





## Distribution pattern and biochemical variability of Irish invasive seaweed across a spatial gradient

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### ABSTRACT

This study updates the distribution of seaweed invasive alien species (IAS) in Ireland and demonstrates the natural spatial variation of their phenolic compounds and fatty acid profiles, coupled with an assessment of biomass availability. We examined the intertidal area of 68 coastal locations and detected the presence of six IAS, but abundant populations (30–50 % cover) were only recorded for *Sargassum muticum* in some western and southern locations along the Irish coast. However, the fact that so many invasive species were widely distributed represents a dormant threat to Irish coastal ecosystems. Regarding distribution, we detected a spatial expansion of *Colpomenia peregrina* and *Codium fragile*, while a contraction was recorded for *S. muticum* and *Asparagopsis armata*. *Undaria pinnatifida* represents a recent introduction, and *Gracilaria vermiculophylla* is spreading to new locations in the south and west. In general, saturated fatty acid content was high in *C. fragile* and *C. peregrina* samples, and higher monounsaturated fatty acid content occurred in the latter. *Sargassum muticum* and *G. vermiculophylla* presented more polyunsaturated fatty acids and n-3 fatty acids (together with *C. fragile*). Statistical analyses showed that, for to *S. muticum*, higher water temperatures decreased metabolite content in all areas sampled, and higher concentrations of metabolites were generally found in northern populations. However, biomass was not abundant at these sites, which poses challenges facing valorisation of these natural resources. This study provides important baseline information of fatty acid profiles and phenolic content of Irish IAS, an essential preliminary step in industrial sourcing of marine bioactive metabolites.

### 1. Introduction

Invasive alien species (IAS) threaten the diversity of marine and coastal ecosystems and may have significant social, economic and health consequences. Thus, their management is crucial for biodiversity conservation and human wellbeing. International institutions have recognized the need to monitor and eradicate biological invasions, as reflected in the Convention on Biological Diversity (CBD COP15, 2022). Therefore, in any given territory, knowing the number of IAS and their abundance is not only the necessary baseline to create conservation programs but also underpins prioritisation of governmental efforts aimed at preserving native biodiversity. Specific impacts of IAS are linked to high growth rates with severe impact on *in situ* light conditions, nutrient levels and substratum availability, in particular in marine systems (Schaffelke and Hewitt, 2007; Engelen et al., 2015). Uncovering

the biotechnological potential of unwanted biomass - a term known as “valorisation” - could be integrated into IAS management plans as a part of mitigation measures. Valorisation of invasive species may be interesting since some represent prolific sources of valuable secondary metabolites, and a common characteristic of invasions by seaweed is the production of abundant biomass. Applying this approach to marine invasive species/processes to date remains novel, and somewhat controversial, though some cases studies have already been undertaken (Milledge et al., 2016; Alburquerque et al., 2019; Amador-Castro et al., 2021; Pereira et al., 2021; Pinto et al., 2022).

In Ireland, the most recent comprehensive marine IAS report incorporating seaweed records is dated 2007 (Minchin, 2007) though recent studies (e.g. (Schoenrock et al., 2019; Bermejo et al., 2020; O’Shaughnessy et al., 2023)) have added few new species in selected locations. The natural content and variability in biochemical composition of a

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species in large geographical areas provides an opportunity to evaluate their chemical potential, and Irish invasive seaweed rarely have been studied in this regard. As a result, their biotechnological potential remains largely unknown but deserves investigation to support future valorisation efforts and expand the knowledge of the potential of invasive species worldwide. For example, fatty acids and phenolic compounds in seaweed have many biological activities and have been target compounds in recent valorisation studies. Phenolic compounds are secondary metabolites found, amongst others, in phaeophytes and are involved in seaweed protection, playing a protective role against biota such as grazers, bacteria, fungi or other epiphytes (Plouguerné et al., 2006; Le Lann et al., 2008; Wijesinghe and Jeon, 2012), and abiotic stressors such as UV-radiation (Cotas et al., 2020). Interesting commercial applications of phenolic compounds relate to their reported antioxidant, antimicrobial, anticancer and anti-inflammatory activities (Jimenez-Lopez et al., 2021; Lomartire et al., 2021). Further, regarding fatty acids, in general, seaweed are characterized by a fatty acid composition that is quite beneficial for animal health, with contents of non-saturated fatty acids usually higher than those of saturated fatty acids (SFA (Pereira et al., 2012)). Some seaweed contain essential polyunsaturated fatty acids that are not synthesized by the human body and need to be obtained through diet, thus are considered essential. Additionally, long-chain monounsaturated fatty acids (MUFA) have antibacterial properties (Zheng et al., 2005) and seaweed derived polyunsaturated fatty acids (PUFA) have been posed as a promising source of prostaglandins, which act as cellular hormones in higher animals and humans (Imbs et al., 2012). Other potential uses of PUFAs are linked to their capacity to exert suppressive effects on patients with cardiovascular, inflammatory and autoimmune diseases (Simopoulos, 2004; Jayawardena et al., 2019). Furthermore, seaweed n-3 fatty acids are unique marine-derived lipids with considerable health and economic consequences (Ackman and McLachlan, 1978). The biochemical range presented by seaweed within phenolics and fatty acids with versatile applications allows us to use them as good proxies for valorisation studies (Pereira et al., 2021; Rocha et al., 2021).

However, despite being theoretically tempting, the commercial exploitation of invasive species is disputable. Particularly, harvesting of wild biomass can be problematic since seaweed settles on public spaces (beaches), which are part of the public domain, thus restricting their use. Additionally, those IAS included in official governmental checklists can have their management regulated. Other challenges include seaweed taxonomy -which possess difficulties-, and ecological, habitat damage and risk of aiding in the dispersal of the invasive organism.

