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A modern perspective on the commercial seaweed landscape of Ireland

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A thesis submitted for the degree of Doctor of Philosophy to the

National University of Ireland, Galway

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Declaration of Authorship

This dissertation is my own original research work. It has not been previously submitted, in part or whole, to any university or institution for any degree, diploma, or other qualification.

Signed: ______________________________ Date: 24.08.2021

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Abstract

In Ireland, seaweed was historically commercially used as a raw material to produce high-volume, low-value commodities, mostly animal feed. More recently, and due to the increasing mainstream acceptance of seaweed, there has been a renewed vigour in the Irish seaweed industry. The harvesting and gathering of “wild” seaweeds continue to play an integral role in many coastal societies, often being intrinsically linked to the cultural identity of those coastal communities. However, given the increasing commercial interest in seaweed, certainly now at a point greater than at any stage in Irish history, it is critically important that the sustainability of the resource is ensured. This thesis describes themes important to the continued evolution of the Irish seaweed commercial landscape. Chapters 2 and 3 focus first on the seaweed resources of Irish waters and how the seaweed industry has changed, adapted, and progressed in the 21st century. The second part (Chapters 4 and 5) focuses on the potential issues relating to levels of arsenic in seaweed. Seaweed has a long history of use as a supplemented livestock feed, providing nutrients and vitamins essential to maintaining animal health. However, seaweeds such as *Ascophyllum nodosum* are well-known accumulators of the metalloid arsenic. As the global demand for livestock produce grows, there exists concern that consumption of livestock produce reared on a diet supplemented with seaweed may pose a threat to the human population due to the potential transfer of naturally occurring arsenic present in seaweed. A population-exposure assessment was carried out using arsenic data from a commercially available seaweed meal from 2012 to 2017. A “Monte Carlo” simulation model was developed to characterise the feed to food transfer of Arsenic from animal feed to animal produce such as beef, milk, chicken, and eggs. To further address potential concerns and provide end-users, including industry, consumers, policymakers, and regulators, with information on the exposure associated with arsenic in commercial seaweed animal feed, the estimated daily intake of arsenic was calculated to evaluate potential human exposure levels. Chapters 6 and 7 describe the use of “Earth Observation” technologies to monitor some native and invasive seaweed blooming species in eutrophic North-East Atlantic estuaries and reconstruct the historical development of seaweeds using free-to-access satellite imagery (Landsat and

Sentinel) utilising appropriate modelling to express the influence of environmental factors on bloom-forming seaweed development. Studies described in Chapters 6 and 7 are the first to utilise satellite imagery to reconstruct the historical development of blooms in European waters. Finally, in Chapter 8, a general discussion of the thesis is provided, concluding the thesis's primary findings while providing recommendations supporting the continued development of Ireland's commercial seaweed industry.

Acknowledgements

The work achieved during this PhD project and presented in this thesis would not have been possible without the kind support I have received from many. Firstly, I’d like to sincerely thank my supervisor, Dr Liam Morrison, for his guidance and support over the years. Your passion for science and seaweeds is evident, and I have taken a lot from what you have taught me over the years.

My benefactors, Louis and J.P. Deveau of Acadian Seaplants, whose financial and personal support was critical to the completion of this thesis.

This project involved collaborations with researchers from different institutions. They are warmly thanked for their contributions to the publications that are part of this thesis.

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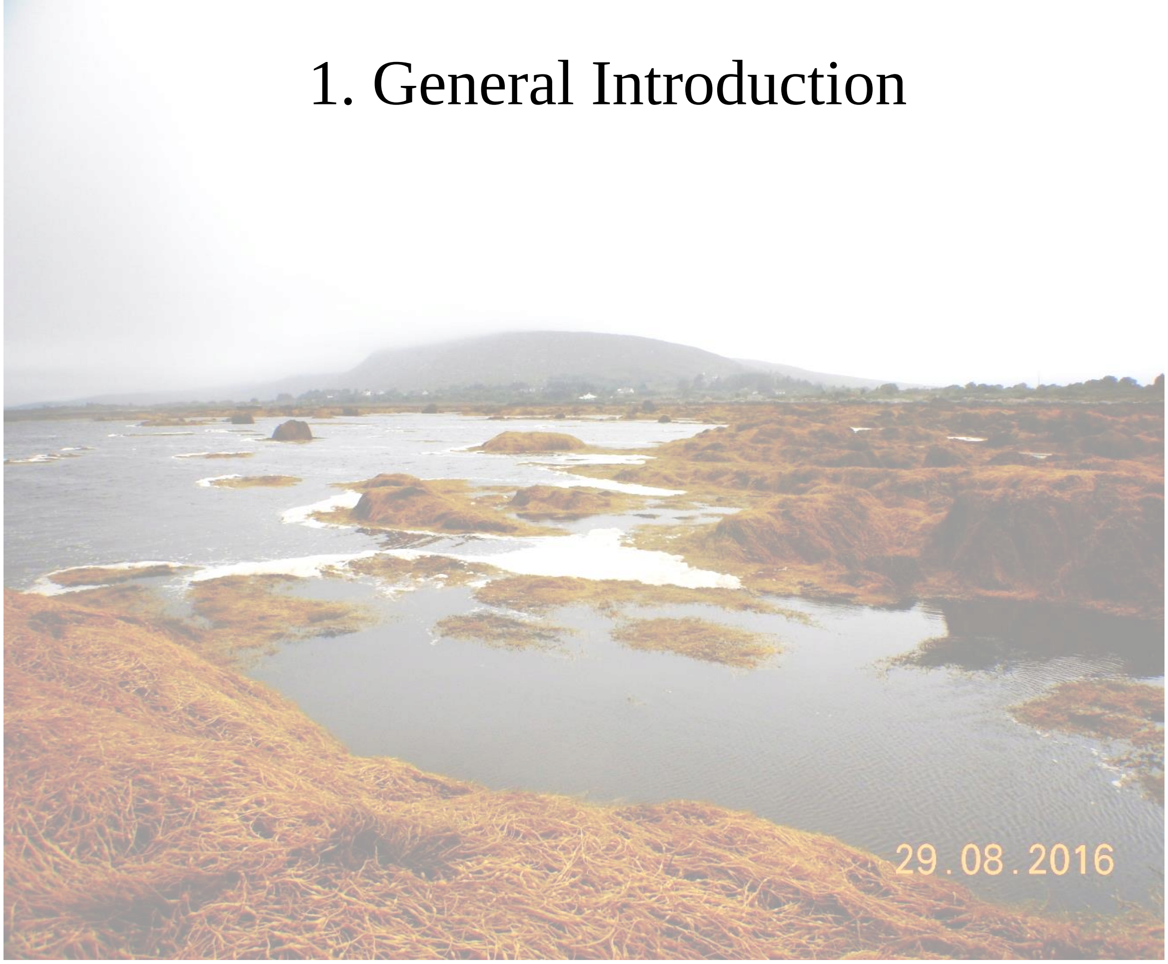
Dedication

In loving memory of my father, Enda, Mac Monagail, R.I.P

1. General Introduction



1.1 Background

The research carried out for this thesis covered several important themes and explored Ireland's evolving commercial seaweed landscape in the 21st century.

The culture of harvesting seaweed in many coastal communities across Europe has a long history (O'Neill 1970, Delaney et al. 2016, Mac Monagail and Morrison, 2019, Araújo et al. 2021). The roots of the Irish seaweed industry can be traced back to the gathering of drift weed (*Laminaria hyperborea* (Gunnerus) Foslie 1885 */ slataí mara*) in the 1930s to the contemporary commercial harvesting of wild *Ascophyllum nodosum* (Linnaeus) Le Jolis for nearly 60 years (Guiry and Morrison, 2013, Mac Monagail et al. 2017).

Today, the Irish seaweed industry provides important materials for agricultural production, with animal feed being the most significant seaweed-based product (Mac Monagail et al. 2018). However, the reported presence of arsenic in a variety of seaweeds and seaweed products (Mac Monagail and Morrison, 2019), together with previous reports of the occurrence of arsenic contaminants in animal feeds (Zhang et al. 2012, Yao et al. 2013), has led to justified concern regarding feed supply and biosecurity (Bryden 2012, Cochrane et al. 2016). Considering the current monospecific reliance of the Irish seaweed industry on the fucoid *A. nodosum* in animal feed production, and in light of historical contamination of animal feed (Kosicki et al. 2016, Pinotti et al. 2016, Abdallah et al. 2017, Aubry et al. 2017, Patriarca and Fernández Pinto, 2017, Pena et al. 2019), the innate ability of certain seaweeds to accumulate arsenic (As) is one of the most concerning issues related to feed quality in Ireland today (Arramara Teoranta, pers. comm.).

Native and invasive bloom-forming seaweed colonisation are also of significant interest to the Irish seaweed industry (Wan et al. 2017, Bermejo et al. 2019, Karki et al. 2021). Their presence or absence of such "nuisance" species in coastal waters has been of particular concern for several decades. Their presence and excessive accumulation can blanket entire estuaries due to eutrophication, ultimately impeding the achievement of EU Water Framework Directive (WFD) "Good Ecological Status" (GES). Additionally, the faster growth rate of species such as *Ulva* and *Agarophyton vermiculophyllum*

(Ohmi) Gurgel, J.N.Norris et Fredericq 2018 can outcompete native perennial fucoids, with large accumulations inhibiting the growth of fucoids through direct competition and increased exposure to grazer pressures (Hammann et al. 2013). These direct impacts can eventually lead to habitat changes (Edgar 1990, Salovius and Kraufvelin, 2004), sudden community shifts and eventual crash of canopy-forming fucoids (Kraufvelin et al. 2006). In the context of what is now accepted as a rapidly changing climate, and the likely increasing presence of these nuisance algae in Irish and international waters (Smetacek and Zingone, 2013), the enhanced monitoring of bloom-forming seaweeds is important for the continuity of the Irish seaweed industry.

The over-enrichment of estuarine environments resulting from excessive agricultural and urban inputs, particularly nitrogen and phosphorus, is known to play a significant role in the development of these bloom-forming seaweeds. However, little is known of the causative climatological factors involved in the development of these species in eutrophic estuaries. To date, the monitoring of native blooming species, such as *Ulva* and invasive species, such as *A. vermiculophyllum*, has traditionally been carried out using traditional field-sampling, "boots on the ground" techniques. Nonetheless, few data are available on their distribution on a large spatial scale due to practical difficulties constraining effective monitoring of estuarine environments.

A comprehensive overview of the Irish seaweed industry has been described in this thesis, with several associated risk factors (both chemical and biological) to the industry investigated throughout.

1.2 The seaweed harvest

Apart from its importance as a raw material in industry, gathering various seaweeds (mainly wracks) and their harvesting continues to play an important cultural role in many coastal inhabitants, particularly on the western Atlantic seaboard of Ireland. The harvesting of seaweeds has several vital socio-economic functions, providing opportunities to coastal and island communities for income and sustainable livelihood (generally combined with several other roles, including fishing, farming etc.) and plays an important role in the persistence of coastal communities (Rebours et al. 2014 and discussed further in Chapter 2). Today, several hundred persons are employed in the harvesting and processing of seaweed in Ireland (Mac Monagail et al. 2017), with this natural resource providing a necessary supplementary income to many living in coastal communities.

The exploitation of a relatively small number of seaweed species (namely, *A. nodosum*, *Chondrus crispus*/*Mastocarpus stellatus*, *Palmaria palmata*, *Laminaria digitata*) has allowed the European industry to grow, albeit slowly, over the last few decades (Mac Monagail et al. 2017). Today in Ireland, the practice of gathering a limited number of seaweeds continues in much the same way as it has historically, being generally carried out following traditional hand harvesting techniques (Mac Monagail and Morrison, 2020). In recent years, however, the implementation of new harvesting strategies is beginning to emerge in Ireland to augment traditional hand harvesting (discussed in Chapter 3). Today, the Irish seaweed industry harvests nearly 30,000 tonnes annually (Mac Monagail and Morrison, 2020). The vast majority of landings come sustainably from wild seaweed stocks, 95% of which is *A. nodosum* highlighting the reliance on this seaweed and the importance of conserving this species. Of this, animal feed is the primary seaweed-based commodity produced in Ireland.

1.3 The production of seaweed-based livestock feed and the relevance of monitoring the presence of natural, elevated arsenic levels in *Ascophyllum nodosum*

Seaweed has a long history of use as livestock feed (Makkar et al. 2016). Seaweed-based animal feeds have been shown to play positive roles in the microbiome of livestock, being rich in amino acids and vitamins and minerals (Pangestuti and Kim, 2015, Kadam et al. 2017) and containing high-quality protein (Angell et al. 2016). The fucoid *A. nodosum* is commercially the most important seaweed species in Ireland (Mac Monagail and Morrison, 2020, Pereira et al. 2020), with wild stocks being exploited since the 1960s for animal feed production (Guiry and Morrison, 2013, Mac Monagail et al. 2017).

Some seaweeds have the ability to accumulate elevated quantities of arsenic in their tissues (Mac Monagail and Morrison, 2019) from the surrounding marine or freshwater environment (van Ginneken and de Vries, 2018, Ownsworth et al. 2019). *Ascophyllum nodosum* is known to play a key role in the biomagnification of arsenic through marine food webs (Morrison et al. 2008, Zhao et al. 2010, Bjørklund et al. 2018). Inorganic arsenic is categorised as a Group A human carcinogen by the United States Environmental Protection Agency (USEPA) and a Class 1 carcinogen by the International Agency for Research on Cancer (IARC) (Straif et al. 2009). Elevated concentrations of arsenic can pose a threat to the general population if consumed directly or indirectly. Moreover, the toxicological effect of some arsenic species, including arsenosugars and thiolated arsenicals, remain poorly understood and may play a more significant role in producing toxicity once consumed than previously reported (See Discussion for Chapters 4 and 5).

It is crucial that feed produced is of the highest quality for the consumer. Animal feed that has been identified as contaminated cannot be fed to livestock to ensure food chain safety (Elliott et al. 2017). Metal contamination is a considerable health risk to both livestock and humans due to the transfer of these contaminants (Arslan et al. 2017). Therefore, it is critical to determine the exposure to metal(loids) as a result of consuming livestock products as “any risk assessment of undesirable substances in feeds needs to consider the occurrence and exposure for consumers of these animal-derived products” (Dorne and Fink-Gremmels, 2012). Correspondingly, research in Chapter 5 has led to an improved understanding of the role of arsenic transfer and human exposure following ingestion of livestock reared on a supplemented seaweed animal feed.

