water body as the inverse of the mean of the per pixel probabilities from the classification model ($\bar{p}$) divided by the global accuracy (G_a Equation 1) of the model when applied to validation data (Davies et al., 2026, 2024a, 2024b; Roca-Mora et al., 2026).

$$\tau = \frac{1 - \bar{p}}{G_a} \quad (3)$$

2.5.2 Oyster Aquaculture

Due to the widely supported hypothesis of the introduction of *G. vermiculophylla* being linked with oyster aquaculture, the presence of aquaculture within a water body was also assessed. The presence of

oyster aquaculture within each different water body was estimated by using the National Register of oyster aquaculture from 2022 (<https://sextant.ifremer.fr/Donnees/Catalogue#/metadata/98a7c90e-33c8-44bc-a27a-9b7b61ae829f>), that was overlaid on top of the different water bodies, and the intertidal area covered by oyster aquaculture was calculated. The levels of aquaculture activity were then grouped into No (Less area than one Sentinel-2 Pixel, i.e. <100 m²) and Yes (>100 m²).

2.6 Trends Over Time

To assess whether there were any inter- or intra-annual variations in red macroalgae cover, two sites where large mats of *Gracilaria vermiculophylla* are known to be present throughout much of the year: Belon Estuary and Bonne Anse (Figure 4). For both sites, all cloud free, low-tide Sentinel-2 L2A images from 2018 to 2024 were selected from the Sentinel-2 Long Term Archive (LTA: Supplementary Material Table 1). A mask was used to isolate only pixels within the intertidal area (Murray et al., 2019). ICE CREAMS v1.2 model was applied to classify intertidal habitats, and all instances of red macroalgae were extracted and summarised as a total area per image. The per image uncertainty (τ) was also calculated as above.

2.7 Statistical Analysis

2.7.1 Change with Water Body Characteristics

A General Linear Mixed-Effects Model (GLMM) was used to assess the proportion of intertidal area covered by red macroalgae within a Water Body Type and whether that was influenced by the Presence of Oyster Aquaculture. Model parameters were estimated within a Bayesian framework using the ‘brms’ and ‘RStan’ packages in R to leverage the Stan language (Bürkner, 2021; Carpenter et al., 2017; Stan Development Team, 2018). Observed proportion, which was centred and scaled ($E * _i = \frac{\kappa_i - \bar{\kappa}}{\kappa_{\sigma}}$, where i denotes each individual sample), of intertidal area covered by red macroalgae ($E * _i$) and its uncertainty

(τ_i) were modelled (Equation 4) as a function of the interaction between water body type (ψ) and the presence or absence of oyster aquaculture (θ), with region as a random factor (R). To account for spatial-autocorrelation between neighbouring areas a two-dimensional tensor product smooth ($f(\Delta)$) was used based on the UTM latitude and longitude with a cubic regression spline with shrinkage (Wood, 2017). The response variable was modelled assuming a Student-t distribution with weakly informative priors. Model parameters were estimated using Markov Chain Monte Carlo (MCMC) sampling, with 4 chains of 10,000 iterations and a warm-up of 500.

$$\begin{aligned}
 E_{*i} &\sim \text{Student}(E_i, \tau_i) \\
 E_i &\sim \text{Student}(\mu_i, \sigma_i) \\
 \mu_i &= a_{R[i]} + \psi: \theta + \psi + \theta + f(\Delta) \\
 a_{R[i]} &\sim \text{Student}(\bar{a}, \delta) \\
 \bar{a} &\sim \text{Student}(3, 0, 2.5) \\
 \psi &\sim \text{normal}(0, 1) \\
 \theta &\sim \text{normal}(0, 1) \\
 \psi: \theta &\sim \text{normal}(0, 1) \\
 f(\Delta) &\sim \text{Student}(3, 0, 2.5) \\
 \sigma &\sim \text{gamma}(2, 0.1)
 \end{aligned} \tag{4}$$