Focusing on the intertidal zone around the Irish coast where seaweed communities are most abundant (Morrissey et al., 2001), this study aimed to: 1) update the distribution and abundance of invasive/introduced seaweed species in Ireland; 2) quantify the phenolic content and fatty acid profiles of Irish populations of *Sargassum muticum* (Yendo) Fensholt, *Colpomenia peregrina* (Sauvageau) Hamel (Phaeophyceae), *Codium fragile* (Suringar) Hariot (Chlorophyta) and *Gracilaria vermiculophylla* (Ohmi) Papenfuss (Rhodophyta), all of which have been previously studied in relation to their biotechnological potential globally; 3) given its widespread presence and biotechnological potential, study the spatial variation of total phenolic and fatty acid profiles of *S. muticum* in relation to temperature and the area where it was collected; and, 4) estimate the valorisation potential of Irish marine floral IAS. These objectives underpin the formulation of the following research questions: to what extent have invasive seaweed species proliferated across the Irish coastal regions? Do these invasive populations exhibit significant biochemical variability within individual species? Specifically, for *S. muticum*, are the most biochemically promising populations uniformly distributed across Ireland, or is there an influence of water temperature variability on their distribution and biochemical profiles?

## 2. Material and methods

### 2.1. Sample collection

On each occasion, sampling was carried out during low tide on foot, covering an area of at least 50 m by 20 m parallel to the coast. Sampling locations and dates are available in Supp. Table 1. Sites were chosen based on previous records of invasive species (*S. muticum*: (Kraan, 2008); *C. fragile*: (Parkes, 1975; Trowbridge et al., 2016); *C. peregrina* (Minchin, 1991)) but also known diversity hotspots, proximity to harbours (due to the importance of maritime transport as the introduction vector of marine invasive species) and locations with distinct landscape features or hydrodynamics. The sampling plan also included sites where previous records indicated presence based on citizen science (National Biodiversity Centre Database, [www.biodiversityireland.ie](http://www.biodiversityireland.ie), Seasearch, <https://seasearchireland.ie>). Sampling was done in May and July in 2019 and 2021 (sampling in 2020 was not feasible due to national COVID-19 lockdown). These months coincided with the biomass peaks reported for most target species (*S. muticum*: (Baer and Stengel, 2010); *C. peregrina*: (Mathieson et al., 2016), *G. vermiculophylla* (Bermejo et al., 2020)). Species identification were done based on morphology using field guides (Bunker et al., 2017) and later confirmed in the laboratory using microscopic characters. Abundance was assessed by visually estimating cover (%) in 0.5 m<sup>2</sup> quadrats at 5 m intervals along 30 m vertical shore transects (n = 4–5) (Ganzon-Fortes et al., 2011), but only when density surpassed 5 ind/m<sup>2</sup>. Constituents of native flora associated with IAS were noted at each sampling location where an IAS was found. When present, three to five replicates of biomass per invasive species were collected at least 5 m apart, bagged and transported to the laboratory in cool dark conditions without seawater. There, samples were cleaned of epiphytes and rinsed twice with tap water to remove salt. They were then frozen for 24 h, freeze-dried (Labconco Freezone®, Kansas City, MO, USA) and ground. All material was stored at –18 °C until analysis which was conducted within two months of algal collection.

At each location we measured *in situ* water temperature using a multiparametric probe (YSI Professional Plus, Ohio, US) due to their importance in shaping metabolic content in seaweed (provided in Supp. Table 1 (Russell and Crawford, 1987)).

### 2.2. Sample biochemical analysis

#### 2.2.1. Total phenolic content (TPC)

*Sargassum muticum* and *C. peregrina*'s TPC was determined using the Folin - Ciocalteu assay by Singleton et al. Singleton and Rossi, (1965) as described by Kenny et al. (2015). Briefly, 20 mg of powdered seaweed was extracted with 2 mL of 70 % EtOH (Fisher Chemical™) at 45 °C for 2 h (twice). Supernatants were dried, weighed and adjusted to 5 mg extract mL<sup>-1</sup> in all samples. 100 µL sample extract (or phloroglucinol standard) were mixed with 100 µL 70 % EtOH, 100 µL Folin Ciocalteu reagent (Fisher Chemical™) and 700 µL of sodium carbonate (Sigma-Aldrich, Sintra, Portugal). After vigorous vortexing, they were incubated in the dark for 20 min at room temperature. Absorbances of supernatants were read at 735 nm in a Cary UV50 Spectrophotometer with a Cary WinUV software (Varian Inc., USA). A calibration curve of phloroglucinol (the basic structural unit of phlorotannins) was created by a serial dilution of 2 mg/mL stock sample (5, 10, 20, 50, 80, 100, 120, 160, 240, 320 mg/mL).

#### 2.2.2. Fatty acid content

Fatty acid (FA) content of all replicates belonging to each species in all sampling events were analysed following Guihéneuf et al. (2015), using Supelco® 37 Component FAME Mix (Sigma-Aldrich, Sintra, Portugal) as a standard to allow fatty acid identification and a known amount of C15:0 (Fisher Chemical™) to allow quantification. Using these data, the  $\sum$ SFA,  $\sum$ MUFA,  $\sum$ PUFA,  $\sum$ n-3,  $\sum$ n-6,  $\sum$ n-6/ $\sum$ n-3,

PUFA/SFA ratios were calculated since these indexes are commonly used in similar valorisation/nutritional studies (Pereira et al., 2012, 2021). In-depth analysis of palmitic, linoleic, palmitoleic and arachidonic fatty acids content were conducted due to their reported biological activities from the *Sargassum* genus (Plouguerné et al., 2010; Martens et al., 2023).

Values of TPC and TFA were expressed as mg/g DW to conduct the statistical analyses but expressed as % in the table to allow comparison with bibliographic data.

### 2.3. Statistical analysis

To rigorously assess the effect of water temperature and sampling location (north, south, east, west; Supp. Table 1) on *S. muticum*, total phenolic content and fatty acid profiles, we employed a robust and comprehensive analytical framework. This approach integrated multivariate analysis of variance (MANOVA), one-way analysis of variance (ANOVA), and multiple regression analysis, enabling a thorough investigation of how thermal variability and coastal location influence these key biochemical profiles (Smith et al., 1962; Potvin et al., 1990; Milke et al., 2008; Saranya and Shanthakumar, 2020).