1.4 Green tides in the Anthropocene; nuisance blooms in European waters and monitoring and reconstructing the spread of native and invasive seaweed species

Estuaries are highly dynamic and complex environments (Joesoef et al. 2017) located at the interface between drainage basins and the coastal ocean (Malta et al. 2017) and support a wide range of marine life, including many species of seaweed (Mathieson et al. 1981, Bryan 1983). Often adjoining urban areas, these marine environments are vulnerable to receiving allochthonous N and P inputs (Malta et al. 2017). The increase in European coastal population and expansion of agriculture since World War II has gone hand in hand with increasing global fertiliser consumption (Steffen et al. 2015), upsetting the global ecosystem by accelerating global cycles of nutrients such as nitrogen (N) and phosphorus (P) (Wang et al. 2021). As a result of reduced water exchange compared to open coastal waters, these estuaries are the first recipients of contaminants from riverine inputs and are more prone to excessive nutrient enrichment, leading to eutrophication (Chapman and Wang, 2001, Pang et al. 2010, Hartnett et al. 2011). The continued eutrophication of coastal waters and subsequent proliferation of problematic bloom-forming species, particularly green macroalgae of the genus *Ulva* (commonly known as 'Sea Lettuce'; Ulvophyceae, Chlorophyta), referred to as “green tides”, can alter the dominance of canopy-forming fucoids as some opportunistic bloom-forming species can suppress the settlement and growth of fucoids (Alestra and Schiel, 2014).

One of the most obvious signs of estuarine eutrophication is the proliferation of opportunistic green algae, particularly *Ulva* spp. *Ulva* blooms, or “green tides”, can occur in considerable assemblages on the top of high water marks and beaches and estuaries annually throughout Europe (Merceron et al. 2007), and their occurrence is increasing almost exponentially (Smetacek and Zingone, 2013). Concurrently, non-native blooming species may also form blooms in eutrophic estuaries (Rueness 2005, Bermejo et al. 2020). Non-native species, including *A. vermiculophyllum*, can alter shallow coastal communities, and their impacts will likely increase due to a range of factors, including further coastal urbanisation across Europe (De Jonge et al. 2002) and intensification of agricultural practices. Certainly, the demonstrable changing climate of the global ecosystem will likely impact bloom dynamics, both native and non-native; however, little is known of the most important climatological factors involved in blooms development in eutrophic waters.

The presence of these problematic species and the associated negative impacts on perennial fucoids will likely be exacerbated further in the context of a warming Earth. Relevant questions about how these problematic species are utilised and whether there is scope for their harvest for commercial purposes need to be addressed. Vigilance monitoring of the arrival and seasonal development of both native and invasive seaweed blooming species into European waters is now critical (discussed further in Chapters 6 and 7).

The relevance of monitoring and reconstructing the spread of native and invasive blooming species holds particular significance considering the Water Framework Directive (WFD) 2000/60/EC and the United Nations Sustainable Development Goals (UN SDGs) aims for good status and management of water bodies. To meet the ideals of such important legislative frameworks, it is crucial that considered and precise monitoring of temperate coastal waters, both in Ireland and across Europe, is conducted. Considering the importance of natural seaweed resources to the livelihood and subsistence of coastal communities along Atlantic coasts, filling of knowledge gaps relating to the spatial extent and magnitude of green tides in European waters and investigating climatological factors controlling the dynamics of these blooms will play a role in meeting the obligations of the WFD for improving aquatic ecosystems, as well as helping to meet sustainability goals set out in the UN SDGs, particularly Goal 8 (Decent Work and Economic Growth) and Goal 14 (Life Below Water).

Traditionally, the monitoring of native and invasive blooms has been performed through field sampling campaigns, shore walks, aircraft flyovers and more recently, unmanned aerial vehicles (UAV) (Pepe et al. 2018). Many of these techniques, however, have specific limitations, particularly related to cost, but also spatial resolution. The use of Earth Observation in monitoring seaweed blooms could provide a practical and inexpensive tool for resource managers to better manage native seaweed resources. Considering the global rise in occurrence of these problematic blooms (Smetacek and Zingone, 2013) and the subsequent negative impacts bloom-forming species have on economically important native perennial fucoids (Kraufvelin et al. 2006), increasing our understanding of bloom-forming species colonisation will play an essential role in the future management of these resources in Ireland and on a continental scale.

1.5 Scope and objective of this study

This thesis investigates and demonstrates varied threats and opportunities concerning the sustainable management of Irish seaweeds. These themes are examined through the following objectives.

1. Investigate the seaweed resources of Ireland, with a focus on the Irish seaweed industry and the sustainable harvest and management of important seaweed resources (Chapter 2 and 3).
2. To provide a synopsis of arsenic speciation in various seaweeds and the effects of cooking and processing on arsenicals present (Chapter 4).
3. To estimate the human exposure to arsenic from consumption of livestock (beef and poultry) and livestock by-products (milk and eggs) reared on a diet of supplemented seaweed animal feed and to use modelling to determine the potential for arsenic transfer to humans (Chapter 5).
4. To reconstruct proliferations of both native and invasive macroalgal blooms in Irish and European waters using an appropriate classification technique coupled with free to access Earth Observation data (Chapters 6 and 7). To assess seasonality and annual variation of seaweed blooms in European estuaries and to utilise appropriate statistical modelling techniques to determine the influence of environmental variables on bloom development (Chapter 7).

1.6 Structure of this thesis

This thesis follows a paper-based format and has been presented in the form of six published or submitted manuscripts included as follows:

Chapter 2, which focuses on the seaweed resources of Ireland and how the industry has changed over the last 20 years, has been published as: Mac Monagail, M. and Morrison, L. (2020). The seaweed resources of Ireland: a twenty-first-century perspective. *Journal of Applied Phycology*, 32, 1287–1300. This work was developed written by MM with key contributions and supervision from LM.

Chapter 3 describes the research published on the sustainable harvesting of wild seaweed resources, published as: Mac Monagail, M., Cornish, L., Morrison, L., Araújo, R. and Critchley, A.T. (2017). Sustainable harvesting of wild seaweed resources. *European Journal of Phycology*, 52(4), 371–390. This work was performed and written by MM with key contributions from co-authors and supervision from LM.

Chapter 4 describes research published on Arsenic speciation in a variety of seaweeds and associated food products and has been published as: Mac Monagail, M. and Morrison, L. (2019). Arsenic speciation in a variety of seaweeds and associated food products. *Comprehensive Analytical Chemistry*, 85, 267–310. This work was performed and written by MM with supervision from LM.

Chapter 5 describes work carried which quantified the feed to food transfer of arsenicals from a commercial seaweed-based animal feed and is published as: Mac Monagail, M., Cummins, E., Bermejo, R., Daly, E., Costello, D. and Morrison, L. (2018). Quantification and feed to food transfer of total and inorganic arsenic from a commercial seaweed feed. *Environment International*, 118, 314–324. This work was performed and written by MM with co-authors helping with statistical and data analyses and manuscript preparation, and supervision from LM.

Chapter 6 describes research carried out on an invasive seaweed species' arrival to a nutrient over-enriched estuary in the south of Ireland. It has been published as: Bermejo, R., Mac Monagail, M., Heesch, S., Mendes, A., Fenton, O., Knoeller, K., Daly, E. and Morrison, L. Assessment and reconstruction of Agarophyton vermiculophyllum (Gracilariales, Rhodophyta), previously known as Gracilaria vermiculophylla, invasion in a nutrient over-enriched Irish estuary. *Marine Environmental Research*, 158, 1-27. For this work, MM performed the earth observation data analysis and interpretation of satellite imagery and the manuscript's writing relating to satellite data analysis.

Chapter 7 Mac Monagail, M., Bermejo, R., Karki, S., Wilkes, R., Miguel Lara-Rayo and Morrison, L. Temporal variability and meteorological influences on the development of green tides in hypertrophic cold temperate estuaries. This work was performed and written by MM with co-authors helping with statistical and data analyses and manuscript preparation, and supervision from LM. For submission to *Nature Communications*.

The final chapter (Chapter 8) contains a general discussion and conclusion to complete this thesis, summarising the project's main findings with further recommendations for future work.

1.7 Compilation of co-authored papers published during the course of the degree

Karki, S., Bermejo, R., Wilkes, R., Mac Monagail, M., Daly, E., Healy, M., Hanafin, J., McKinstry, A., Mellander, P-E., Fenton, O. and Morrison, L. (2021).
Mapping Spatial Distribution and Biomass of Intertidal Ulva Blooms Using Machine Learning and Earth Observation. Frontiers in Marine Science, 8(633128), 1–20.
Michéal Mac Monagail contribution: Reviewing and preparation of the manuscript

Araújo, R., Vázquez Calderón, F., Sánchez López, J., Costa Azevedo, I., Bruhn, A., Fluch, S., Garcia Tasende, M., Ghaderiardakani, F., Ilmjärv, T., Laurans, M., Mac Monagail, M., Mangini, S., Peteiro, C., Rebours, C., Stefansson, T. and Ullmann, J. (2021).
Current Status of the Algae Production Industry in Europe: An Emerging Sector of the Blue Bioeconomy. Frontiers in Marine Science, 7, 1-24.
Michéal Mac Monagail contribution: Writing and preparation of the manuscript. Contributing all data and data analysis on section "Ireland."

Cornish, M.L., Mac Monagail, M. and Critchley, A.T. (2020).
The Animal Kingdom, Agriculture....and Seaweeds. Journal of Marine Science and Engineering, *8*(8), 574.
Michéal Mac Monagail contribution: Reviewing and preparation of the manuscript

Abreu, H., Alberti, J., Azevedo, I., Barrento, S., Billing, S.L., Bouma, T., Bruhn, A., Buschmann, A., Campbell, I., Chopin, T., de Clerck, O., Cottier-Cook, E., Critchley, A., Edwards, M., Emblemsvåg, J., Engelen, A., Funderud, J., Gachon, C., Golberg, A., Handå, A., Heldens, J., Hurtado, A., Kyoung Hwan, E., Ingle, K., Ktari, L., Loureiro, R., Macleod, A., Mohammady, N.G., Mac Monagail, M. et al. (2019)
PEGASUS- PHYCOMORPH European Guidelines For A Sustainable Aquaculture Of Seaweeds. COST Action FA1406 (B. Barbier, M. and Charrier (ed.)), Roscoff, France. 1-173.
Michéal Mac Monagail contribution: Writing and preparation of the manuscript. Contributing all data and data analysis on section "Republic of Ireland."

Bermejo, R., Heesch, S., Mac Monagail, M., O'Donnell, M., Daly, E., Wilkes, R.J. and Morrison, L. (2019).
Spatial and Temporal Variability of Biomass and Composition of Green Tides in Ireland. Harmful Algae, 81, pp 94-105.
Michéal Mac Monagail contribution: Fieldwork and seaweed sample collection, data processing, help with manuscript writing and preparation

Mac Monagail, M., Bermejo, R. and Morrison, L.
The Potential Application of Unmanned Aerial Vehicle Remote Sensing Techniques in the Spatial and Temporal Determination of Ulva Species Blooms in South-west Ireland. (2019). This work has been published as part of the EPA report No. 285. Nutrient Dynamics and Ecophysiology of Opportunistic Macroalgal Blooms in Irish Estuaries and Coastal Bays (Sea-MAT).
Michéal MacMonagail contribution: Fieldwork and remote sensing experimental work, data processing, writing and preparation of the report

1.8 Compilation of presentations delivered in the course of the degree

Mac Monagail, M. and Morrison, L.
Harvesting of the resource Ascophyllum nodosum in Ireland: Implications for its increased demand
Oral presentation: The International Conference on Natural Product Biotechnology (ICNPB)", October 2019, Aberdeen, Scotland

Mac Monagail, M., Cummins, E., Bermejo, R., Daly, E., Costello, D. and Morrison, L.
The potential transfer of arsenic species from a seaweed animal meal
Oral presentation: The 23rd International Seaweed Symposium (ISS) – Jeju island, Korea, April 2019

Mac Monagail, M., Bermejo, R., Daly, E. and Morrison, L.
The potential monitoring of Ulva sp. blooms in Ireland using both satellite and drone-based aerial surveys
Poster presentation: Martin Ryan open day, The Martin Ryan Institute, National University of Ireland, Galway February 2019

Mac Monagail, M., Cummins, E., Bermejo, R., Daly, E., Costello, D. and Morrison, L.
Quantification and feed to food transfer of total and inorganic arsenic from a commercial seaweed feed
Oral presentation: Seaweed4health conference – Galway Mayo Institute of Technology, Galway, Ireland, July 2018

Mac Monagail, M., Cummins, E., Bermejo, R., Daly, E., Costello, D. and Morrison, L.
Arsenic in seaweed animal feed: A negligible threat from arsenical species present in seaweed animal feed
Poster presentation: Martin Ryan open day, The Martin Ryan Institute, National University of Ireland, Galway, February 2018