2.7.2 Change Over Time

A General Additive Model (GAM) (Wood, 2017) was used to assess trends of red macroalgae extent across two sites; model parameters were estimated, as above, within a bayesian framework. Centred and scaled observed total red macroalgae cover ($E_{*i} = \frac{\kappa_i - \bar{\kappa}}{\kappa_\sigma}$) and its uncertainty (τ_i) were modelled (Equation 5) as a function of Time with a basis spline ($f(t_i)$) across Locations (ρ) and Day of the Year with a cyclic basis spline ($f(DOY_i)$) across Locations (ρ). The response variable was modelled assuming a Student-t distribution with weakly informative priors. Model parameters were estimated using MCMC sampling, with 4 chains of 10,000 iterations and a warm-up of 500.

$$\begin{aligned}
E_i &\sim Student(E_i, \tau_i) \\
E_i &\sim Student(\mu_i, \sigma_i) \\
\mu_i &= f(DOY_i): \rho + f(t_i): \rho \\
f(DOY_i): \rho &\sim Normal(0,1) \\
f(t_i): \rho &\sim Normal(0,1) \\
\sigma_i &\sim Student(3,0,2.5)
\end{aligned} \tag{5}$$

3. Results

3.1 Validation Comparison

Agreement between ICE CREAMS v1.2 and the *in situ* sampling visually was evident, especially in the Belon and Bonne Anse sites (Figure 4), although finer-resolution patterns evident from the high-resolution RGB imagery of Belon were not clear from the prediction on coarser resolution sentinel-2 imagery (Figure 4 a & c). A formal validation comparison of ICE CREAMS v1.1 and v1.2 across ~25,000 Sentinel-2 pixels also shows v1.2 is superior at detecting red macroalgae, with both versions achieving acceptable global accuracies (v1.1: 80.1 % & v1.2: 93.2 %; Figure 5). However, this similarity in accuracy was due to the high number of True Negatives accurately predicted by v1.1, while this version of model failed to accurately predict a single True Positive. Conversely, ICE CREAMS v1.2 accurately predicted around 4,000 of the 5,000 *G. vermiculophylla* pixels. This significant increase in accurate prediction was reflected in the far greater F1 score achieved by v1.2 (0.824) compared to v1.1 (0).