The application of MANOVA is particularly advantageous for its capacity to concurrently evaluate multiple interrelated dependent variables, thereby enhancing the detection of interaction effects that may not be apparent in univariate analyses (Scheiner, 2020). This multivariate approach was employed to determine whether collective response variables -total fatty acids (TFA), total phenolic content (TPC), saturated fatty acids (SFA), monounsaturated fatty acids (MUFA), polyunsaturated fatty acids (PUFA), the omega-6/omega-3 ratio, and specific fatty acids such as palmitic, palmitoleic, linoleic, and arachidonic acids- exhibited significant variations attributable to the predictors: water temperature, used as a continuous quantitative variable, and coastal location, the categorical factor. Following the identification of overall significant differences via MANOVA, we conducted one-way ANOVAs to pinpoint which specific response variables were driving these differences. This step was crucial, as MANOVA alone does not specify the individual contributions of each response variable to the observed effects (Milke et al., 2008). ANOVA thus allowed for a more granular analysis of the data, isolating the influence of each predictor on individual biochemical profiles (Milke et al., 2008).

To further refine our analysis, multiple regression was employed to model each trait independently, accommodating both continuous (water temperature) and categorical (coastal location) predictors. This analysis involved calculating the coefficient of determination ( $R^2$ ) to quantify the proportion of variability explained by the model, providing a nuanced understanding of the predictors' influence on each response variable. Model validation was rigorously performed to ensure adherence to statistical assumptions, including independence, homogeneity of variances, and normality of residuals. This was accomplished through the application of the Durbin-Watson test (Zeileis and Hothorn, 2002), Breusch-Pagan test (Zeileis and Hothorn, 2002), and Shapiro-Wilk test (R Core Team, 2024). Additionally, MANOVA assumptions were evaluated using the Henze-Zirkler test for multivariate normality (Korkmaz et al., 2014), Box M test for homogeneity of variance-covariance matrices (Friendly et al., 2024), Levene's test for equality of variances (Kassambara, 2023) and scatter plots for linearity assessment. Assumptions were considered satisfied when  $p > 0.05$ . In instances where data insufficiency precluded certain analyses, as indicated by preliminary Box M test results, Pillai's trace was employed as a robust alternative (Kassambara, 2019). All statistical analyses were conducted within the RStudio statistical programming environment (R Core Team, 2024). This comprehensive approach provided a detailed and precise understanding of the environmental and geographic influences on the biochemical traits of invasive species, contributing valuable insights to the field of algal research.

## 3. Results

### 3.1. Distribution and abundance of invasive species in Ireland

A total of six invasive seaweed species: *Gracilaria vermiculophylla*, *Asparagopsis armata* (Rhodophyta), *Codium fragile* (Chlorophyta), *Colepomenia peregrina*, *Sargassum muticum* and *Undaria pinnatifida* (Phaeophyta) were found after visiting 68 sampling locations around Ireland (Fig. 1, see Supp. Table 1 for new records and which localities define the south, east, north and west coasts). Their distribution is provided in Fig. 1.

The most ubiquitous invader was *S. muticum*, having been found in more than half of the locations sampled. However, in general, densities were below 5 ind/m<sup>2</sup>, allowing measurement of coverage by transects in only in six locations: Kilmore Quay (23.79 ± 13.39 %), Boyce's Bay (32.49 ± 17.15 %) in the south, and Mullaghmore (50.30 ± 24.79 %), Quilty (52.29 ± 26.73 %), Spiddal (48.77 ± 29.51 %) and Finavarra (46.79 ± 16.51 %) in western Ireland. All specimens were sterile at the time of sampling. In Boyce's Bay, Quilty and Spiddal *S. muticum* was confined to rockpools, thus a discontinued patchy distribution was observed, but in Kilmore Quay, Finavarra and Mullaghmore, continuous belts were found growing on sand-covered substrata. The second most widespread taxon after *S. muticum* was *C. peregrina*, despite low abundances preventing biomass quantification. In the case of *A. armata*, no gametophytes were found in the intertidal at any site, which contradicted previous reports for the life stage of this species in Ireland despite consideration of suitable sampling time. Though present in 19 locations in the north, west and south of Ireland (Supp. Fig. 1), in general, densities of *C. fragile* were very low (2–5 individuals at the site, precluding biomass collection in most locations except three: Finavarra (west), The Boat Strand and Harry Blaney Bridge (north). Notably, very large individuals (each one >5 kg wet weight) of *C. fragile* were found in Harry Blaney Bridge (Co. Donegal), but these were not abundant (less than 5 ind/m<sup>2</sup>); other invasive species like *S. muticum* and *C. peregrina* were also found at the same location, at low densities.

We confirmed the presence of *G. vermiculophylla* in the Clonakilty estuary (southern Ireland (Bermejo et al., 2020)), and we report two further locations in the south (Red Strand Beach and Saint Helen's), one in the west (Bantry) and a population in the northeast (Strangford Lough). Finally, *U. pinnatifida* was confined to one location.

All invasive species were found settled among common components of the Irish intertidal flora (Supp. Table 2 (Guiry and Guiry, 2023)) and it was not uncommon to find several IAS cohabiting in the same rockpool or using each other as a substratum for growth (Supp. Fig. 2).

### 3.2. Fatty acid profiles and total phenolic content

TFA content in *Sargassum* ranged from 7.28 ± 2.24 mg/g DW in Boyce's Bay (south) to a 5-fold of that value in Keel Beach (west; 39.33 ± 3.87 mg/g DW, Supp Table 2). Details on specific FA profiles are provided in Supp. Table 3. TPC content greatly varied around the island, from maximum values of 64.7 ± 1.8 mg/g DW in Lough Hyne (Southern Ireland) to a minimum of 2.9 ± 0.3 mg/g DW in Strangford Lough (north-east). The MANOVA analysis applied to *S. muticum* met all required assumptions except for the homogeneity of covariances, which was attributed to certain locations having fewer observations than variables (Supp. Table 4, Supp. Fig. 3). However, this limitation did not compromise the validity of the analysis, as shown by the results of the multivariate Pillai statistic employed. This analysis assessed the impact of temperature and coastal location (northern, eastern, western and southern coasts) on the biochemical composition of the species. The results indicate that temperature had a significant effect on the biochemical compounds (Supp. Table 5), suggesting that thermal conditions modulate the concentrations of the various biochemical compounds. By contrast, coastal location showed a marginally significant effect (Supp. Table 5), indicating a potential spatial influence on the