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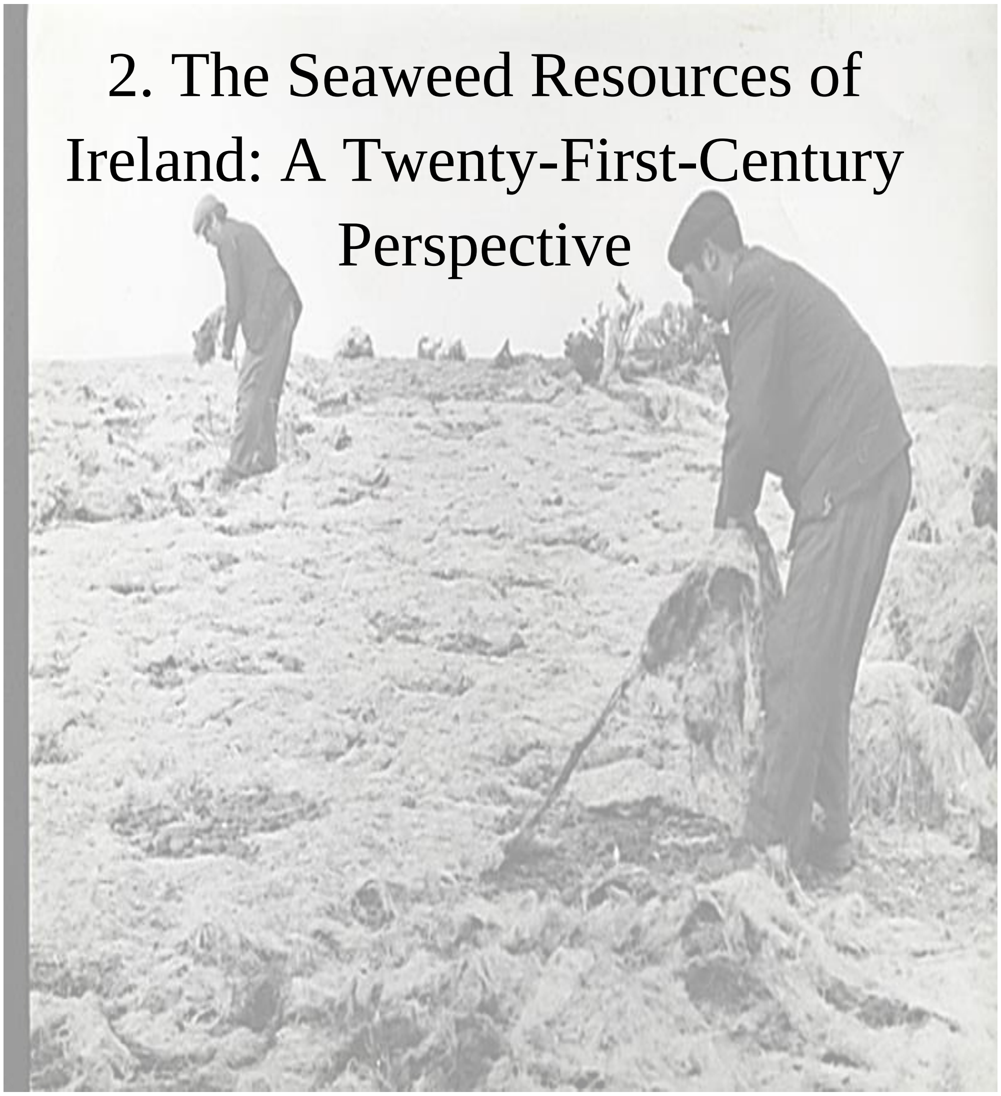
2. The Seaweed Resources of Ireland: A Twenty-First-Century Perspective



2.1 Abstract

The harvesting of wild seaweeds continues to play an important cultural and socioeconomic role for many coastal communities on Ireland's Atlantic seaboard. Although Irish waters contain a diverse and substantial benthic seaweed flora, only a few species are exploited commercially. Historically in Ireland, seaweed was commercially used as a raw material in the production of high-volume, low-value commodities such as animal feed and raw material for alginate production. Recently, with increasing acceptance of seaweed as a sea vegetable and its ever-increasing role as a raw material in the cosmetic and pharmaceutical industries, there has been a renewed vigour in the Irish seaweed industry, particularly with new entrants into the human nutrition and cosmetic markets producing high-quality, high-value products. Although many of Ireland's native seaweed species can be sustainably exploited if well managed, the fucoid *Ascophyllum nodosum* maintained its prominent role in the Irish seaweed industry. The traditional harvesting of *A. nodosum* in Ireland continues, although the recent introduction of new harvesting techniques, along with the expected expansion of the Irish seaweed cultivation sector, undoubtedly marks a shift in the Irish seaweed seascape. We focus here on the seaweed resources in Irish waters and how the industry has changed in the last 20 years.

2.2 Introduction

The classic folkloric account of the shores of Connemara, *Cladaigh Chonamara*, Séamas Mac Con Iomaire (1938), originally published in Irish, attempted to "bury the myth that the people of Ireland were a race of thalassophobes incapable of observing their natural surroundings" by describing the diverse marine flora and fauna and the coastal traditions of the west of Ireland. The collection and harvesting of seaweed is an historic practice that remains an important cultural and socioeconomically activity, particularly along Ireland's western seaboard. The practice of collecting seaweed or *ag baint feamainne* provides a supplementary income to harvesters (Macken-Walsh, 2009, Morrissey and O'Donoghue, 2012), and it has supported a native industry for almost 300 years in Ireland (Hession et al. 1998).

The seaweed biodiversity in Irish waters is considerable, with only 76 fewer recorded seaweed species than Great Britain, with a comparatively much smaller coastline (Guiry 2012). A systematic catalogue of the Irish seaweed species referred to as the Rhodophyta, Chlorophyta, and Ochrophyta was produced by Guiry (2012), who recorded some 570 species of benthic seaweed native to Irish waters, of which 161 were Phaeophyceae, 303 Florideophyceae and Bangiophyceae, and 93 Ulvophyceae together with 13 species of *Vaucheria* (Xanthophyceae). A healthy 7.5% of the world's known seaweeds have been reported from Irish waters (Guiry 2012).

Ireland's Atlantic coast has the most diversity of Irish seaweed species (Morrissey et al. 2001), and the lowest biodiversity is found on shores bordering the Irish Sea due to a range of physical, geomorphological, and anthropic factors resulting in unsuitable conditions for the establishment of large seaweed assemblages (Rae et al. 2013). Except for a few restricted areas in the vicinity of the few large cities, Ireland's shores are still relatively pristine (Morrison et al. 2008).

Some kelps, including *Saccharina latissima* (Linnaeus) C.E.Lane, C.Mayes, Druehl and G.W.Saunders and *Himanthalia elongata* (Linnaeus) S.F.Gray, can be found in extensive bands growing along the Irish coast, have yet to be commercially harvested in

Irish waters. Others (for example, *L. digitata* (Hudson) J.V.Lamouroux) have been put forward as promising alternative sources of biofuels, having some of the highest biomethane yields of Irish fucoids (Tabassum et al. 2017). Another species that has never been exploited commercially Araújo in Ireland, *Fucus vesiculosus* Linnaeus, has only recently been harvested from counties Galway and Mayo (approx. 200 tonnes harvested in 2021: pers. obs.). One of the larger red seaweeds, *Dilsea carnosa* (Schmidel) Kuntze, commonly referred to as the poor man's weather glass, while another familiar species, *Porphyra umbilicalis* Kützing, continue to be harvested by hand on a limited scale. Locally referred to as sloke, some coastal households boil and eat the small red alga as a jelly. Although with the recent exception of *F. vesiculosus*, none of these seaweeds are harvested commercially; several are now harvested on an artisanal scale and found in a range of dried edible products; See https://wildirishseaweeds.com/). Irish shorelines contain diverse seaweed flora; however, only a very limited number of species have economic and/or cultural importance (e.g., *Chondrus crispus Stackhouse* and *Palmaria palmata* (Linnaeus) F.Weber and D.Mohr, amongst others; further described in the text).

We here provide an update on Ireland's seaweed resources, with a focus on the most commercially important species. We examine how the Irish industry has changed over the last two decades and what developments are required to make full use of Irish seaweed resources and further expand the Irish seaweed industry.

2.3 *Ascophyllum nodosum*: Ireland’s most commercially important seaweed species

Seaweed processing in Ireland has been relatively stable for the past two decades, allowing Ireland to remain one of Europe’s largest seaweed producers. Since 1966, the Irish seaweed industry has been mostly reliant on the harvesting of *Ascophyllum nodosum* (Linnaeus) Le Jolis (*Feamainn bhuí*), following the cessation of the drying for export of sea rods (*Laminaria hyperborea* (Gunnerus) Foslie) in Ireland which had occurred from 1948 to 1965 (Guiry and Morrison, 2013). All *A. nodosum* harvesting occurs sustainably from wild stocks, with most material cut by hand using traditional techniques (Mac Monagail et al. 2017). In 1999, *A. nodosum* accounted for 94% of the total Irish seaweed landings. In 2016, the proportion grew marginally to 95%, highlighting the continued fundamental role *A. nodosum* plays in the Irish seaweed industry.

In 1999, 36,100 t of *A. nodosum* were harvested in Ireland, equal to 10.5% of total European seaweed production. In 2016, the tonnage landed in Ireland was 28,000 t, equivalent to 10% of the overall European seaweed market (FAO 2018). Harvested seaweed was virtually all from the wild harvest, making Ireland the third most productive country in Europe, behind Norway and France (Table 2.1) (FAO 2018).

Table 2.1 Top European producers of wild seaweed 2016 (FAO 2018)

Country	Species	Tonnage
Norway	Aquatic plants, Brown seaweeds, Rockweed	169,407
France	Brown seaweeds, North European Kelp, Tangle	55,041
Ireland	North Atlantic rockweed, North European kelp, Red seaweeds	29,500
Iceland	Rockweed, North European Kelp, Tangle	17,985
Russian Federation	Aquatic plants, Brown seaweeds, North European kelp, red seaweeds	14,022
Spain	Brown seaweeds, *Gelidium* seaweeds, Green seaweeds, Ribboned nori, Wakame	3493
Portugal	Red seaweeds	2328
Italy	Green seaweeds, Red seaweeds	1200
Estonia	Red seaweeds	348

2.4 Harvesting of *Ascophyllum nodosum*

Some 75% of landed biomass harvested of *Ascophyllum* is from counties Galway, Mayo, and Donegal (Fig. 2.1), with smaller amounts from counties Sligo, Clare, and Kerry. Several harvesting techniques are now employed by the harvesters of Ireland, depending on local conditions and tradition. When harvesting *A. nodosum* in Connemara, for example, harvesters cut seaweed (Fig. 2.2a) at low tide using a sickle or a small, sharpened knife, referred to as a *corrán* (literally a crescent) or a *scian bheag* (little knife). The harvested material is placed upon two crossed ropes, which are used to tie the stack of seaweed in place into a 2 to 4-t *climín* (literally a bundle, plural *climíní*) (Fig. 2.2b). The *climín* is then allowed to float with the incoming tide and is usually towed to the nearest pier using a traditional boat (*currach*) from where it is transported for processing by lorry (Fig. 2.2c). In counties, Clare and south Galway, the use of a flat *climín* or a *téad* (literally a rope) (Fig. 2.2d) is more common than the use of *climíní* when harvesting *A. nodosum* due to the nature of the shoreline. Depending on their experience and skills, seaweed harvesters are typically capable of cutting between 1 and 4 t in a single tide cycle, although it has been known for some cutters to harvest as much as 7 t "on a good tide". Further information on the sustainable harvesting of *A. nodosum* in Ireland has been described in Guiry and Morrison (2013).

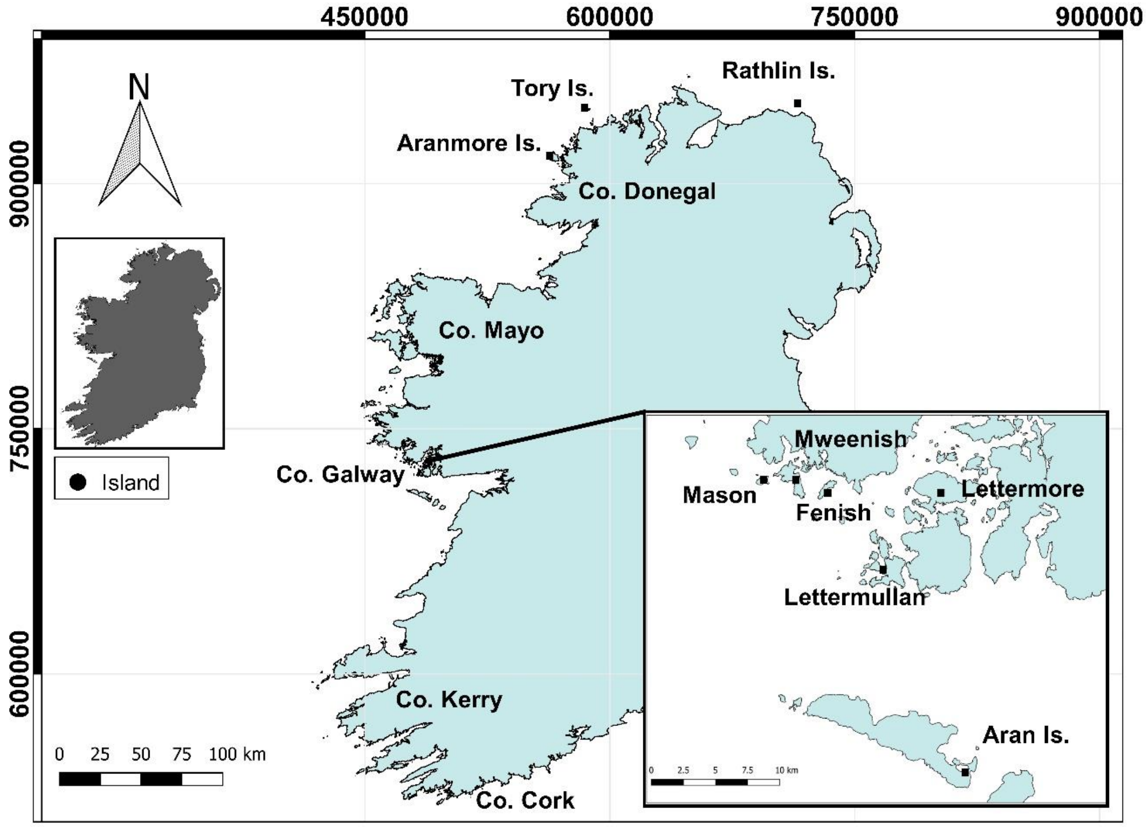


Fig. 2.1 Map of Ireland showing locations of *Ascophyllum nodosum* and *Laminaria hyperborea* harvesting mentioned in the text

Fig. 2.2 (a) traditional hand harvesting of *A. nodosum* on the west coast of Ireland, (b) *Climíní* stored on local piers awaiting collection and transportation to *A. nodosum* processing factory (c) traditional *Climíní* being tower ashore at high water, Co. Galway, (d) flat *Climín* (rings) being towed ashore in Co. Donegal

After cutting, beds are left fallow for 3–7 years to allow regeneration, depending on the harvesters' local knowledge and experience. In counties Galway and Donegal, this period is generally between 3 and 4 years, while in Co. Mayo, it can be between 5 and 7 years. This practice was recorded by the Norwegian researcher Egil Baardseth while working in the west of Ireland, who reported the opinion of cutters that recently harvested areas of *A. nodosum* should fallow for a period of "3–6 years" to allow the seaweed to recover properly. Recovery also depends on the exploitation rate and the amount of actively growing shoots remaining (Baardseth 1955, 1970). There are also significant economic benefits associated with sustainable harvesting and allowing adequate recovery times (Rebours et al. 2014). The self-imposed implementation of fallow periods following harvest ensures the recovery of seaweed beds and allows for a well maintained and sustainably exploited resource (Morrissey et al. 2001).