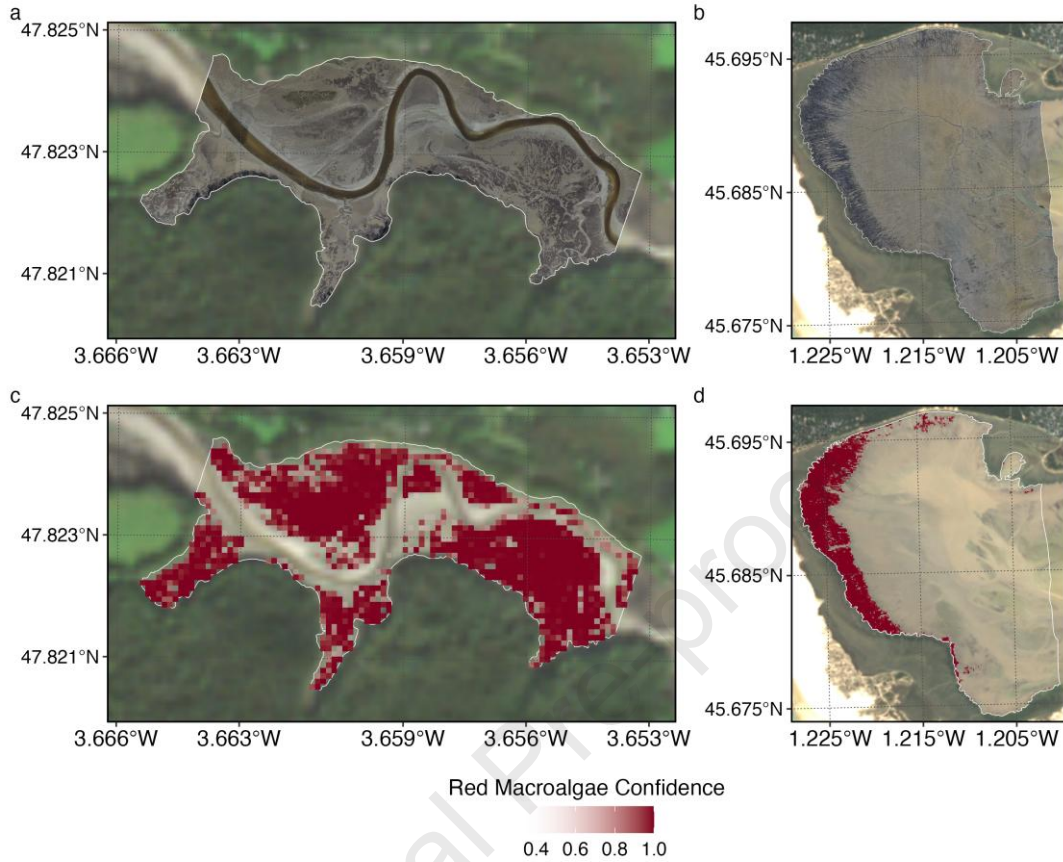


Figure 4: Visual comparison between ultra-high resolution drone imagery (Belon: a & Bonne Anse: b) and ICE CREAMS v1.2 predictions for temporally similar dates (Belon: c & Bonne Anse: d). Drone imagery were taken on the 26-11-2024 for Belon and 27-03-2025 for Bonne Anse, while Sentinel-2 imagery that ICE CREAMS v1.2 predicted on were taken on the 05-10-2024 for Belon and 02-04-2025 for Bonne Anse. ICE CREAMS v1.2 predictions show all pixels predicted as red macroalgae, with the intensity of colour being the confidence in prediction.

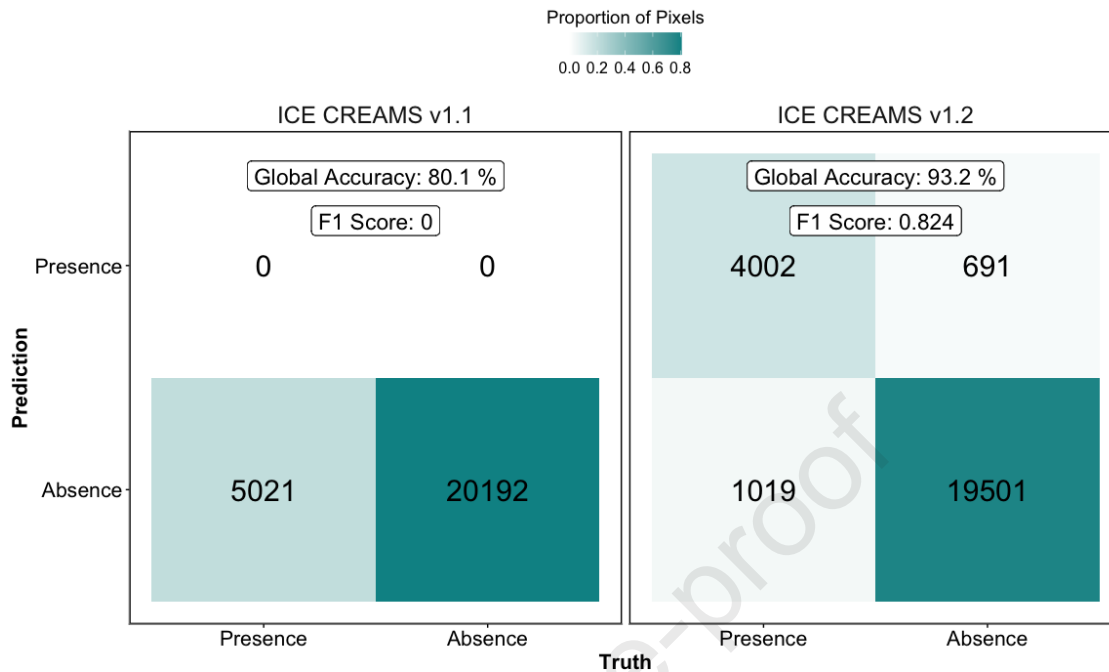


Figure 5: Validation results for both v1.1 and v1.2 of ICE CREAMS, showing Global accuracy and F1 Score. Colour denotes the proportion of the total pixels for a specific group and labels show how many pixels for a specific group.

3.2 Intertidal Red Macroalgae Hotspots

The majority of the hotspots of intertidal red macroalgae were found in the Brittany area of France (Figure 6), although the highest densities were found more south, in Arcachon Bay and Bonne Anse. Generally, the majority of hotspots were located within estuaries, with only 4 of the top 10 hotspots not in estuarine locations (Arcachon, Sillon de Talbert, Île de Batz and Paimpol).