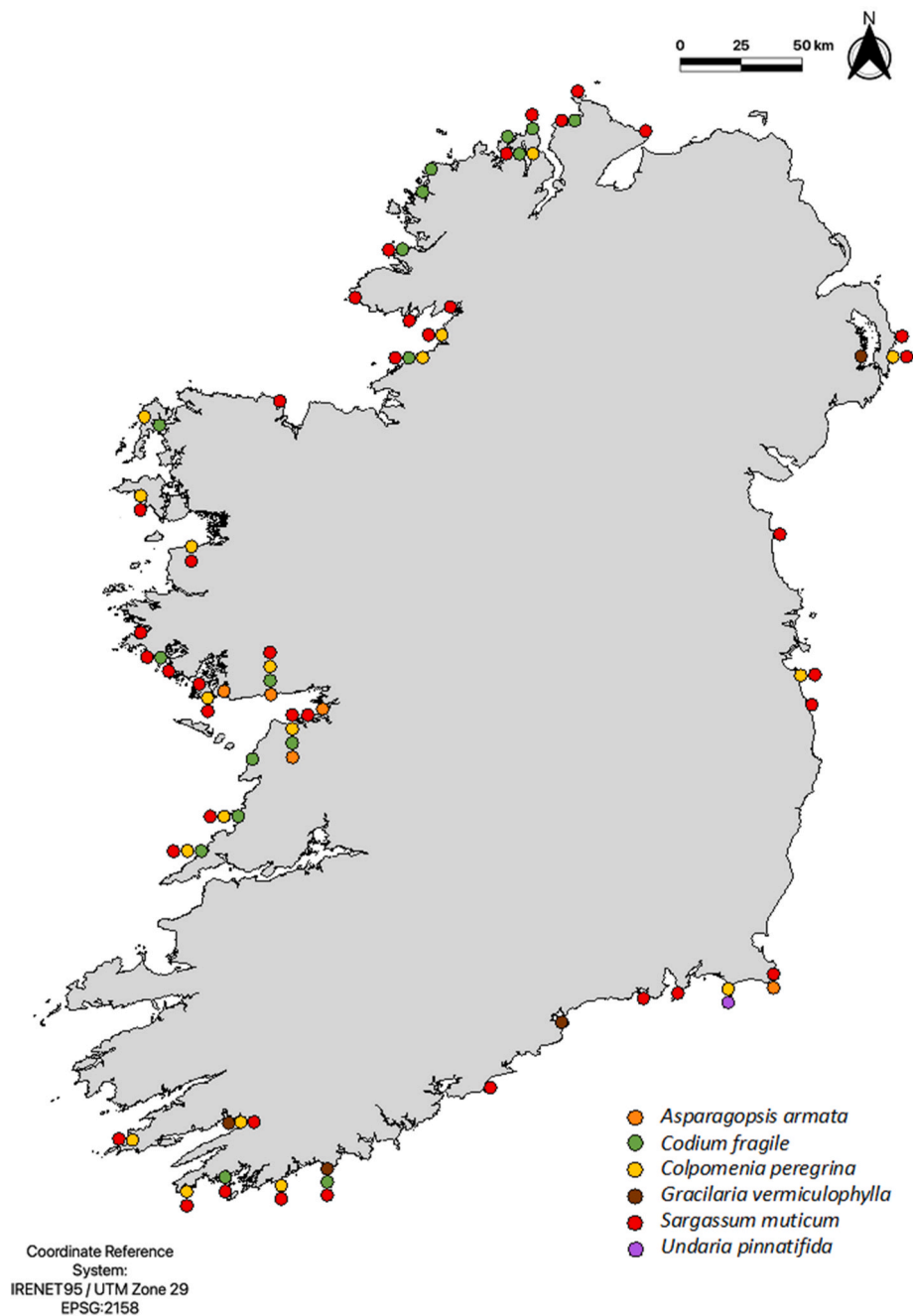
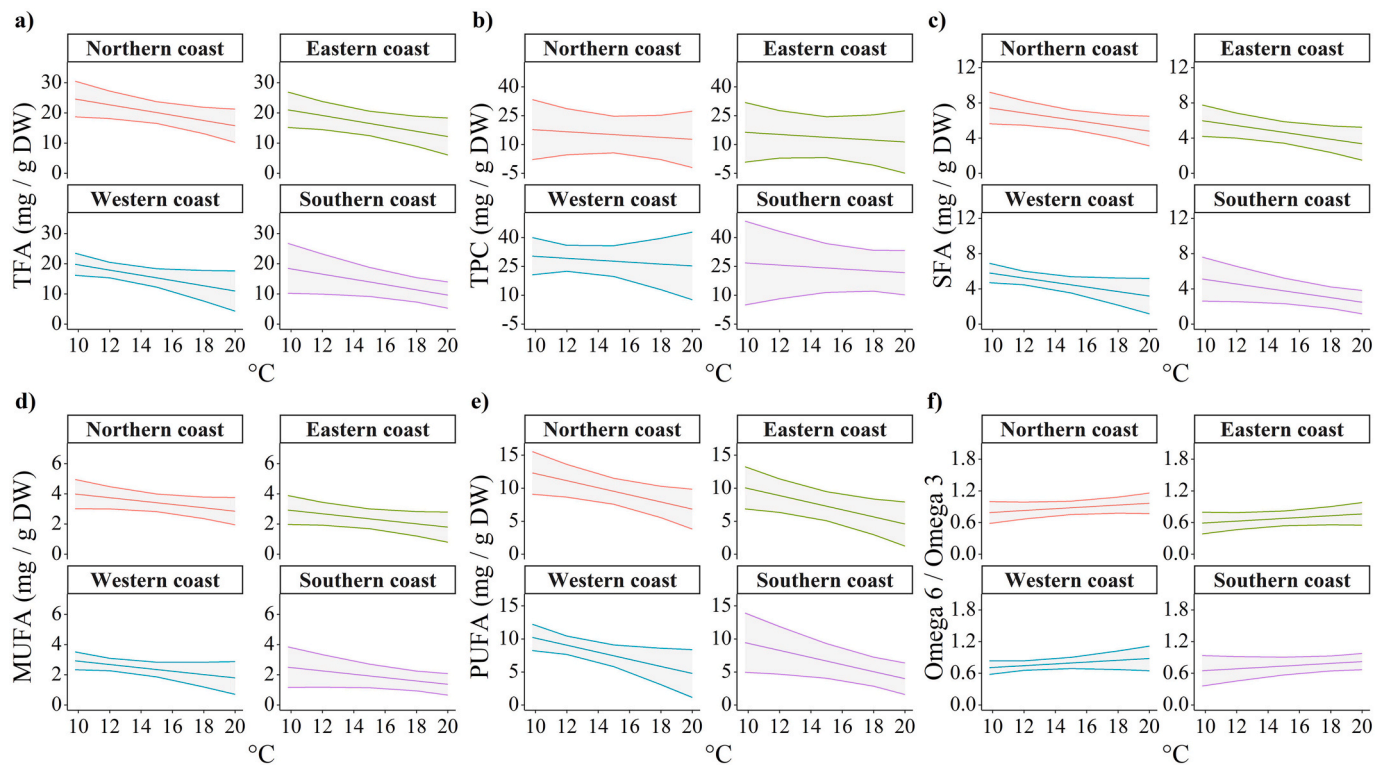