2.5 *Laminaria hyperborea*

Important kelps in Irish waters include *L. hyperborea*, of which 1400 wet tonnes were harvested from wild stocks in 2016 (FAO 2018). The harvesting from wild stocks of this kelp occurs mostly in Cork and Kerry's southern counties (Buschmann et al. 2017).

The harvesting of “sea rods” (*L. hyperborea*/*slataí mara*/*budógaí*) played a meaningful role for Irish coastal inhabitants from the mid-eighteenth century for about 100 years. The manufacture of “kelp” from seaweed was a profitable undertaking for many island residents in the north and northeast of the country, particularly in areas such as Aranmore Island, Tory Island and Rathlin Island (Fig. 2.1), where it is said that “persons of every age and sex [were] employed collecting seaweed or carrying it off the beach on the small island horses” (Forde 1926, Forsythe 2006). In Ireland, the progress of the bleaching trade created a demand for alkali (Clow and Clow, 1947). In the west of the country, on the Aran Islands and the islands of Lettermullan, Lettermore, Mweenish, Fenish and Mason, inhabitants took advantage of kelp burning and the use of “black weed” harvested and brought from the shore in “back loads” by “the women who join in all fieldwork and seem to be the hardest worked members of the community” (Browne 1900).

2.6 Rhodophyta

Of the Rhodophyta, some native species, including *P. palmata*, *Chondrus crispus*, *Mastocarpus stellatus* (Stackhouse) Guiry and the red coralline algae collectively referred to as maerl, have historically been utilised by coastal communities, either as a food source (Mouritsen et al. 2013) or as a source of fertiliser (as in the case of maerl; O’Reilly et al. 2012). According to FAO (2018), “red seaweeds” accounted for < 0.5% of the total national landings by volume (approximately 100 t) in Ireland (Table 2.2). Both *C. crispus* and *M. stellatus* are important carrageenophytes (Necas and Bartosikova, 2013) and are harvested at low tide by plucking or cutting the small plants from the lower intertidal using either a sharpened small knife or scissors. Irish harvesters collect both seaweeds indiscriminately as carrageen (*carraigín*). Most harvesting occurs during the autumnal equinoctial spring tides (Pybus 1977). The harvesting of the delectable alga *P. palmata* (Dulse or Dillisk) occurs on only a small scale throughout Ireland's Atlantic coast (Edwards and Dring, 2011).

Table 2.2 Irish seaweed landings 2016 (FAO 2018)

Species	Tonnage landed
North Atlantic rockweed	28000
North European kelp	1400
Red Seaweeds including *Chondrus crispus*/*Mastocarpus stellatus, Palmaria palmata* and Maerl	~100

Several species of maerl are present in Irish waters (Fig. 2.3a), but only two are of current economic importance (*Phymatolithon calcareum* (Pallas) W.H.Adey and D.L.McKibbin ex Woelkering and L.M.Irvine and *Lithothamnion corallioides* (P.Crouan and H.Crouan) P.Crouan and H.Crouan). Sizeable deposits of both occur at more than 60 locations along the west coast of Ireland (De Grave et al. 2000). Maerl is also found washed up on shores known as “coral strands” (Hession et al. 1998), such as Trá an Dóilín near Carraroe, Co. Galway and Mannin Bay, Co. Galway.

Fig. 2.3 (a) maerl, (b) storm cast kelp rods, Co. Mayo, (c, d) newly adopted boat and rake harvesting technique, Co. Galway

The gathering of drift weed or storm cast material (*racálach*) (Fig. 2.3b) from the upper part of the beach was historically an essential source of raw material as a soil treatment or as an additive for animal feed (Guiry and Morrison, 2013). This resource was seen as a readily available source of biomass, the right of which to gather in particular areas was given to the first family down to the shore in the morning (O'Neill 1970). In recent years, however, and as a response to industry demands for improved raw material quality, the gathering of cast weed has almost disappeared except for personal use.

2.7 Introduction of new harvest techniques

Although to date the Irish seaweed industry has been wholly reliant on traditional hand harvesting, some new harvest methodologies are beginning to emerge in Ireland to augment traditional hand harvesting, particularly using rakes from boats for *Ascophyllum* and the use of mechanical harvesting for kelps.

2.7.1 Hand-harvesting into a boat

Though the practice of harvesters cutting seaweed using a *croisín* (a pole with a hook and crosspiece for harvesting seaweed) into a traditional currach or *húicéir* boat has occurred in the past, increasing water safety regulations in Ireland has curtailed these practices. Following its introduction into the Canadian Maritimes in the 1960s (Chopin and Ugarte, 2006), the boat and rake method for commercial *A. nodosum* harvesting was introduced in Ireland in 2016. Purpose-built boats are operated by experienced harvesters, while specially designed rake heads produce minimum changes to the habitat architecture following harvest (Ugarte et al. 2006) (Fig. 2.3c, d). This harvest method also allows individuals to take advantage of the rising tide offering improved socio-economic opportunities for harvesters. Due to several factors, however, including the slope of the shoreline, the geomorphology of the area, and the experience and skills of harvesters working under challenging conditions, the traditional hand-harvest is still the only viable harvest option in many areas. The boat and rake harvest method has provided to date only a limited amount of biomass to the industry in Ireland.

2.7.2 Mechanical harvesting

The mechanical harvesting of Irish seaweed resources, for both *A. nodosum* and kelps, has previously been identified as a key area of development for the domestic seaweed industry (Werner and Kraan, 2004). In recent years, the proposed introduction of mechanical harvesting methods in Ireland has attracted considerable interest from both the industry and local communities (Baker 2017, Roseingrave 2017).

Mechanical harvesting of seaweeds is carried out in some parts of Europe (Kadam et al. 2015), particularly in northern European countries such as Iceland and Norway, which are at the forefront of developing mechanical harvesting techniques (Tiwari and Troy, 2015). Mechanical harvesting provides the vast majority of Norway’s national seaweed output (Meland and Rebours, 2012), with seaweed trawlers operated for the harvest of *L. hyperborea* capable of harvesting 50–150 t day^{-1} (Vea and Ask, 2011). Smaller paddle wheel cutters are operated for the *A. nodosum* harvest (Meland and Rebours, 2012). In Iceland, *A. nodosum* is harvested using mechanical harvesters equipped with adjustable rotating cutting blades and a conveyor platform that feeds chopped material into net bags (Gunnarsdóttir 2017). In Brittany, depending on the species, the harvesting of kelp is either carried out by boat with gear called “scoubidou”, which is used to uproot the kelp or by using large rake-like devices which are dragged through seaweed beds where the larger kelps are uprooted (Mesnildrey et al. 2012). Meanwhile, Maerl is harvested mechanically in some parts of Brittany using a “sablier” suction dredge that removes the calcareous algae from the sea bottom (Mesnildrey et al. 2012).

Several mechanical harvesters operated in the Canadian Maritimes between the years 1976 and 1990. Older, less efficient mechanical harvesters consisting of a reciprocating cutter mounted on a paddlewheel driven barge (Ugarte and Sharp, 2001) were replaced in 1985 by ultra-efficient Norwegian suction cutter harvesters, which were capable of harvesting 33.6 wet t day^{-1} of *A. nodosum* (Sharp and Ang, 1994). Since 1993, harvesting has reverted to boat and rake methods in southwestern Nova Scotia (Chopin and Ugarte, 2006).

Mechanical harvesting has the potential to present challenges for fisheries management in terms of protecting marine biodiversity (Kelly 2005). Understanding the impact of mechanical harvesting on the harvester population is crucial in determining the correct management strategy (Ang et al. 1993). Examples of successfully implemented management strategies exist in Europe. In Norway, a sustainable management program for the harvest of *L. hyperborea* has been in place for 60 years, which is based on a clear understanding of the ecology and life cycle of the kelp as well as the ecosystem (Vea and Ask 2011).

The National Parks and Wildlife Service (NPWS) at the Department of Culture, Heritage, and the Gaeltacht in Ireland are responsible for the conservation and protection of Ireland's seaweed resources and for advising the licensing authority (Marine Section within the Department of Housing Planning and Local Government) regarding the issuing of harvest licenses to new entrants (Kelly 2005). The NPWS has repeatedly expressed its opposition to mechanical kelp harvesting in Ireland, stating that "… such activities are not compatible with the conservation objectives of and should not be permitted in Natura 2000 sites".

In June 2009, an application was submitted to the licensing authority to harvest mechanically over an area of 1800 acres 5000 t of kelp (*L. hyperborea*) per annum from Bantry Bay, Co. Cork using a purpose-built vessel equipped with a winch, suction pump, and cutter. Approval in principle was first granted in 2011, with a licence subject to conditions granted in 2014. However, following local opposition to the plan (Keogh 2018a), a judicial review was secured in May 2018. Separate High Court proceedings were also launched, seeking an order that the harvesting operation should come under the Planning and Development Act 2000 and not just the provisions of the Foreshore Act 1933 (as amended) under which the license was initially granted. That issue was heard in May 2019, and a judgement was handed down on 6 June 2019, with the High Court dismissing the action and finding in favour of the applicant. However, concerning the Judicial Review proceedings, the High Court was of the view on 29 July 2019 that the State's failure to adequately publish notice of plans to grant a license for large-scale mechanical kelp harvesting off Bantry Bay meant that the license had not yet been effectively issued (Sargent 2019).

Further hearings were carried out on 8 October 2019, when the High Court heard submissions from the applicant who are a notice party to the proceedings. Judgement is yet to be made. Should the Court confirm its view by way of ruling, then it is likely that the Minister will appeal the ruling to the Supreme Court. Therefore, with regard to the Judicial Review proceedings, the matter is still before the Courts, and harvesting has yet to commence.

2.8 Seaweed harvesters

It is important to note that few people (if any) make their sole income through seaweed harvesting, and very few people officially declare themselves as harvesters (Delaney et al. 2016). Harvesters, or *bainteoirí*, are effectively seen as sole traders not contracted by any one enterprise and who are free to harvest for whom they wish. In some parts of the country, particularly some areas of Connemara, the harvesting of seaweed is both an income-generating activity and a cultural commodity (Macken-Walsh 2009). Income-generating activities such as seaweed harvesting are not only economically significant in coastal communities but are also seen as crucial for realising “real” rural development (Macken-Walsh 2009). Most commonly, harvesting seaweed is an income-generating activity that complements a diverse range of other activities, including fishing or dredging, lobster potting, wall building, small-scale farming, or turf cutting, depending on the time of the year.

The age structure of harvesters in the Connemara region in 1997–1998, as reported by Kelly et al. 2001, was such that 13% of harvesters were under the age of 40, while only 3% were under 30. Twenty years on, and this demographic is still apparent (pers. obs.). Seaweed harvesting is challenging and labour-intensive work, and for the most part, the younger generations migrate away from rural coastal areas in search of higher paid employment. The average harvesters' age profile and the difficulty in recruiting the younger generation to harvest seaweed pose a threat to this traditional practice. A paucity of harvesters will likely threaten the ability to ensure raw material supply to the industry in the near future. New (biotechnological applications) or recovered (traditional food) uses of seaweeds, in addition to the increased price of the raw material, may encourage the uptake in this activity in the near future.

2.8.1 Harvester rights and regulations

Some specific regulations, such as the EU Council Directive 92/43/EEC of 21 May 1992, exist relating to conserving natural habitats and wild fauna and flora. However, for the most part, little regulation exists in Ireland relating to either harvestable seaweed species or allowable harvestable quantities. In Northern Ireland, the Crown Estate issues licenses for the sustainable, commercial harvesting of seaweed from foreshore and seabed areas under their ownership. In the Republic of Ireland, however, the seabed and the shore below the line of high water at mean tide and extending outward to twelve nautical miles are the State's responsibility under the 1933 Foreshore Act (revised and amended up to 2017). Under the original 1933 Act, persons are prohibited from gathering seaweed material unless in possession of a “foreshore licence” from the relevant Minister, with the result being that “many people having no foreshore rights must buy the seaweed or go without” (O’Buachalla 1937). Under this Act, seaweed constitutes “beach material”, whether growing or rooted on the seashore or deposited or washed up by the action of waves, winds, and tides. A foreshore licence is required from the Minister to remove organic beach material from the foreshore. Therefore, any individuals or companies seeking to harvest wild seaweed are required to first obtain a foreshore licence under Section 3 of the Act.

However, one exception is where traditional rights to harvest seaweed are in place under one’s property. These “seaweed rights” or “folio rights”, recorded in landowner folios (which include property details, its ownership and any burdens affecting ownership) dating from the breakup of estates under the Land Commission in the 1920s, have historically ensured access to harvest seaweed material adjacent to some coastal properties in the west of Ireland (O’Neill 1970, Mac Monagail et al. 2017). These “traditional rights” have since been rigorously preserved by the Irish State (Dermody 2018).

Traditional harvesters may, in some cases, have established rights known as profit-à-prendre rights. The Minister may not grant a licence to harvest wild seaweed where such a licence would interfere with either an appurtenant or *profit-à-prendre* right to take seaweed or where the foreshore is privately owned. Where an appurtenant or *profit-à-*

prendre right exists, the requirement to hold a foreshore licence under the Foreshore Act does not apply to the individual holding the appurtenant or *profit-à-prendre rights*, although the rights holders still must comply with the requirements of the Birds and Habitats Directive. In his speech given at the Our Ocean Wealth Summit in Galway in June 2019, the Minister has stated, "... my Department cannot licence seaweed harvesting in an area where there is an existing right to harvest seaweed… existing seaweed rights holders can continue to exercise their right to harvest seaweed and do not require consent under the Foreshore Act". Where the foreshore is privately owned, the Foreshore Act provisions do not apply to the taking of seaweed from the foreshore.

Speaking at the Oireachtas (Irish Parliament) in January 2019, the Minister of State for Local Government stated that "it is now necessary for applicants [to] undertake a search of the Land Registry folios in respect of the area of the foreshore for the which they apply to harvest". Some 6500 folios along the west of Ireland have been identified as containing seaweed harvesting rights (Siggins 2018).