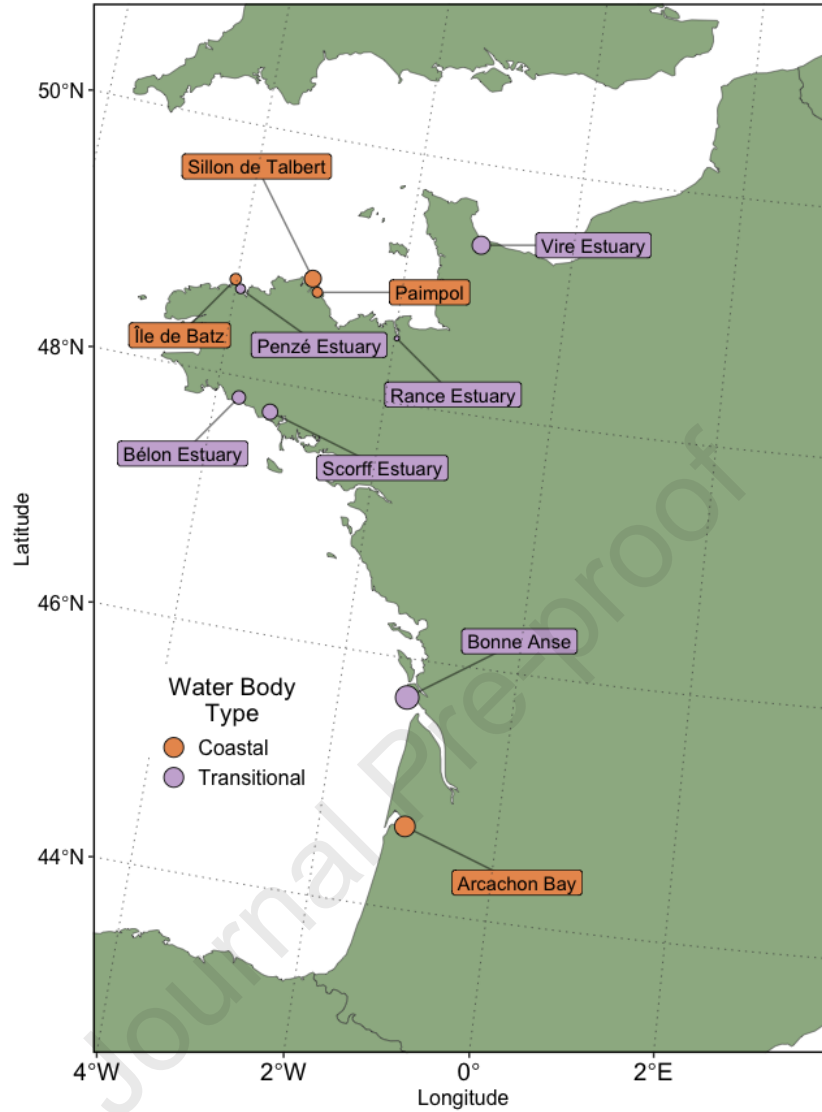


Figure 6: Intertidal red macroalgae hotspots across the Atlantic coastline of France. Size of points denote the density of predicted red macroalgae of the hotspots, given a kernel density resolution of 500 m and a bandwidth of 2,000 m. Colour denotes whether the site is found within a coastal (orange) or transitional (purple) water body.

3.3 Coastal vs Transitional Water Bodies

The estimated percentage of the intertidal area covered by red macroalgae in coastal water bodies (2.43 ± 3.3 & 2.68 ± 3.26 %, for areas with and without oyster aquaculture, respectively) was consistently lower than in transitional water bodies (5.71 ± 3.58 & 4.88 ± 4.31 %, for areas with and without Oyster aquaculture, respectively). This was regardless of the level of oyster aquaculture activity; aquaculture activity in transitional waters was associated with marginally greater estimated cover of the intertidal area (Figure 7). While the estimated uncertainty was generally large, the estimated cover of intertidal areas of transitional waters was ~ 2.1 times greater than coastal waters.