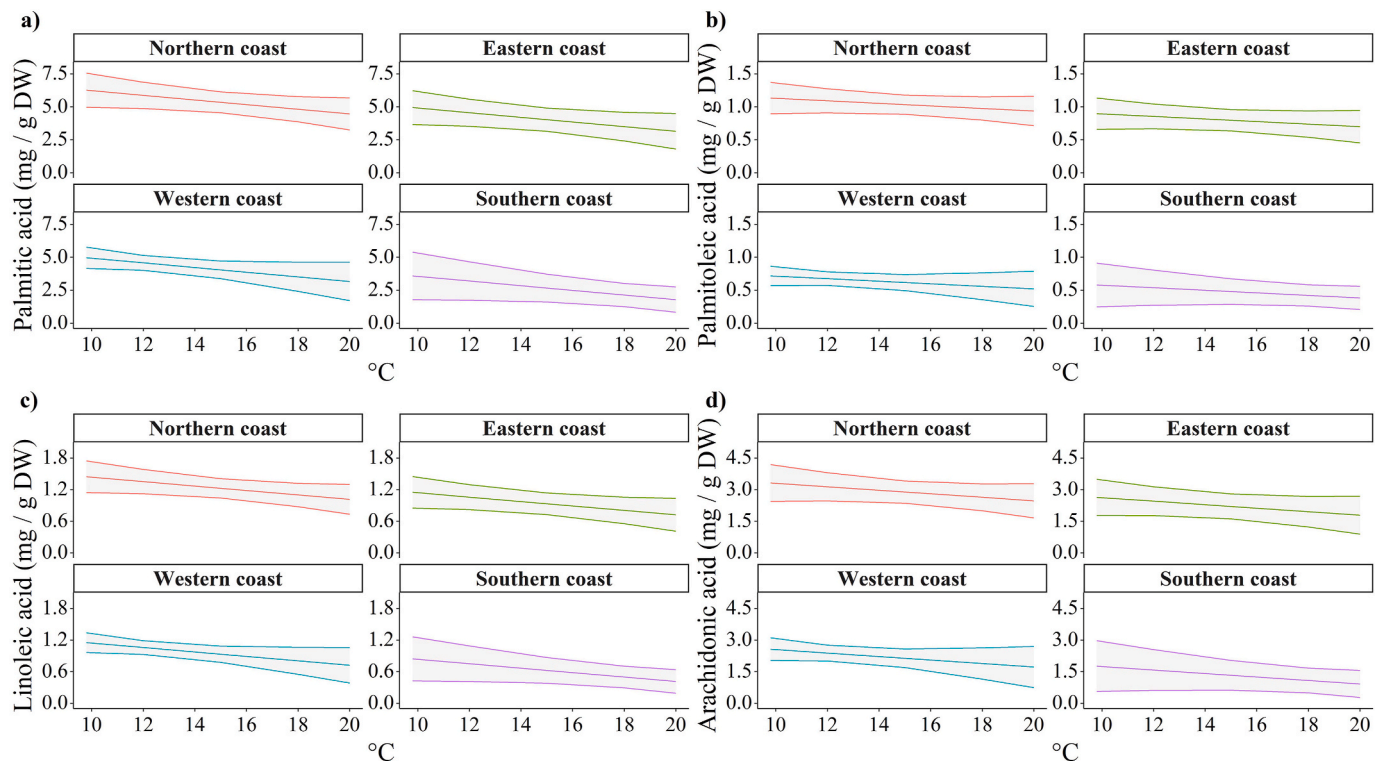
Fig. 1. Distribution of invasive seaweed in Ireland (detailed locations in [Supp. Table 1](#)).

biochemical composition of *S. muticum*. The subsequent ANOVA confirmed and further detailed the observed effects, demonstrating that temperature significantly impacted most biochemical compounds, except for TPC, omega-3/omega-6, and, marginally, palmitoleic acid ([Supp. Table 5](#)). The effect of coastal location, while less consistent than that of temperature, was found to be significant for SFA, MUFA, and specifically palmitic, palmitoleic, linoleic, and arachidonic acids ([Supp. Table 5](#)). The multiple linear regression models indicated that the temperature and the coastal location explained between 27 % and 67 % of the variability in the biochemical compounds of *S. muticum*. The highest  $R^2$  values were obtained for palmitic acid ( $R^2 = 0.66$ ) and palmitoleic acid ( $R^2 = 0.67$ ), while the variables with the lowest  $R^2$  were omega-3/omega-6 ( $R^2 = 0.27$ ) and TPC ( $R^2 = 0.34$ ) ([Supp. Table 6](#)). Regarding temperature, significant effects were observed for PUFA and marginally significant effects for TFA, SFA, palmitic acid, and linoleic

acid. By contrast, coastal location, with the northern coast used as the reference level, showed significant effects on most biochemical compounds. Regional differences were more pronounced, with a higher number of significant locations in SFA, MUFA, palmitic, palmitoleic, linoleic and arachidonic acids ([Supp. Table 6](#)). Lastly, [Figs. 2 and 3](#) display the estimated effects of multiple linear regression models on the concentrations of the different biochemical compounds of *S. muticum*. As shown in [Fig. 2](#), a general decrease in TFA, TPC, SFA, MUFA, and PUFA variables with increasing temperature was observed, while omega-3/omega-6 showed the opposite trend. Regarding coastal location, regional differences were identified, with a general trend for concentrations of most biochemical compounds to decrease with temperature. However, TPC exhibited a less pronounced reduction compared to the other compounds, and omega-3/omega-6 increased with temperature across all four regions. [Fig. 3](#) displays a trend for different fatty acids to



**Fig. 2.** Effects of the predictor variables, water temperature (°C) and geographic location (northern, eastern, western sand southern coasts) on the response variables for the species *S. muticum* of: a) TFA (mg/g DW), b) TPC (mg/g DW), c) SFA (mg/g DW), d) MUFA (mg/g DW), e) PUFA (mg/g DW) and f) omega-3/omega-6 ratio (unitless). The middle line represents the estimated effect from the multiple linear regression model and the shaded area corresponds to the 95 % confidence interval around the estimated effect.