2.9 Two decades of change and development within the Irish seaweed industry

The Irish seaweed industry has developed from one whose roots can be traced back to the 1930s (Bixler and Porse, 2011, Delaney et al. 2016), with commercial seaweed processing beginning in early 1948. By 2020, the Irish seaweed industry is expected to be worth 30 million € (Sea Change 2006).

Ireland's seaweed industry continues to mature and plays a fundamental role in the marine and coastal economies (Morrissey et al. 2011) and is expected to expand (McMahon 2017, Keogh 2018b). Ireland's ocean economy employs 30,176 full-time employees (Vega and Hynes, 2017), with an estimated 700 people engaged in the seaweed sector at the end of the twentieth century (Lyons 2000). As these industries are typically based near the coast, the continued expansion of the Irish seaweed industry will likely promote employment opportunities to the 40% of the Irish population who reside within 5 km of the coast (O'Donoghue et al. 2014, CSO 2017).

A new report on "The global status of seaweed production, trade and utilisation" (Ferdouse et al. 2018), which provides an update of the global seaweed market, including production figures from culture and capture, does not, unfortunately, include Ireland. A report “Valuing Irelands Blue Ecosystem Services” valued seaweed harvesting at 4 million € to the Irish economy (Norton et al. 2014).

There appeared to be little development of the seaweed industry in Ireland in the early part of the twenty-first century, with most biomass directed towards industrial processes and the commercial value of seaweeds being limited to high volume, low-value products such as animal feeds and alginates (Walsh and Watson, 2011, Guiry and Morrison 2013).

Despite an abundant and diverse native resource, only a minimal number of species are exploited commercially, particularly *A. nodosum*, *L. hyperborea*, *L. digitata*, Irish Moss (*C. crispus*/*M. stellatus*), *P. palmata* and Maerl (See Table 2.2). However, many Irish producers have found niche markets where purchasers are willing to pay higher prices for these products.

There exists a diverse indigenous seaweed industry within Ireland. There have been significant shifts in the Irish seaweed landscape within the past decade. The largest seaweed processor in Ireland is Arramara Teoranta, which has been largely responsible for developing the seaweed industry in the country (Hession et al. 1998) and is the predominant processor of *A. nodosum* (Walsh and Watson, 2011) and, as of 2021, has begun processing *F. vesiculosus*. The company was acquired by the Canadian group Acadian Seaplants Ltd. in 2014. A second Irish processor, Oilean Glas Teo (OGT), a company based in Kilcar, Co. Donegal, was founded in 2004 and specialises in producing a range of *A. nodosum*-based horticultural products for plants and grass, golf courses and playing fields. The company was acquired by the Spanish group TradeCorp Ltd. in 2014.

There are significant burdens associated with raw material procurement and chemical and energy-related costs to seaweed production (Bixler and Porse, 2011). Despite this, changing public perception and acceptance of seaweed as a valuable commodity (Mouritsen 2017) have prompted new entrants to the Irish market. Growth in this industry has been driven mainly by processing higher value products and, more recently, by price increases in the harvested raw material (Tsakiridis et al. 2019). In the recent past, there has been an increase in the number of seaweed producers and microbusinesses, marketeers, and artisanal retailers, specialising in the production and packaging of seaweed raw materials and finished products in Ireland (Delaney et al. 2016). Many of these small enterprises are concentrated on the west coast of Ireland, producing a variety of seaweed-based products for both the domestic and international food, cosmetic and thalassotherapy markets. Some Irish SMEs, such as This Is Seaweed and Voya, based out of counties Dublin and Sligo, respectively, have successfully developed an internationally recognised brand (Keough 2015, Keogh 2018b).

In Northern Island, several small companies such as Islander Kelp and the Irish Seaweed Company, both based in Co. Antrim produces food products from wild local resources. Several Connemara-based companies, including the Connemara Seaweed Company Ltd. and Mungo Murphy's Seaweed Ltd., produce products from a range of locally harvested seaweed species, including dulse, carrageen moss and *Sargassum*, for both cosmetic skincare and food markets. Some indigenous organisations, such as Nutramara Ltd. and Aquaceuticals Ltd. (based in Co. Kerry and Co. Galway, respectively), create and commercialise a diverse range of cosmeceutical and food supplement products and formulations for human health from sustainably harvested seaweed. Cybercolloids Ltd., operating in Carrigaline, Co. Cork since 2002, is a company working in developing high value, seaweed-based flavour ingredients for the food industry (Reis et al. 2016). In Co. Kerry, since 1998, Brandon Bioscience Ltd. has been focused on developing A. nodosum–based products to improve the yield and quality of crops. An enterprise based in Co. Clare, Wild Irish Sea Veg, has been operating for over a decade to produce seaweed products for human consumption and cosmetic markets. In Cork, Irish Seaweed utilises native species such as dulse, kelp, sea lettuce, Irish moss, and wild nori (*Porphyra*) into the brewing process of fruit wine (Walsh and Watson, 2011). The range and diversity of the Irish seaweed industry highlight the impressive fluidity in which Irish SMEs can dovetail between high-end food, human nutrition, and cosmetic markets.

2.10 Cultivation of seaweed in Ireland

Seaweed aquaculture is seen as an integral part of Ireland's coastal economy (Department of Housing Planning and Local Government, 2018). Growth in the Irish seaweed industry will likely result from an expansion of seaweed cultivation in Irish waters (Werner and Kraan, 2004). Although likely to be adjusted according to local Irish conditions (Campbell et al. 2019), Irelands favourable climatic conditions and suitable shoreline show considerable potential for cultivation expansion in Irish waters (Werner et al. 2004). As with the majority of Europe, the Irish seaweed cultivation industry is still in its infancy and has yet to reach anywhere near its full potential (Murphy et al. 2013, Jansen et al. 2019). However, requiring no fresh water or fertiliser inputs, cultivating seaweeds in Ireland can be relatively resource-efficient and possesses a low carbon footprint (Taelman et al. 2015). The first commercial seaweed pilot farm in Ireland was established in 1996 by Sliog'eisc Mhic Dara in Ard Bay (Campbell et al. 2019) to cultivate *Asparagopsis armata* Harvey. This venture has since been discontinued (Kraan and Barrington, 2005). More recently (since 2015), the Daithi O'Murchu Marine Research Station has been granted a seaweed licence to cultivate native marine algae in Bantry Bay, Co. Cork. However, production in Ireland remains limited, with total Irish production through cultivation in 2016 some < 50 t (FAO 2018).

The cultivation of several seaweeds, including *P. palmata* and *L. digitata*, is required to meet the demand of several sectors, including the requirements of abalone and finfish farmers (Schmid et al. 2003, Edwards and Dring, 2011, O'Mahoney et al. 2014) and even to provide raw material to establish a seaweed biogas industry in Ireland (Tabassum et al. 2017).

Currently, there are 17 applications submitted to the DAFM for seaweed licences to cultivate and process a range of native species in Ireland (Cadogan 2018). In the south of the country, several enterprises, including Allihies Seafood Ltd., Emerald Seaweed Ltd., and Dingle Bay Seaweed Ltd., have applied for seaweed aquaculture licenses to cultivate a significantly varied range of species, including *Alaria esculenta* (Linnaeus) Greville; *S. latissima*; *L. digitata*; *P. palmata*; *Porphyra* sp.; *C. crispus*; and *M. stellatus* on long seeded lines. This activity is expected to grow substantially with the granting of further cultivation licenses.

Open sea cultivation can provide an enormous quantity of biomass for several sectors, particularly relevant as demands for contaminant-free seaweed for use in nutraceuticals and pharmaceuticals appears to be increasing (Engle et al. 2018). While wild harvesting can result in variation in the availability and quality of the finished product, and the possibility of heavy metal contamination is a significant issue (Edwards and Dring, 2011, Ferdouse et al. 2018), several challenges also exist for the guaranteed supply of seaweed through sustainable cultivation. Biotic and abiotic stressors are significant challenges to global seaweed aquaculture (Ding and Ma, 2005, Loureiro et al. 2015), with cultivation very dependent on any outbreak of seaweed disease of pest species (Borlongan et al. 2011). An infestation of epiphytes and parasites can result in considerable quality deterioration (Stévant et al. 2017), with the grazing of seaweed tissues by herbivores resulting in inconsistent crop yields (Ganesan et al. 2006). Infestations of the parasitic epiphyte *Polysiphonia* sp. can drastically alter farmed *Kappaphycus alvarezii* (Doty) Doty ex P.C.Silva growth and can even cause farming activity to collapse (Critchley et al. 2004, Tsiresy et al. 2016).

With the further development of new markets in pharmaceutical and human health applications, the production of high-quality health and food products with recognised traceability and testable safety standards will be of utmost importance to the successful commercialisation of contaminant-free raw material (Winberg et al. 2011, Hafting et al. 2012). The continued refinement of existing cultivation techniques will likely improve products' quality control and traceability (Hafting et al. 2015).

2.11 Seaweed as a source of food in Ireland

One of the goals of the National Marine Research and Innovation Strategy 2017–2021 is the continued contribution of seaweed to Ireland’s food production and processing sector, which incidentally is Ireland’s largest indigenous industry sector. Until the last decade or so, seaweed consumption in Ireland, except in some localised hotspots, appeared to have more or less discontinued. Seaweeds in Ireland were historically regarded as a food source for the poor due partly to their consumption during the great famine in the 1840s (see, for instance, Mokyr and O’Gráda, 2002). More recently, however, seaweeds have undergone a renaissance in Ireland and across Europe and are now viewed as both a nutritious and versatile food adding taste and mouthfeel to innovative dishes (Mouritsen 2017, Lucas et al. 2019).

Edible seaweed products may be available to consumers in various forms, either fresh or dry, powdered and flaked (Buschmann et al. 2017). The nutritional composition of several edible Irish seaweeds have exceptional potential as valuable commercial food products (Skrzypczyk et al. 2019), holding nutritional and therapeutic promise (MacArtain et al. 2007, Mendez et al. 2019), with many native Irish seaweeds finding a place in the functional food market (Holdt and Kraan, 2011, Wells et al. 2017).

Certain seaweeds have specific and diverse sensory characteristics, providing consumers with a large variety of sensory qualities (Chapman et al. 2015). Only a small number, however, are exploited for human consumption in Ireland. *Palmaria palmata* is considered a food delicacy, with much of this edible seaweed harvested and consumed within Ireland (15–30 t) (Walsh and Watson, 2011).

Harvested quantities are influenced by market demands as well as seaweed availability (Bixler and Porse, 2011), with demand for *P. palmata* as a snack in Northern Ireland regularly outstripping supply from natural populations (Edwards and Dring, 2011). *Chondrus crispus* is also used as a traditional herbal remedy in some coastal households in the west of Ireland (Mac Monagail and Morrison, 2020). Barring some limited usage, it would appear that some species, including *Porphyra* and *Pyropia* species (*sleabchán*), have all but fallen out of household use.

2.12 Invasive species

The number of introduced seaweed species to Irish waters is relatively small (Guiry 2012, Rae et al. 2013). Many, such as *Asparagopsis armata* (first recorded in 1941 in Galway Bay (De Valera 1942)), *Melanothamnus harveyi* (first recorded in 1990 by Maggs and Hommersand (1990) (previously *Polysiphonia harveyi* Bailey) and *Codium fragile* subsp. tomentosoides and subsp. *atlanticum* (first recorded in 1941 in 1911, respectively in Ireland) (Parkes 1975, Provan et al. 2008), are now common species throughout Irish waters. A recent arrival to Irish waters is the *Undaria pinnatifida* (Harvey) Suringar that was first recorded on the east coast of Ireland in Kilmore Quay, Co. Wexford, in July 2016 (Kraan 2017). More recently, the presence of *Agarophyton vermiculophyllum* (Ohmi) Gurgel, J.N.Norris and Fredericq (previously *Gracilaria* *vermiculophylla* (Ohmi) Papenfuss) was confirmed by molecular means in an estuary located in Clonakilty, Co. Cork in 2019 (Bermejo et al. 2019).

Invasive seaweeds can be in direct competition with native biota (Hammann et al. 2013), and they have the potential to alter habitat structure (Dijkstra et al. 2017). Some of the chief concerns relate to direct competition with native Irish biota and the potential to alter habitat structure (Stokes et al. 2004, Hammann et al. 2013, Dijkstra et al. 2017).

The first recorded arrival of *Sargassum muticum* (Yendo) Fensholt in Irish waters was documented in Northern Ireland in Strangford Lough, Co. Down, and in the Republic of Ireland in Cashel Bay, Co. Galway, in 1995 and 2001, respectively (Boaden 1995, Loughnane and Stengel, 2002), although it most likely occurred in Irish waters a decade before then (Kraan 2008). *Sargassum muticum* has since spread from Co. Donegal (Kraan 2008) to Co. Cork (Salvaterra et al. 2013). It is thought unlikely to cause widespread ecological impacts in Scotland (Harries et al. 2007), with *S. muticum* showing a limited impact on native algal assemblages from rocky intertidal shores from Northern Spain (Olabarria et al. 2009). However, few studies have been carried out in Ireland to substantiate these opinions, and the impact on native *Cystoseiraceae* and sea-grass beds remains to be assessed. High abundances of *S. muticum* can result in space monopolisation and reduced resources for native species (Schaffelke and Hewitt, 2007), thus changing indigenous seaweed assemblage communities' functional behaviour and structure. *Sargassum muticum* may interact and replace native eelgrass and the brown seaweed *H. elongata* though this effect may be site-specific (Den Hartog 1997, Baer and Stengel, 2010). It has also been suggested that this species could have more wide-reaching effects on coastal ecosystems than direct effects (DeAmicis and Foggo, 2015).

The increasing annual proliferation of nuisance *Ulva* spp. blooms in Irish waters result from the enrichment of nutrients and metals in seawater associated with anthropogenic activities (Wan et al. 2017). Some significant and persistent blooms occur annually in a number of estuaries in counties Cork, Dublin and Donegal, and several other counties (Bermejo et al. 2019).

It can be challenging to define invasive species' transmission pathway in Irish waters with certainty, with the quantity and quality of invader propagules determining invasion success (Johnston et al. 2009). The spread and transmittance of invasive species in Irish waters may be through several vectors, such as attachment to leisure or fishing vessels (Miller et al. 2007, Vega Fernández et al. 2019) and aquaculture installations (Naylor et al. 2001, Minchin 2007). Marine litter such as floating plastic debris (Rech et al. 2016) can also carry attached alien biota, thereby acting as a gateway for invasive seaweed species (Gregory 2009).