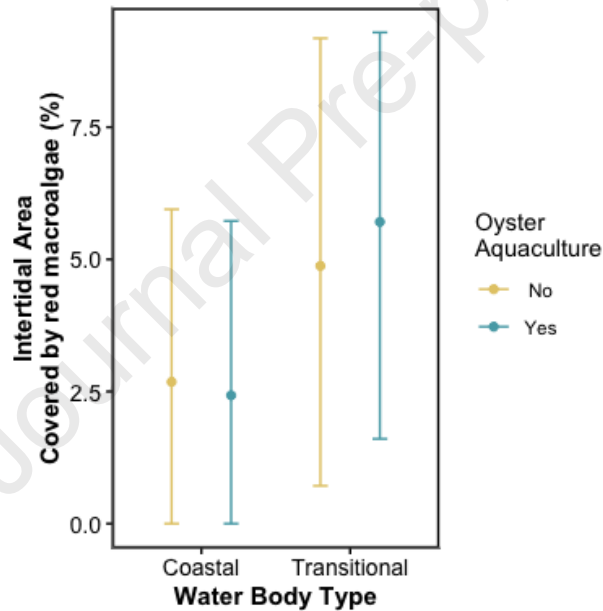


Figure 7: The modelled percentage of the intertidal area predicted to be red macroalgae between Coastal and Transitional Water Bodies, and the level of Oyster Aquaculture activity (No: Yellow and Yes: Blue). Points show median modelled GLMM estimates, while error bars show 89 % confidence intervals.

3.4 Change Over Time

Across the two sites assessed, there were very different inter- and intra-annual variations in the area of red macroalgae predicted (Figure 8). Inter-annually, Belon estuary showed a marginal increase in area from 2018 to 2024, while Bonne Anse showed an inverse pattern, with a decrease over the same time period. Intra-annually, Belon appeared to show phenology-like patterns, with seasonal increase and decrease in area, while no such patterns were found in Bonne Anse. Belon showed greater areal cover during boreal winter, i.e. December-January, compared to summer, i.e. July-August, yet there were consistently red macroalgae present throughout the year. Conversely, Bonne Anse showed individual images of almost zero red macroalgae cover.