**Fig. 3.** Effects of the predictor variables, water temperature (°C) and geographic location (northern, eastern, western and southern coasts) on the response variables for the species *S. muticum* of a) palmitic acid (mg/g DW), b) palmitoleic acid (mg/g DW), c) linoleic acid (mg/g DW) and d) arachidonic acid (mg/g DW). The middle line represents the estimated effect from the multiple linear regression model and the shaded area corresponds to the 95 % confidence interval around the estimated effect.

be reduced at increased water temperatures at all locations. Finally, model validation assumptions were generally met (Supp. Fig. 4). However, the independence condition was not met for palmitic and linoleic acids ( $p < 0.05$ ) but visual validation of the residuals revealed random patterns and therefore independence (Supp. Fig. 4g and i).

Of the 17 locations where *C. peregrina* was found, enough biomass for chemical analysis could only be collected in only 8, which prevented the detailed analysis we applied to the *S. muticum* dataset, as determined by violations of statistical assumptions and Box M test results. The range of TFA content in *C. peregrina* varied from  $12.77 \pm 1.66$  mg/g DW on Kilmore Quay (south) to a fourth of those values in The Cove (west;  $3.27 \pm 0.0$  mg/g DW). Details on specific changes in the FA profile can be found in Supp. Table 7. Compared to *S. muticum*, TPC content was similarly low (mean values of  $0.55 \pm 0.1$  mg/g DW) across the localities sampled, except in Old Head (southern Ireland) where we determined a TPC content of  $2.02 \pm 0.47$  mg/g DW.

As for *C. peregrina*, no statistical analysis was performed on *G. vermiculophylla* or *C. fragile* samples given insufficient data points ( $n = 3$ ) for the geographical variation analyses. However, *G. vermiculophylla* samples from eastern and western coasts presented twice the content of TFA compared to those samples gathered from the south (Supp. Table 8). The most abundant PUFA was arachidonic acid (C20:4), and palmitic acid (C16:0) and oleic acid (C18:1) most abundant among the SFA and MUFA, respectively. Our samples of *C. fragile* maintained a consistent metabolite content (Supp. Table 9, Supp. Fig. 1), but specimens collected at Finavarra (western Ireland) presented higher values of PUFA (linolenic acid, specifically) and n-3 fatty acids.

The natural biochemical variability of *Asparagopsis armata* and *Undaria pinnatifida* in Ireland could not be assessed given the low abundance of the two species in the locations visited.

#### 4. Discussion

Attending to the research questions laid out in this study, we provide a comprehensive view of the IAS distribution in Ireland, finding them conspicuously present along all shores visited, however, distribution patterns strongly depended on the species. While *Sargassum muticum* and *Colpomenia peregrina* were found on all coasts sampled, *Codium fragile* was absent from the east coast, and *U. pinnatifida* remains restricted in its distribution to southern sites. *Gracilaria vermiculophylla* was found to be actively spreading into new habitats on western and southern coasts. Statistical analyses revealed that the northern coast of Ireland harbors metabolically rich populations of *S. muticum*. This heightened activity appears to be predominantly influenced by variations in water temperature and coastal location, which play a crucial role in modulating the biochemical composition of these populations. This in-depth analysis of *S. muticum* is further justified because of the big size of *S. muticum* in relation to the other IAS and its high FA and phenolic content, and thus, its valorisation potential. Unfortunately, this aspect could not be verified for the remaining species. Thus, this aspect should be further addressed in countries/areas where these IAS species are more abundant and widespread, which would allow for the identification of potential heterogeneities within the populations, contributing to a deeper understanding of the effects of environmental variability and geographic location on the species' biochemical characteristics.

##### 4.1. IAS distribution in Ireland

Though no new seaweed IAS were found during this study, we detected recent significant changes in distribution. For most species, this might be due to the specific methodic sampling effort that was applied, but for species like *S. muticum* - subject of several studies in the past (Kraan, 2008; Baer and Stengel, 2010; Boaden, 1995; Strong et al., 2006) - it may also capture the species dynamics around the coast. We report new sightings of *S. muticum* in three locations of the east coast (Co. Dublin), two from the south (Co. Cork) and new populations on the west

coast (Co. Clare). In other locations within Strangford Lough (Co. Down) and Co. Derry, previously recorded high abundances of *S. muticum* appeared to be greatly reduced or virtually disappeared. While abundant and widespread populations were reported in 1995 (Boaden, 1995) we found only free-floating specimens in two locations of the area, despite a close inspection of 11 locations covering the western and southern shores of Strangford Lough. This suggested that, despite being widespread, *S. muticum* is likely to be causing a significant impact predominantly in the south and west of Ireland, but its presence represents a dormant menace to native ecosystems in the rest of the country. Regarding abundance, *S. muticum* was the only species that presents sufficient biomass to impose a potential impact to cohabiting native species; however, this does not diminish the threat that other species pose to native Irish ecosystems. Their widespread presence at low abundance may imply either that they have become naturalised (and thus are not colonising new territories) or they are latent, due to sub-optimal environmental conditions which may change in the future. This is a similar case to *C. peregrina*, which is present in Ireland since 1987 (Minchin, 1991). While we detected an expansion in its distribution, for example on the east coast (where it was considered absent, and now occupies at least three locations), all 18 populations encountered around Ireland presented low abundance. Preliminary statistical analysis rendered that the presence of *S. muticum* and *C. peregrina* could not be explained by temperature or type of substratum, therefore indicating that other biotic or abiotic factors not considered in this study play a role in the distribution of these invaders.