2.13 Effect of global change on seaweed biodiversity in Ireland

The threat of climate change to Irish waters' native flora species biodiversity is inadequately understood with little emerging consensus. Warming Irish waters may result in pressures placed on elements of the native flora and may significantly influence the biodiversity composition of nearshore benthic communities (Harley et al. 2012, Donnelly 2018).

Many kelp species, for example, are negatively affected by ultraviolet radiation, particularly in shallow tidal conditions (Huovinen et al. 2004, Roleda et al. 2006), with projected climate change and warming waters threatening ancient kelp forests in the north Atlantic (Assis et al. 2018). Many cold-water species are likely to be affected by warming waters as sexual reproduction in most kelps will not occur above 20 °C (Dayton et al. 1999), meaning some native kelp species, such as *A. esculenta*, *S. latissima* and *L. hyperborea*, are likely to decrease in abundance and range (Simkanin et al. 2005). As a result of increasing water temperature, a latitudinal retreat in the distribution of some coldwater kelp species such as *A. esculenta* and poleward expansion of warmer water species such as *S. latissima* and *L. digitata* (Merzouk and Johnson, 2011) is likely. The kelp *Laminaria ochroleuca* Bachelot de la Pylaie has been recorded for the first time in Irish waters in Belmullet, Co. Mayo (Schoenrock et al. 2019). Climate change will likely affect the standing crop of fucoids in Ireland, with an expected shifting northward of these species as the North Atlantic warms faster than all other ocean basins (Jueterbock et al. 2013). It has been suggested that increasing water temperatures will likely negatively impact growth rates and therefore canopy cover of *A. nodosum*, with *F. vesiculosus* displaying a higher tolerance to warming waters relative to *A. nodosum* (Wilson et al. 2015).

2.14 Future scenarios

As laid out in the integrated marine plan for Ireland, “Harnessing Our Ocean Wealth”, “ocean wealth will be a key element… generating benefits for all our citizens, supported by coherent policy, planning and regulation, and managed in an integrated manner”. It is a challenge to forecast the future of the Irish seaweed industry. Many domestic factors, including an ageing workforce, higher demands from industry for raw materials and unpredictable economic conditions, are immediate threats to the industry.

The Irish seaweed industry has always been viewed as having “potential” (Hafting et al. 2015), and it is appropriate that Ireland takes full advantage of its enormously valuable yet underutilised national asset (Shields et al. 2005). It is critical that we improve our fundamental knowledge of biomass quantities and economically significant species to fill knowledge gaps relating to the development of Irelands sustainable bioeconomy (Sánchez et al. 2018).

Many seaweeds native to Ireland, including *A. nodosum*, *L. hyperborea*, *L. digitata*, *P. palmata* and carrageen moss, continue to play vital cultural and industrial roles. The challenges now lie in the further development of cost-effective methodologies to expand the national harvest. Expected industry growth and increasing automation, coupled with higher drying and scaling up capabilities, will likely reduce overheads.

A new report, “PEGASUS: Phycomorph European Guidelines for a Sustainable Seaweed Aquaculture”, calls for the development, improvement and diversification of seaweed aquaculture practices across Europe (Barbier et al. 2019; *See Section 1.7 Compilation of co-authored papers*). Seaweed cultivation, if properly managed, can help develop underutilised marine resources throughout Europe (Campbell et al. 2019). Consequently, increasing emphasis on seaweed cultivation may allow wild harvesters a diversification opportunity to augment their income and transfer their skills and equipment to other species (Burrows et al. 2018). The large-scale roll-out of cultivation facilities in Irish waters requires thoughtful consideration for the location of cultivation sites.

As the popularity of Irish seaweed products increases along with numerous new entrants into the Irish seaweed market, uninhibited exploitation of a resource will likely lead to additional stress placed upon the resource. Irish authorities must be vigilant and forward-thinking towards managing Ireland’s seaweed resources as historically most management strategies of natural resources generally occur immediately before imminent collapse or after the evident decline of populations (Vásquez 2008). The effects of climate change and continued invasive seaweed colonisation on the abundance, diversity and range of Irish benthic flora have yet to be fully elucidated. We recommend vigilance with regard to the monitoring of invasive species, such as the possible effects of *A. vermiculophyllum* on native *F. vesiculosus* beds (Hammann et al. 2013) and *L. ochroleuca* competition with native *L. hyperborea* assemblages (Smale et al. 2015).

A fundamental impediment to a growing industry is the guaranteed steady supply of high-quality raw material. As Ireland (and Europe) slowly moves away from the harvesting of wild resources and begins to increasingly utilise cultivated raw material, a shift from low-value commodities such as animal feed towards higher-value products in the cosmetic, functional food, nutraceutical, and pharmaceutical markets can be expected. A cultivation industry likely needs to be developed to compete in these markets.

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3. Sustainable Harvesting of Wild Seaweed Resources

3.1 Abstract

Macroalgae have played an important role in coastal communities for centuries. In the past, they have been harvested and gathered from shorelines worldwide for traditional uses such as food, animal feed and crude fertiliser (marine manure). Today, seaweeds are used in a multitude of applications with expanding global industries based on hydrocolloids, cosmetics, and food supplements, and also as a potential biofuel source. However, of the approximately 10 000 algal species reported to exist, only a small number are commercially utilised. While representing only a small fraction of total global seaweed production, harvesting and gathering 'wild' seaweeds has had and continues to have an integral role in many coastal societies, often being intrinsically linked to the cultural identity of those coastal communities. Today, 32 countries actively harvest seaweeds from wild stocks, with over 800 000 t harvested annually from natural beds. It is vitally important that seaweeds are utilised sustainably, and those coastal communities effectively manage natural resources with vested interests around the world. As the popularity of seaweeds increases and the use of less traditional species with novel applications come to the fore, it is critically important to make certain that the sustainability of the resource is ensured, given the increased pressures of harvesting. Issues exist regarding ownership of the resource and its over-exploitation, and the implementation of environmentally damaging harvesting techniques must be avoided. Resource scientists, managers, conservationists, governments, and other stakeholders need to be proactive in the sustainable management of these vulnerable yet valuable resources.

3.2 Introduction

The increasing popularity of seaweed-based products, coupled with seemingly endless industrial possibilities, may lead to and in some cases has led to their exploitation, putting a strain on natural resources worldwide (Avila and Seguel, 1993, Feeney 2001, Khan and Satam, 2003). Seaweeds are multicellular, macroscopic, marine algae, and their harvesting has played a crucial role in developing coastal communities for centuries (Rebours et al. 2014), providing sources of food, fuel, feed, and fertiliser to those who harvest or gather the plants. As examples, the harvesting of the brown fucoid, *Ascophyllum nodosum*, which dominates the rocky intertidal of the North Atlantic, has taken place for hundreds of years (Hallsson 1961, Sharp 1987, Hession et al. 1998), while *Laminaria digitata*, *Chondrus crispus* and *Palmaria palmata* are species which share equally rich histories of utilisation by humans (Kain and Dawes, 1987, Vea and Ask, 2011, Mouritsen et al. 2013, Collen et al. 2014).

However, over-harvesting of natural resources to meet commercial demand has led to the deterioration of seaweed beds in some regions (Buschmann et al. 2014) and has given rise to genuine concerns regarding over-exploitation of these natural resources (Ugarte and Sharp, 2001), thereby highlighting the need for management strategies and stakeholder accountability to be adopted and monitored.

The increasing uses of seaweeds in agriculture, animal feeds, and human food are expected to maintain the long-term growth of the seaweed industry. The commercial availability of seaweeds falls into two categories: resource-based, wild-collected enterprises and, similar to commercial agricultural production activities, cultivated seaweeds (Bixler and Porse, 2011, Hafting et al. 2012). Seaweeds have experienced a renaissance in popularity, prompted in part by the media's take on their applications as 'superfood', with newspapers asking: 'Is seaweed the new kale?', or 'the next superfood?' (Goodyear 2015, Sbhimani 2016). This review explores the current human utilisation of selected examples of wild resources and different harvesting strategies adopted and will examine the sustainable management practices and initiatives driving further expansion of the wild seaweed harvest.

3.3 The commodity-based seaweed industry

Escalating global demand for seaweeds and their products fuels the expansion of industrialised processing of these resources, with 42 countries reporting commercial seaweed activity prior to 2005 (Khan and Satam, 2003). White and Wilson (2015) estimated the value of the seaweed industry to be US $10.1–16.1 billion, with some projecting that the market will reach US$17.59 billion by 2021 (www.marketsandmarkets.com, 2016). Total annual global seaweed production in 2014 was 28.5 million tonnes (FAO 2014), with cultivation accounting for 96% of this figure (1.2 million t harvested wild versus 27.3 million t from aquaculture). The increasing demand for seaweeds as food products can only be adequately met by cultivation (Freitas et al. 2015), and the high production and cultivation costs are offset by the higher market prices achieved for algal foodstuffs than for other algal products (Hafting et al. 2012, Little et al. 2016).

3.4 Wild harvest of seaweeds

The wild harvesting of seaweeds has played an important role in many coastal communities worldwide for centuries (Kraan 2020). Globally, total macroalgal production has increased by approximately 5.7% per annum (Critchley et al. 1993, FAO 2014, Rebours et al. 2014). Global harvesting production from natural beds or wild stocks remains relatively stable, fluctuating between 1–1.3 million t per year.

Table 3.1 Global seaweed production from wild stocks 1950-2014 (FAO 2014)

Total seaweed produced via capture (tonnes)	Europe	Asia	Africa	North and South America	Oceania
1950–1959	2 467 334	2 708 688	275 000	1 405 962	2500
1960–1969	3 919 564	3 419 110	434 000	2 106 645	40 500
1970–1979	4 017 962	3 232 250	518 138	2 955 364	89 067
1980–1989	4 353 710	3 429 709	265 344	2 866 262	158 372
1990–1999	3 602 827	5 045 122	227 679	3 216 902	244 238
2000–2009	2 823 367	4 321 926	313 290	4 128 532	103 145
2009–2014*	1 286 809	1 928 988	101 158	2 384 646	14 525

Table 3.2 Global red seaweed production from wild stocks 1950-2014 (FAO 2014)

Red seaweed produced via capture (tonnes)	**Europe Main genera: *Palmaria palmata*; *Gelidium*; *Pyropia* sp.; 'Red' seaweeds**	**Asia Main genera: Laver (Nori); *Gelidium*; *Gracilaria***	**Africa Main genera: *Gracilaria*; *Gelidium***	**North and South America Main genera: *Gigartina*; *Gelidium*; *Gracilaria*; *Carrageen Moss***	**Oceania Main genera: 'Red' seaweeds**
1950–1959	528 991	275 387	168 000	192 623	2500
1960–1969	882 274	371 288	258 100	628 926	4500
1970–1979	523 086	416 478	137 258	1 006 275	4108
1980–1989	418 260	785 367	97 878	1 195 122	<100
1990–1999	288 969	1350223	160 187	782 804	<600
2000–2009	79 260	286 608	158 524	1 551 301	1077
2009–2014*	10 773	105 886	40 396	657 794	1618

Table 3.3 Global green seaweed production from wild stocks 1950-2014 (FAO 2014)

Green seaweed produced via capture (tonnes)	**Europe main genera: *Dunaliella salina*: Eel grass**	**Asia Main genera: *Codium fragile*; Green laver; Lacy sea lettuce**	**Africa**	**North and South America Main genera: *spirulina* nei**	**Oceania Main genera: Sea Lettuce**
1950–1959	0	120 600	0	200	0
1960–1969	0	23 400	0	700	0
1970–1979	0	13 325	0	839	256
1980–1989	16 521	168 230	0	12 232	1744
1990–1999	21 059	551 911	0	13 802	4378
2000–2009	19 415	76 736	0	0	2704
2009–2014*	6159	4974	0	0	2334

Table 3.4 Global brown seaweed production from wild stocks 1950-2014 (FAO 2014)

Brown seaweed produced via capture (tonnes)	**Europe Main genera: North Atlantic Rockweed (*Ascophyllum nodosum*); North European Kelp**	**Asia Main genera: Japanese Kelp (Kombu); Wakame**	**Africa Main genera: 'brown' seaweeds**	**North and South America Main genera: Giant Kelps; North Atlantic Rockweed; Bull kelp**	**Oceania Main genera: *Lessonia* spp; Bull Kelp**
1950–1959	1 407 199	1 729 900	94 000	1 213 139	0
1960–1969	2 378 322	2 200 996	162 700	1 476 019	36 000
1970–1979	2 629 986	2 034 741	380 148	1 928 267	84 577
1980–1989	2 711 605	1 685 284	162 619	1 658 224	156 290
1990–1999	3 284 707	1 520 045	67 492	2 417 385	239 410
2000–2009	2 682 510	1 013 454	154 706	2 576 618	98 396
2009–2014*	1 236 976	361 623	60 762	1 726 666	10 573

since 2000 (Tables 3.1–3.4; FAO 2014). Global fisheries capture statistics for 2014 reported that there were 20 countries worldwide involved in the harvesting of brown seaweeds, totalling 624 136 t, with landings of Chilean and Norwegian kelp alone accounting for 60% of global brown seaweed harvest (FAO 2014). In the mid-1980s, Chile also annually supplied one-third to one-half of the world's demand for *Gracilaria* spp. (Santelices and Ugarte, 1987). Alginates extracted from brown algae have been used in a wide range of applications such as thickening and gelling agents in the food and feed processing industry, in the pharmaceutical industry as stabilisers of colouring agents, for waterproofing in the textile industry, paper coating and wastewater treatment (Lee and Mooney, 2012, Mesnildrey et al. 2012, Gao et al. 2017). Today, Chile supplies approximately 10% of the raw materials for alginates, primarily through the annual harvesting and collection of 314 661 dry t of kelp from natural stocks (Buschmann et al. 2014).