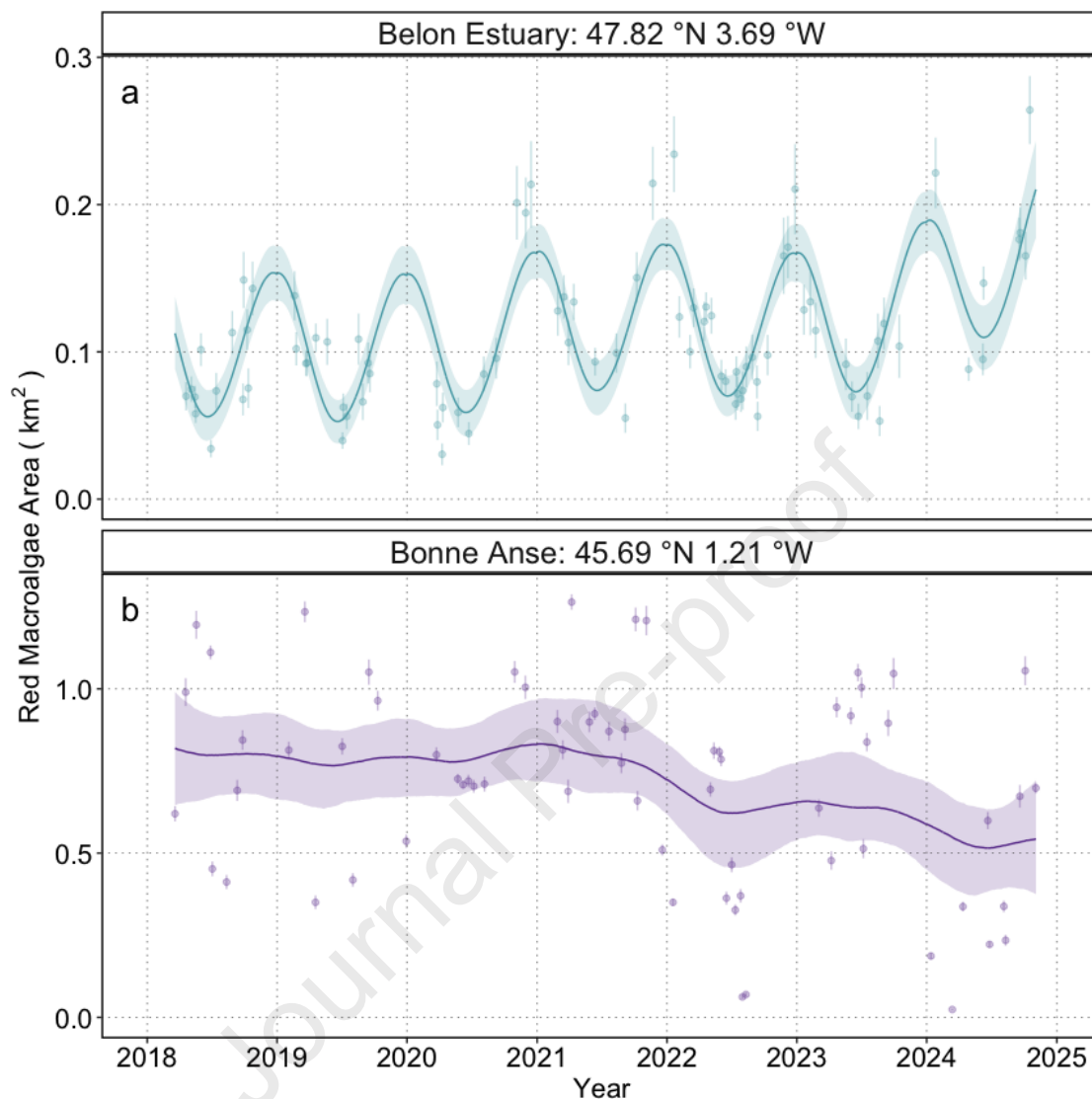


Figure 8: The modelled intertidal area predicted to be red macroalgae over time for the Belon Estuary and Bonne Anse. Lines show modelled median GAM estimates with shading showing 89% confidence intervals, while points show raw estimates with error bars showing 89 % confidence intervals.

4. Discussion

This work has shown the successful improvement of an open access intertidal remote sensing classification model at discriminating an invasive red macroalga, *Gracilaria vermiculophylla*, at the national scale of France. By applying this model to a composite of Sentinel-2 imagery, hotspots of this red macroalgae have been identified across France, notably within the Gironde Estuary and Arcachon Bay, as well as multiple estuaries and bays in Brittany. Furthermore, this work highlights the greater proportion of intertidal areas covered by this invasive red macroalgae in transitional water bodies compared to coastal areas, yet showed little pattern of influence by the presence of local aquaculture activity. Finally, the work is the first description of temporal dynamics in *G. vermiculophylla* that take into consideration both inter- and intra-annual variation, and showed that these temporal patterns are not consistent between the two sites assessed.

4.1 Invasive Species Management

The fundamental first step of effectively managing any natural or non-natural system is to understand spatial and temporal dynamics within that system. Temporal information is vital to detect real changes in ecosystems as opposed to seasonal fluctuations, while spatial and temporal dynamics can provide relevant information for management, both at local and regional scales. These data are vital for most forms of mechanistic modelling, which can provide essential insights, such as spread rate, ecosystem effects of that spread and the efficacy of different management strategies (Baker and Bode, 2021; Thompson et al., 2021). The large spatial and temporal scales that remote sensing can provide for marine invasive species monitoring come with a relatively poor, lower detection limit, especially when you compare the size of a Sentinel-2 pixel (100 m²) to that of an individual plant (~ 5 cm²). This would likely make it ineffective at early detection of invasions. While higher resolution remote sensing data, both optical and radar, are available, they are not freely available; ultra-high resolution data usually cost the end user and are rarely

systematically acquired, meaning historic or temporal analyses are difficult to perform. Therefore, these lower resolution remote sensing methods should be combined with *in situ* sampling methods that can provide greater sensitivity, even if at smaller spatial extents.