Previous records of *C. fragile* in Ireland are patchy (Parkes, 1975; Trowbridge, 2001; Provan et al., 2005) which may explain the substantial increase in distribution reported here. Remarkably, no specimens of *C. fragile* were found on the east coast, despite visiting suitable habitats (i.e. rockpools and/or rocky substratum). Our updated records for *C. fragile* support those observations by Trowbridge et al. (2016) in terms of low abundance, which were explained by these authors to low fecundity and low recruitment. It is not uncommon for invasive populations to thrive and persist by means of asexual reproduction alone (Zanolla et al., 2017). The oversize of individuals sampled in Harry Blaney Bridge may be due to the proximity (>1 km) of this location to a mussel farm, which likely increased the input of nutrients.

In the case of *A. armata*, both life stages were widely reported across Irish shores in the past (Kraan and Barrington, 2005). Though we did not survey the subtidal, which could account for the recorded absence of the species in some locations, our results likely support an ecological shift in the upper bathymetric limit inhabited by the species, being displaced to deeper areas rather than indicating a significant reduction in the distribution of *A. armata*.

##### 4.2. Phenolic and fatty acid spatial variation

Understanding the natural plasticity of the biochemical composition in marine populations is a challenge of marine chemistry which can be addressed by monitoring them along spatial gradients and variable temporal scales, to display their potential as valuable sources of marine bioactive compounds in a sustainable way. Whilst temporal variability could not be fully captured in this study, seasonal changes in metabolites in seaweed species are commonly reported. *Sargassum* represents an interesting source given the size of the individuals and the studies availing optimization of extraction protocols of bioactive metabolites (Anaëlle et al., 2013). Its widespread distribution in Europe provides an opportunity to capture the spatial variability of the content in phenol compounds at different geographical scales. On a regional scale, northern populations contained higher phenolic levels than southern ones (Plouguerné et al., 2006) which corresponds to the trend observed here in Ireland. These findings may be related to 1) the role of these compounds as a mechanism of protection against light and grazing stress (Stengel et al., 2011), or 2) the negative correlation of temperature with TPC found on all shores in this study. At larger scales, the fact that at

higher latitudes the curvature of the Earth causes the atmosphere to become thinner, resulting in a higher level of UVB absorption (Herman et al., 1999), may shape phenolic content in seaweed. Our data is also consistent with field data from other Fucales species, *Ericaria amentacea* (C.Agardh) Molinari & Guiry (Mannino et al., 2016), where an opposite relationship for phenolic content with increasing seawater temperature was reported, with lower values observed in winter. Conversely, Tanniou et al. (2014) found Portuguese samples to have higher TPC contents than those from Norway. We hypothesize that spatial differences are attributed to the fact that in brown seaweed phenolic profiles are species-specific (Connan et al., 2004; Mannino et al., 2014) and change both spatially and temporarily according to environmental abiotic factors such as salinity, nutrients and biotic pressure rather than the influence of irradiance or UV; this coincides with Norwegian samples presenting higher TPC content than those from lower latitudes (Ireland, France and Spain).

Similar to TPC, TFA content and profiles exhibited strong geographic variation. Differences between levels and profiles reported here might be explained by exposure to diverse abiotic factors that are known to influence the content of PUFA in algae such as temperature (Harwood et al., 1984; Khotimchenko et al., 2002; Kumari et al., 2014) and incident light (Sanina et al., 2004). For example, for *S. muticum* lower PUFA levels were observed in southern Irish populations (e.g., Lough Hyne and Kilmore Quay) and higher in northern locations (e.g., Strangford Lough) coinciding with higher and lower seawater temperatures measured, respectively, indicating changes in the structural lipids as a part of temperature response (Kim et al., 1996; Schmid et al., 2021). The high content of palmitic, palmitoleic, linoleic and arachidonic fatty acids in northern populations of *S. muticum* enhances their potential for nutritional and pharmaceutical applications, given the highest content of this species when compared to other species of the genus, as *Sargassum vulgare* C.Agardh (Pereira et al., 2012), *S. thunbergii* (Mertens ex Roth) Kuntze and *S. confusum* C.Agardh (Narayan et al., 2005). Further, extracts rich in these lipids have shown antibrowning activity on B16F10 murine cells and inhibition of lipogenesis in SW872 liposarcoma cells (Conde et al., 2015). Together, our results suggest that thermal and spatial differences are key factors shaping the biochemical profile of *S. muticum*. The observed variations may reflect the existence of environmental heterogeneity, which should be considered to better understand the adaptive and functional mechanisms of the species under different geographical and thermal conditions.

Total phenolic and TFA contents in *C. peregrina* were lower compared to those obtained for *S. muticum*, and no information on natural spatial variation on these compounds is available - to our knowledge - at any scale. Thus, while with caution, our results provide evidence that spatial variation does occur, but the drivers shaping it remain unknown. Levels of palmitic, palmitoleic, linoleic and arachidonic acids in *C. peregrina* in some locations in the west and south of Ireland (e.g., Finavarra, Kilmore Quay) were twice or 3-times higher than those described for samples from the same species from Quebrado Beach (Portugal) collected in October (Rocha et al., 2021); they also resembled levels reported for *S. muticum* in some locations in this study but it remains to be ascertained if these FA perform equally well in bioactivity tests reported for *Sargassum* species.

Spatial variability in the TFA and fatty acid profiles of *Codium fragile* samples could not be assessed in this study, while the three locations that allowed for biomass collection were relatively uniform. For *C. fragile*, TFA content was higher in Finavarra (west) compared to other locations sampled, but similar conclusions to those elaborated for *S. muticum* could not be made, given the low number of replicates in the spatial study. Spatial variation has previously been reported for other *Codium* species, such as *C. tomentosum* Stackhouse (Rey et al., 2020), *C. dwarkense* Børgesen and *C. taylorii* P. Silva (Chlorophyta) (Dembitsky et al., 2003).

In contrast to our results, lipid content in *G. vermiculophylla* was found not to vary on a geographical scale in France, but temporal

variations could be observed (Surget et al., 2017). Given that our sampling design prevented us from addressing this specific issue in detail, we encourage further study of this aspect and highlight higher TFA content in southern populations.