Comprising only a small portion of the global seaweed market today, the harvesting of seaweed from wild stocks still plays an important role in many cultures. For example, European macroalgal production accounted for 1% of the worldwide biomass supply, with 275 390 t produced in 2014 (FAO 2014). Harvesting of wild stocks supplied approximately 99% of the biomass during this period highlighting the importance of wild seaweed resources, particularly to the European seaweed industry. Meanwhile, the rest of the world heavily relies on biomass derived from aquaculture (see Buschmann et al. in press). The largest seaweed producers in Europe are France, Norway, Ireland, Iceland and the Russian Federation, accounting for 98% of total biomass supplied in 2014. Smaller-scale production occurred in Spain, Italy, Denmark, and Portugal (see www.algaplus.com). In Europe, kelps' commercial harvesting is currently carried out in Norway and France (Frangoudes and Garineaud, 2015, Steen et al. 2016), with some smaller-scale harvesting taking place on the southern coast of Ireland (1400 t in 2014). This figure will probably rise in the coming years as an experimental licence to mechanically harvest some 1800 acres (c. 730 hectares) of kelp (*Laminaria hyperborea*) from Bantry Bay, Cork has been granted to the Irish biotechnology company BioAtlantis Ltd (O'Sullivan 2017). The granting of this licence by the Marine Licence Vetting Committee was considered 'not likely to have a significant negative impact on the marine environment, would not adversely impact marine Natura 2000 sites'. However, granting a licence to harvest seaweed in Ireland mechanically has divided opinion amongst local people and environmental groups (Robinson 2017).

Norway leads the harvest and production from wild stocks in Europe with 154 230 t of brown seaweeds harvested (primarily *L. hyperborea* and *A. nodosum*), corresponding to 56% of the European macroalgal biomass production in 2014 (Stévant et al. 2017). Annual landings from almost exclusively wild-harvested stocks of North European kelps in France in 2013 and 2014 were 17 891 and 33 919 t, respectively (FAO 2014).

Red seaweeds, meanwhile, are wild harvested from 32 countries, indicating their widespread popularity, with a total of 216 456 t harvested worldwide (FAO 2014). Chile and Indonesia are the world's largest harvesters of red seaweeds, producing 76% of total global capture (i.e., >165 000 t in 2014). In Europe, the harvesting of red seaweeds from wild stocks has continued to decline since its peak of over 500 000 t harvested between 1960–1969, down to <80 000 t harvested between 2000 and 2009. Spain is now the largest producer of red seaweeds from wild stocks (i.e., 1643 t harvested annually) (FAO 2014). Globally, the wild harvest of green seaweeds was by far the lowest, with 11 countries producing 1660 t annually, the majority of which was green laver (*Ulva* spp.) harvested in Korea (FAO 2014).

'Wild' harvesting of seaweed resources generally occurs by the selective cutting from monospecific stands of seaweed (e.g., rockweeds and kelps) or, alternatively, the gathering of storm-cast fronds (which would result in multiple mixed species, along with contaminating flotsam and jetsam). Whether using nets, horses, bulldozers or tractors, the gathering of storm-cast material from beaches, although highly variable and unreliable, can constitute the use of an important, passive local commodity on shores all around the world. In Ireland, for example, 10 000 wt. (wet tonnes) of opportunistic macroalgal bloom biomass (*Ulva* spp.) is annually cleared from a single beach in west Cork and disposed of (Tabassum et al. 2017, Wan et al. 2017), while in Namibia 15 000 wt. of *Gracilaria* were regularly washed ashore at Lüderitz (Critchley et al. 1993). South Africa has built its seaweed industry on the beach collection of both *Gracilaria* and kelps (Amosu et al. 2013). Beach wash-ups of *Gracilaria* in southern Africa, as a whole, have declined considerably, and the industry was significantly reduced as of 2017 (Rothman et al. 2009; H. Rothmann, pers. comm.). Similar declines in *Gracilaria* wash-ups were also noted at traditional Argentinian collection sites, but this decline's causes remain unknown (G. Soriano, pers. comm.).

3.5 Historical utilisation of wild seaweeds

While the utilisation of seaweeds has probably been carried out by coastal dwellers since time immemorial, only a few categorical accounts exist. The gathering of seaweeds as food, for example, has occurred in Iceland for at least 1000 years, with reference made in the Icelandic sagas of the gathering of 'Sol' (*Palmaria palmata* – as *Rhodymenia palmata* in the text) for food (Hallsson 1961). Pliny meanwhile noted in AD 79 the gathering of 'Margo*'* (thought to be maërl) by 'peoples of Britain and Gaul' in order to fertilise their soils (Augris and Berthou, 1990, Grall and Hall-Spencer, 2003), while in the 600s, Scottish written records made reference to the collection of dulse (*Palmaria palmata*) by the monks of the small Hebridean island of Iona (www. ambaile.org.uk). Similarly, the Welsh delicacy laver (*bara lawr*) (*Porphyra*/*Pyropia*) has been consumed since at least 1600. In Portugal, the gathering of seaweed species washed up along the shore, collectively called '*sargago'*, has occurred since at least 1308 and was regulated under King D. Dinis (Veiga de Oliveira et al. 1975, Santos and Duarte, 1991). In Asia, the gathering and trade of seaweeds has taken place for centuries. In the 18th century, shipping documents recorded how Japanese merchants traded raw sugar in return for 'kombu' (*Saccharina japonica*) along the so-called 'kombu road' for trade with Chinese merchants (Sho 2001). In China, the use of 'Tsu-Tsai' (*Porphyra*) as a food and pharmaceutical was first recorded by Si Zuo in the book Odes of Wu Capital, written some 1700 years ago (Yang et al. 2017). Meanwhile, Dillehay et al. (2008) reported the remains of nine species of seaweed recovered from hearths in a human settlement at Monte Verde II, Chile, dated to approximately 14 000 years ago, assumed to be used for food and medicinal purposes.

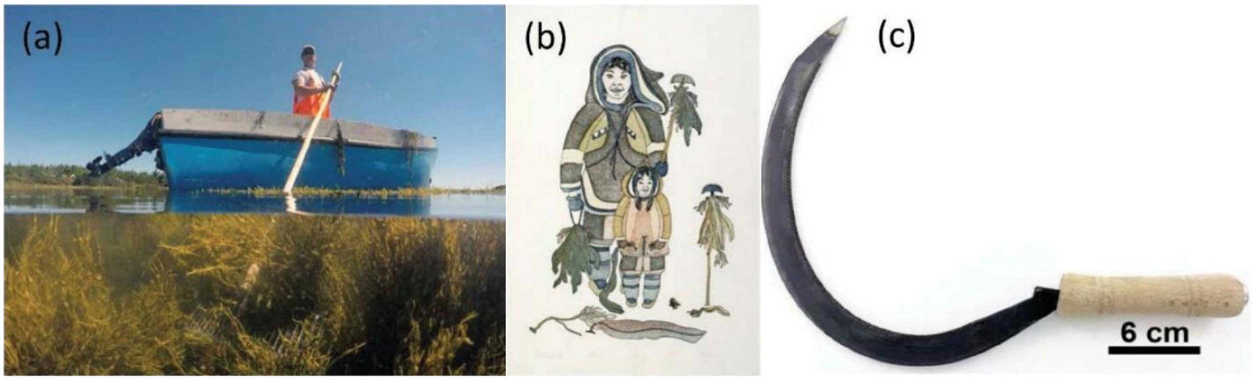

Fig. 3.1 (a) A rockweed harvester in the Canadian Maritimes; (b) Image of indigenous Canadian family gathering kelp; (c) *Corrán*; Irish rockweed cutting implement

3.6 Present-day utilisation with a focus on North Atlantic seaweeds

The utilisation of wild-harvested macroalgal biomass largely depends on the species, some being used by the food-processing industry and sold as “sea vegetables” preserved dry, fresh, frozen, canned, or salted (Mesnildrey et al. 2012, Schreiber 2014). Consumption of wild-gathered seaweeds forms part of some cultures' traditional, staple diet, particularly throughout Asia. Currently, China and the Republic of Korea are the largest consumers of edible seaweeds. Although more than 10 000 species of macroalgae are reported to exist (Guiry and Morrison, 2013, Guiry et al. 2014), as few as 200 species are consumed worldwide, mainly as sea vegetables (Pereira and Neto, 2015). Currently, following the introduction of regulation EC 258/97, 21 macroalgal species are considered edible in Europe (Mesnildrey et al. 2012, CEVA 2014).

Seaweed extracts and powders made from these natural resources are used widely in organic farming as feed supplements, biofertilisers and biostimulants for soils in agriculture and horticulture (Wang et al. 2016). The main algal species used in Europe as fertiliser are the brown seaweeds *A. nodosum*, *Fucus* spp., *Laminaria* spp. (including *Saccharina*) and maërl (free-living calcareous red algae) (Mesnildrey et al. 2012). Products derived from these seaweeds are considered to promote improved seedling success rates, increased crop yields and resistance towards diseases and insect pests (Raghavendra et al. 2007, Sathya et al. 2010, Vijayanand et al. 2014).

Wild harvested seaweed species are also popularly used in biostimulant formulations (Khan et al. 2009), feed formulations (Evans and Critchley, 2014, Makkar et al. 2015), for hydrocolloid production (Porse and Rudolph, 2017), or food supplements (Forster and Radulovich, 2015), cosmetics (Balboa et al. 2015, Sarkar et al. 2016), bioremediation (Volesky 2001) and as a potential biofuel source (Smith and Ross, 2016, Tabassum et al. 2017).

3.7 The harvesting of the wild seaweed resource: wild-harvesting techniques

Judged on their catch per unit effort and chosen as a consequence of the target seaweed species, a range of techniques and cutting implements are at the disposal of commercial harvesters. A greater income can be made by harvesting the seaweed using boats, rakes or by diving than by hand-harvesting from the shore at low tide (Fig 3.1a-3.1b) (Rebours et al. 2014). The techniques, intensity of exploitation and homogeneity of the harvest all influence the regenerative and recovery capacity of the cut seaweed beds and their associated communities (Kelly et al. 2001). While the first commercial harvesting of seaweeds in the USA appears to have been initiated by the Irish fishers, Daniel Ward and Miles O'Brien of Scituate, Massachusetts, between 1848 and 1850, this was short-lived (see www.stmar yscituate.org/aboutus_history.html). Coinciding with the increased demand for seaweed biomass in the middle of the 20th century came the evolution of harvesting methods and tools. The next wave of commercial harvesting of wild seaweeds in the Western world began in the early 1940s on the shores of the North Atlantic, particularly along Nova Scotian and Irish coasts, and the first traincar load of *Chondrus crispus* from Canada to the USA came out of Nova Scotia (10 000 lb = 4500 kg) in 1940 (Humm 1951). A drag-rake was the preferred harvesting tool of the day for the delicate carrageen moss (*C. crispus*), but ultimately its use caused immense damage to the standing crop. The use of appropriate and well-maintained tools markedly influences the health and sustainability of a resource. A hand-held seaweed cutting implement is generally small and lightweight, such as the sickle used to cut *Palmaria palmata* (*dileasc*) in Scotland, the small kombu cutting Nejiri tool (Japan), or the *Corrán* (Irish hook) used to cut *an Feamainn bhuí* (*A. nodosum*) in Ireland (Fig. 3.1c).

Prior to harvesting natural seaweed beds or purchasing the rights to harvest seaweed beds from landowners, harvesters are required to estimate the amount of time and materials necessary to extract the resources (Salo et al. 2014) successfully. There are certain additional costs, such as transportation and extra labour, which must also be considered. Several factors can influence productivity on any given day. When gathering on foot, access is important. In contrast, when harvesting by boat, productivity may be affected by tide times, wave height and current, weather, access to wharves, transportation to processing, even the sharpness of the cutter blade and bottom conditions, including substratum and shore geomorphology.

For decades, mechanical harvesting of seaweed beds has been successfully carried out in several northern Atlantic countries. Using a range of custom-built devices and boats, mechanical harvesting has been the method of choice in Iceland, Norway, Brittany and Maine, USA (Hallsson 1992, Ugarte and Sharp, 2001, Vea and Ask, 2011, Mesnildrey et al. 2012). Recent collapses of some important fisheries in Atlantic Canada have created strong public concern regarding management policies for marine resources in general. Accordingly, a precautionary approach has been urged for these resources, and as a consequence of its important role as habitat for invertebrates and vertebrates, a new approach to the management of rockweed was applied (Ugarte and Sharp, 2001). In 1995, under a four-year pilot plan, the *A. nodosum* harvest expanded from Nova Scotia to the previously unexploited areas of southern New Brunswick. A new joint federal/provincial management strategy for rockweed was implemented after reviewing existing biological information covering 30 years of harvesting history and experience in Nova Scotia. The maximum exploitation rate, cutting height, gear restrictions, and protected areas were management measures employed within a precautionary pilot-harvest plan. A research and monitoring programme involving the industry, universities, and the provincial and federal governments was simultaneously initiated to evaluate the effect of the harvest on the resource and associated species and provide information on improving the management of rockweed. A scientific peer committee reviewed this information in April 1998 and 1999. The consensus was that the impact of harvest on the habitat architecture was minimal and of short duration, and therefore it was advised that the harvest could continue, but to clearly maintain the precautionary approach to management. The overall objective of efficient mechanical harvesting is to improve the catch per unit effort over hand-harvesting methods. The ‘seaweed trawler’, the first purpose-built boat for seaweed harvesting, was launched in Norway in 1969. Today, 11 seaweed trawlers annually harvest 130 000–180 000 t of brown seaweed every year on Norway’s south-western shore, with a peak harvest of 192 426 t in 2000 (FAO 2014). This high exploitation rate was made possible by the use of trawlers capable of operating in shallow water (>2 m) and with an increased hull capacity, allowing for harvests of 50–150 t per day (Vea and Ask, 2011). Based on studies by Per Svendsen of the Biological Station at the University of Bergen, Norway, in 1972, an initial 4-year harvest rotation was implemented. Following further investigations, this period was increased to a 5-year rotation in 1992. The Continental Shelf Act (1994) ensured the Norwegian resource's sustainability and an appointed management committee comprised of seaweed industry representatives, harvesters, fishermen’s associations, and marine research institutes. This Committee previously concluded that: ‘so far, it is not shown that seaweed harvesting represents unacceptable or irreversible injury on other organisms or ecosystems’ (Vea and Ask, 2011).