4.2 Transitional over Aquaculture

Transitional water bodies, coastal areas that are in proximity and therefore highly influenced by freshwater inputs, are dynamic systems, with large natural variations in temperature, salinity and oceanographic regimes, but are also vulnerable to accumulated human impacts. This vulnerability stems largely from their close proximity to human activities and has historically led to these systems, alongside coastal areas, being in poor ecological state (Ferreira et al., 2007). Being highly degraded but also extremely changeable ecosystems makes them vulnerable to invasions (González-Ortegón and Moreno-Andrés, 2021), especially when species with elevated physiological plasticity are concerned (Johnston et al., 2017; Surget et al., 2017). Our results seem to agree with this, with higher proportions of the invasive red macroalgae in transitional water bodies than coastal waters. Though it has been suggested that the original introduction of *G. vermiculophylla* was associated with aquaculture activities, we found little difference between areas with aquaculture and those areas without, likely due to the large time lag between the current study and the initial introduction, likely fifty years ago (Oiry et al., 2025). This might imply that once established in an area, the vector of spread is not exclusively aquaculture derived. It should be noted that oyster aquaculture was represented using a simplified binary variable due to limitations in the availability and spatial resolution of open-access data, and therefore the absence of a clear relationship should be interpreted with caution, as finer-scale information on aquaculture intensity, type, and history could not be incorporated.

4.3 Model Transferability

The underlying aim for many habitat classification and ecosystem mapping machine learning models is to transfer that model to different scales or resolutions. This may be by spatially transferring a model from one location to another, applying it at a larger spatial scale or even at different spatial resolutions (Oiry et al., 2024), or applying the model across different temporal scales whether inter- or intra-annually, or even across decades (Zoffoli et al., 2021). Yet, less emphasis has been given to transferring models to different taxonomic scales or resolutions (But see: Bridges et al., 2025; Oiry et al., 2025). Here, the ICE CREAMS model was used to map red macroalgae, even though this model was created to map intertidal seagrass across Europe (Davies et al., 2026, 2024a, 2024b), allowing the mapping of the invasive red macroalga *G. vermiculophylla* at the scale of France. However, this was only facilitated by the low diversity of red macroalgae in Europe that cover soft-bottom tidal flats at the scales of Sentinel-2 pixels, although there are a few exceptions with combined mixtures of multiple red macroalgae species as well as the potential to confuse with other species in the same genera, although these species are most prevalent in rocky rather than soft bottom coastal areas (Supplementary Material). The same approach could not be used to detect invasive green or brown macroalgae, for which the discrimination from native species would be extremely challenging. Likewise, this approach would be less effective for the detection of non-vegetation or non-vegetation like species. Furthermore, given the spectral resolution of Sentinel-2, similarities between this red macroalga and some brown macroalgae in some particular ecosystems may cause model confusion or inaccuracy. Finally, this national-scale distribution map is based on a single seasonal composite (July–October 2024) and therefore represents a snapshot of peak biomass conditions rather than a baseline or long-term trend; as such, the results should be interpreted as an initial assessment demonstrating the potential of the approach rather than a temporally integrated product.

5. Conclusions

By improving the training data of a published intertidal habitat classifier, we achieved high levels of classification accuracy at predicting an invasive red macroalgae (93.2% global accuracy and F1 score of 0.82), which colonises mudflats. This improved model, being a pixel-based classifier relying solely on Sentinel-2 reflectance, meant the entire intertidal area of France could be assessed from the summer of 2024, while specific sites were assessed from 2018-2024. The lack of latitudinal spatial pattern showed a ubiquitous cover of the invasive red macroalga *Gracilaria vermiculophylla* across France, but a greater association with transitional water bodies than coastal areas was found. Likewise, no pattern was detected in relation to aquaculture practices, which have been linked to the original invasion of this species in Europe. By assessing temporal patterns we showed that this invasive algae shows inconsistent inter- and intra-annual patterns in areal extent, with general increases alongside seasonal fluctuations in the Belon Estuary, but no clear seasonality and general decline in area in Bonne Anse. These data and the described framework for intertidal invasive species mapping provide useful information for management of this and potentially other invasive species. However, the spatial resolution of these data require associated high resolution *in situ* data to supplement and provide the full picture. In particular, the sites where *Gracilaria vermiculophylla* was estimated to be absent from a satellite point of view should be investigated with particular attention in the near future in order to confirm the findings of the current study and monitor any potential development of this invasive algae. Therefore, future work should focus on combining a range of methods and data to be able to fully assess how to effectively assess and mitigate the effects of invasive species.

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