#### 4.3. Valorisation potential

Giakoumi et al. (2019) proposed that the most efficient way to control IAS negative impacts was by raising public awareness for their commercial potential use, which is achieved through valorisation of invasive seaweed species. However, while in theory this implies positive environmental and economic outcomes by removing biomass temporarily, the physical removal of biomass of any species, and particularly that of invasive seaweed, needs to follow a detailed study of its environmental suitability, for several reasons. Firstly, because misidentifications with cohabiting native algae are common. For example, *Codium* and *Colpomenia* species are identified based on microscopic morphological characters (Trowbridge, 2001; Clayton, 1975); *Sargassum* species can resemble those of many *Cystoseira*/*Ericaria* species (Guiry and Guiry, 2023); and the similarity of *C. peregrina* with the native *Leathesia marina* requires expert knowledge (Mathieson et al., 2016). Secondly, without the development of safe removal protocols, the local habitat may be damaged which would, ultimately, further weaken the condition of the invaded ecosystem. Thirdly, the manual removal of the algal biomass, from which unintentionally liberated propagules may aid the dispersal of the species, may exacerbate problem (Critchley et al., 1986). Thus, valorisation as a tool in mitigation strategies requires careful consideration and should be guided by the principle of environmental conservation, and also benefit those sectors affected by invasive species blooms, including local fisheries and tourism. In order to assure this, for example, IAS biomass removal (attached or beach-casted) - if proven sustainable and conducted only by trained staff -, can be considered and may be mediated by environmental agencies, local governments for downstream commercial processing.

*Sargassum muticum* has invaded many locations of the northern hemisphere (Engelen et al., 2015) and several valorisation studies have highlighted its multiple industrial uses (e.g., Milledge et al., 2016; Plouguerné et al., 2010; Stiger-Pouvreau et al., 2014; Susano et al., 2022). Previous studies of phenolic compounds in *S. muticum* outlined significant spatial variation across samples from Portugal, Norway, France, Spain and western Ireland - collected in the same season as the present study, with maximum values observed in Almogrove, Portugal (Tanniou et al., 2014). We recovered significantly higher values than those from Almogrove. These values, however, were similar to those reported by Pinteus et al. (2017) who analysed populations 290 km south of Almogrove, Portugal. Considering their abundance and TPC in the present study, *S. muticum* populations at Mullaghmore, Quilty, Spiddal and Finavarra appear to present the most promising valorisation potential. We accurately quantified the content in phenolics and fatty acids in July, when the highest biomass peak occurs and the individuals are larger, since the onset of thallus fragmentation in Ireland occurs in August (Baer and Stengel, 2010), thus indicating the best time to collect wild biomass provided that further spread of the species from disturbance can be prevented.

Overall TFA content in Irish *C. peregrina* were low. Slightly (14 %) higher values have previously been recorded in south-west England (Beacham et al., 2019), and, remarkably, values 10-fold higher were recorded in Portugal (but harvested in October 2020 and not in May 2021, like this study (Rocha et al., 2021)). By contrast, Irish samples appeared to contain TPC levels twice those of Portuguese samples (Pinteus et al., 2017). *Colpomenia peregrina* has been also reported to have high content of ash, zinc and iron (Beacham et al., 2019).

Regarding fatty acid contents of *C. fragile*, in Irish samples, while SFA were similar, PUFA and MUFA double that of Chilean populations (Goecke et al., 2010). Compared to South Korean individuals, they showed a diminish content of SFA and omega-6 fatty acids but higher

MUFA, PUFA and omega-3 (Seo et al., 2019).

In *G. vermiculophylla*, arachidonic acid (C20:4 n-6), a prostaglandin precursor, and palmitic acid (C16:0) were the predominant fatty acids in the total lipid profile. This agrees with the proportions reported for this species (Honda et al., 2016). However, absolute values recorded in this study for Strangford Lough (east) are 1.5 times higher than those reported for *G. vermiculophylla* from Japan, Vietnam and France (Imbs et al., 2012; Surget et al., 2017). Regarding valorisation potential for this species, although biomass quantification was not possible in this study due to the unsteady substratum upon which this species settles, we did observe abundant biomass, especially in Bantry (south) and seasonal blooms are reported to occur also in Clonakilty Estuary (Bermejo et al., 2020). This species is also easily culturable, and cultured biomass maintains its prostaglandin levels as those collected from natural populations (Imbs et al., 2012) thus making it a promising source of this essential FA.

## 5. Conclusions

1. While populations of invasive seaweed species are well spread along the Irish coastline, this survey revealed recent changes in their distribution pattern. For example, *Sargassum muticum*, previously recorded at high abundances appears to be greatly reduced or virtually disappeared, being very abundant only in some locations of the west and south of the country. By contrast, we report an apparent expansion of *Colpomenia peregrina* and *Codium fragile* which is likely linked to the fact that distribution data of these species had not been updated since the 1990's, but abundant populations were very localised. For other, more recent, invaders such as *Gracilaria vermiculophylla*, this study provides new records, which indicates an active dispersal of the species.
2. TPC and TFA contents varied geographically for all species. While this appeared to be at least in part related to variations in ambient *in situ* temperatures at the time of collection, further in-depth studies are needed to account for the observed variability.
3. Our analysis revealed that the northern coast of Ireland is where the most productive populations of *S. muticum* inhabit and that temperature is involved in shaping their metabolic content. Considering their abundance, biomass and TPC in the present study, some western *S. muticum* populations appear to present the most promising valorisation potential but only if appropriate management and monitoring protocols are implemented. Regarding *G. vermiculophylla*, the most abundant PUFA was arachidonic acid, as previously reported for these species (Imbs et al., 2012), which portrays this species as a promising source of prostaglandins.

## CRedit authorship contribution statement

**Marianela Zanolla:** Writing – review & editing, Writing – original draft, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Claudia L. Cara-Ortega:** Writing – review & editing, Writing – original draft, Investigation, Formal analysis, Data curation. **Víctor Sanz-Fernández:** Writing – review & editing, Writing – original draft, Software, Methodology, Formal analysis. **Dagmar B. Stengel:** Writing – review & editing, Writing – original draft, Supervision, Project administration, Investigation, Funding acquisition, Conceptualization.

## Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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## Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.ecss.2025.109406>.

## Data availability

Data will be made available on request.

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