Mechanical harvesting of wild seaweeds seems to have reached its peak during the 1980s and 1990s worldwide. Again, using Nova Scotia as an example, since it is well documented, mechanical harvesting of rockweed peaked between 1986 and 1992. During this time, the use of highly efficient Norwegian suction harvesters was in place, capable of exploitation rates of 40–60% (Sharp et al. 2006, Vea and Ask, 2011). These suction harvesters increased the catch per unit effort, and rockweed landings rose from 9448 t in 1985 to a peak of 30 000 t in 1989 (Sharp et al. 2006). In France, the scoubidou trawl has been used since 1974 (Mesnildrey et al. 2012); this method of harvesting kelp species, including *S. latissima* and *L. digitata,* uses a crochet-hook-like implement, which rotates around the fronds and uproots them to be pulled on board (Perez 1973). The scoubidou has played a key role in the fresh seaweed industry, annually harvesting 60 000–80 000 t (FAO 2014). The use of suction-based mechanical harvesters in the Canadian Maritimes ceased in 1994 due to uncontrolled over-harvesting (Sharp et al. 2006).

Conversely, the introduction of mechanical harvesters in Norway resulted in the decline of rake harvesting of *Laminaria hyperborea and L. digitata* (Vea and Ask, 2011). Kelly et al. (2001) reported that mechanical harvesters were unsuitable for operation in all areas. As an alternative, boat and rake harvesting was implemented in the early 1970s in the Canadian Maritimes and now accounts for 100% of seaweed landed in Eastern Canada (Ugarte and Sharp, 2011, 2012). With its long handle and specially designed serrated cutting head with steel guards, the rake is deployed by the harvester from the side of a suitable boat and slowly drawn through, thereby cutting the floating seaweed canopy, which is then landed (an example is shown in Fig. 3.1a). This harvesting method removes large clumps at the upper, distal end of the canopy where the majority of the biomass is to be found, whilst leaving behind some meristematic tissue to allow for regrowth of the canopy, which generally happens within a year or two (Sharp et al. 2006). It has a similar effect to the pruning of terrestrial crops by encouraging fuller, more robust regrowth. Rockweed rake harvesters can harvest 3–5 t of rockweed per tide (rockweed harvester, personal communication), with some harvesters cutting on ‘two-tides’ when daylength permits in summer.

3.8 Over-exploitation – including criticisms of mechanical harvesting

Over-exploitation, i.e., removing seaweed biomass beyond its annual or seasonal rate of renewal, of wild seaweed beds could lead to potentially significant, negative ecological responses (Rebours et al. 2014). Lessons must be learned from past mistakes. Maërl (mostly composed of *Lithothamnion corallioides* and *Phymatolithon calcareum*) has a long history of harvest along France's Atlantic coast. Historically, this assemblage of coralline algae was used as a soil conditioner and replacement for lime in agriculture. However, maërl beds are also valuable, biodiverse marine habitats. These calcareous seaweeds are effectively present as large subtidal beds which can be mined mechanically via a sablier, which dredges the seafloor. Unfortunately, this method of harvesting has negatively affected maërl beds to such an extent that the assemblage of calcareous algae are now a Convention for the Protection of the Marine Environment of the North-East Atlantic (OSPAR) listed ‘seaweed’ as a result of declining natural status and abundance (Barbera et al. 2003).

It is well known that over-exploitation can result in significant reductions in marine biota biomass (Buschmann et al. 2001). Over-harvesting can lead to a reduced seaweed thalli density, skewing the population mix and increasing impurities (i.e., other, unwanted seaweed species) in the harvested seaweed loads. If the biomass continues to be used ‘as is’, reduced purity of the harvest thereby leads to impaired quality of the finished product (Kelly et al. 2001, Werner and Kraan, 2004).

In the Canadian Maritimes, the Norwegian suction harvester was discontinued in 1994 following widespread over-exploitation in the early 1990s (Ugarte and Sharp, 2012), only eight years after its introduction. In the USA and Canada, harvesters reverted to manual rake harvesting (from boats) for three of the most economically important seaweeds, e.g., Irish moss, rockweed, and kelps, in a bid to restore resource balance.

Registration of Natura 2000 sites in Europe (Fock 2011) resulted in the restriction of mechanical harvesting practices in the Basque Country, while in Ireland, local NGOs opposed the introduction of mechanical harvesting techniques due to their being considered ‘not compatible with the conservation objectives of Natura 2000 sites’ (Netalgae 2012, Baweja et al. 2016), although as stated above, some concessions have been made. Northern Ireland took a similar stance, with the Environment and Heritage Service (EHS) declaring its requirement for long-term studies to ‘demonstrate[d] that it (mechanical harvesting) will not have an adverse impact on the environment’ (EHS 2007).

3.9 Impacts of over-harvesting on resources

As is the case with the use of all-natural resources, the wild harvest of seaweeds inevitably has ecological implications for the species targeted and the associated community of flora and fauna, leading to varying degrees of change (Lorentsen et al. 2010, Phillippi et al. 2014, Salo et al. 2014). As foundational species and important contributors to primary production, the large canopy-forming fucoids and laminarians provide food, habitat, nursery refugia and shelter to a wide range of intertidal species, thereby supporting complex food webs in coastal habitats (Sharp et al. 2006). The large structural seaweeds offer protection from predation to some species while allowing refuge from desiccation at low tide, and they can also be involved in reducing tidal surge and waves affecting coastline erosion and sedimentation rates by dampening the incoming energy (Mendez and Losada, 2004, Phillippi et al. 2014).

Seaweeds exert a strong influence on intertidal and subtidal community structures (Thompson et al. 2010). Large-scale canopy removal of marine macroalgae directly influences marine biodiversity, particularly the abundance and biomass of associated organisms from other trophic levels such as mobile megafaunal invertebrates, fish, and apex predators (Kelly et al. 2001, Migné et al. 2014, Phillippi et al. 2014). This can negatively affect recruitment (Levitt et al. 2002) and reduce contributions to the marine carbon cycle (Thiel et al. 2007). These habitats also provide several other important ecological services to coastal areas, such as the transfer of organic materials between ecosystems (Krumhansl and Scheibling, 2012), natural, temporary carbon sequestration (Thiel et al. 2007, Hill et al. 2015, Raven 2017), removal of dissolved nutrients, thereby decreasing eutrophication of coastal waters, and coastal protection from erosion and hazardous waves (Arkema et al. 2013).

Data analysis for a single year from 10 sites around Nova Scotia suggested that removing biomass of *Ascophyllum nodosum* from coastal environments by harvesting was associated with a reduction in the amount of detrital material entering the food web (Halat et al. 2015). This detritus is typically released through epidermal shedding, and if not consumed by herbivores or microbes before reaching the upper intertidal zone, it contributes to coastal, terrestrial fertility. However, the actual amount and impact has been debated (Garbary et al. 2017, Ugarte et al. 2017). Repeated intensive removal of the seaweed canopy can also have a gradual negative effect on population dynamics, altering the availability of resources such as light and space (Vásquez 1995) and potentially changing the overall structure/architecture of the beds (Kelly et al. 2001, Thompson et al. 2010).

Following long-term, extensive rake harvesting of Irish moss on Prince Edward Island and Nova Scotia, once-extensive *Chondrus crispus* beds have gradually transformed from domination by *Chondrus* to *Furcellaria lumbricalis* (Hudson) J.V.Lamouroux (Sharp et al. 2006). Using ecological models, Rinde et al. (2006) calculated that trawling in Norwegian kelp forests substantially affected primary and secondary production, calculating that primary production could be reduced by 45% and secondary production by 70–98% within trawled areas (recovery rates unknown).

Himanthalia elongata has been harvested in Europe for centuries for fertiliser, food, and hydrocolloid extraction. It is currently harvested in France, Ireland, and Spain, mainly for human consumption (Stagnol et al. 2016). In Brittany, between 2009 and 2013, the annual harvesting of *H. elongata* increased by 35% (Stagnol et al. 2016). In France, the collection of seaweeds for personal consumption is not regulated nor managed. The situation is similar in Portugal, where *H. elongata* populations suffer from reduced local abundance and even some local extinctions (Lima et al. 2007, Araujo, personal observations).

Some natural biotic influences, such as ice scouring and grazing pressure by sea urchins (Echinoidea) or top shells (Trochidae), have been reported to exert severe strains on certain seaweed resources. The largescale removal of predators for export markets increased sea urchin abundances and promoted the decline of kelp forests over vast areas (Steneck et al. 2002). Extensive grazing of kelp beds by sea urchins created the phenomenon of ‘sea urchin barrens’; stretches carved through kelp forests characterised by low primary productivity areas, which may extend for thousands of kilometres within a given kelp bed (Filbee-Dexter and Scheibling, 2014). For example, Nova Scotian and Norwegian kelp beds have undergone several cycles of over-grazing by sea urchins creating barren grounds that may take decades to recover (Sharp et al. 2006, Norderhaug and Christie, 2009, Rinde et al. 2014).

3.10 Constraints to the wild harvesting industry

Unlike the customary cultivation of high-value seaweeds in Asia for use in food, medicine, and as raw materials for the pharmaceutical industry (Hurtado et al. 2014, Chellaram et al. 2015, Liu et al. 2016), harvesting of seaweeds in western countries is typically rooted in providing biomass for industrial processes, primarily as animal feed, fertilisers and thickening agents (Kılınç et al. 2013). The harvesting of wild seaweed resources, particularly the larger fucoids and laminarians has, to date, been used to supply animal food supplements, soil conditioners and biostimulant formulations (e.g., Hebridean Seaweeds Ltd, Stornoway, Isle of Lewis, The Outer Hebrides, Scotland; see www.hebrideanseaweed.co.uk). Numerous smaller cottage industries based upon wild-collected seaweeds are also appearing in the entrepreneurial landscape, and these will play important educational/accessibility roles at local levels, although care must be taken not to overexploit here as well.

A lack of adequate resource supply could result in a country not reaching its capacity for seaweed production and associated processing and would likely be a serious hindrance to the further development and investment required for a sophisticated, sustainable seaweed industry (Kelly et al. 2001, Hafting et al. 2012). As a consequence of the requirements for industrial amounts of raw material, demand in many regions has far outstripped the capacity that traditional harvesting of wild stocks can supply. Indeed, there is already industrial and commercial concern regarding the inability of traditional harvesting methods to adequately meet current, and especially future, global demand for seaweed products. The demand is expected to grow as the broad range of benefits derived from seaweeds become more universally appreciated, and their human health benefits are more widely known and exploited. Grounds for these concerns relate primarily to the efficiency of traditional harvesting methods, and secondarily to an increasing harvester age profile, lack of recruitment of young harvesters and the corresponding reduction in the number of seaweed harvesters (i.e., manual labourer) workforce (Kelly et al. 2001).

To exploit seaweed species commercially, it is necessary to have suitable labour and harvesting technologies (Hafting et al. 2012). There are three main constraints to the development of commercial wild harvesting operations. Firstly, the presence of an accurately quantified seaweed resource (standing crop) is essential. A major hindrance to the large-scale economic exploitation of seaweeds results from knowledge gaps relating to a lack of basic data on standing crops. Knowledge gaps exist from the ground up, with a chronic lack of long-term biomass data in most countries for even the most popular seaweed species already exploited. Estimating seaweed standing crops is difficult, and there is often a large margin of error in estimates, in some cases of ±40%. However, acquiring accurate data on standing crops is an essential foundation for building robust harvest management plans (Bruton et al. 2009). Secondly, reliable access to the resource is of great importance, and there may be confusion regarding seaweed exploitation and ownership, often exacerbated by ambiguous laws. Thirdly, the not insignificant costs associated with the seaweed biomass, including drying and transportation to the point of processing, need to be accurately assessed as they can be a hurdle to developing an economically viable industry (Tabassum et al. 2017). Significant costs such as drying and transportation can be mitigated by a warm climate and good location of the processing factories (i.e., near the resource; Buschmann et al. 2014).

Fig. 3.2 (a) Loading trailers on the shore, Connemara, Ireland; (b) Beach collection of *Gracilaria* after wash up, Bahia Bustamante, Argentina, (1960); (c) women of Praia collecting seaweed, Portugal

3.11 The role of seaweed gathering and community

Considering the importance of seaweed gathering and harvesting solely in monetary terms does not adequately express the harvest's importance. Harvesting from wild seaweed beds is a key component of many countries' culture and tradition, playing an important role in the identity of its harvesters and rural coastal communities. The gathering of seaweeds has traditionally been a domestic task carried out by multiple family members, with basic processing occurring near or within the home. Both men and women may carry out harvesting (Fig. 3.2a - 3.2b). Women's role is central to many harvesting societies (Marinho-Soriano, 2016, Msuya and Hurtado, in press).

In Brazil, women comprise a significant portion of the harvester workforce (estimated at 80%), and in Japan, the picking of nori (*Pyropia* spp.) is customarily carried out by women. At the same time, the famous Ama ladies have a long history of freediving for fish, pearl oysters and seaweed (Nakuda 1965). In Malaysia, women dominate the seaweed industry even though the majority of the workforce are men, and they play an important role in enhancing seaweed production and generating revenues (Kunjuraman et al. 2019). In Hawai'i, wild seaweed gathering is traditionally considered to be the role of women and children (Hart et al. 2014), and in coastal communities around Portugal, women typically controlled seasonal seaweed harvests (Cole 1991) (Fig. 3.2c). Similarly, in South Africa, the majority of seaweed harvesters are women (Amosu et al. 2013), whose average annual income was cited as US $5000. Women of the British Columbian (Canada) and Alaskan First Peoples often travelled together in their hand-crafted canoes to the seaweed beds, both for companionship and safety (Turner 2003). The 19th-century historian Robin Flower recounted how Irish women kept a supply of *dileasc* in their pockets and a Dr Browne, visiting Co. Mayo (Ireland), in the 1880s, described how women 'attended to all of the housework and the needs of their children, helped in the fields and on the bog and gathered and dried *carraigin* and *dileasc'*. This was sold in the neighbouring towns – to which the women walked barefoot, as they were expected to save their boots for market days and holidays – for two shillings a stone. The men, on the other hand, suffered no such hardship (Rhatigan 2009). Fundamentally, the long-term, sustainable harvesting of wild seaweeds is a societal issue. As such, sustainable management plans can result from self-imposed harvesting restrictions brought down from the community level, e.g., in the kombu harvesting villages of the Hidaka District, Japan, harvesters followed the instructions of the hatamochi, i.e., the person authorised to define harvesting times and periods (Lida 1998). In Ireland, harvesting practices for *A. nodosum* have remained relatively unchanged for centuries. Harvesting of familial patches of the foreshore or 'stripes' has been practised since the 19th century, with strategically placed rocks, 'mearing stones' marking individual stripes' margins helping regulate rotational cutting (McErlean 2007, Skeffington et al. 2013). In fact, it was the common practice of many historic estates to give shore rights to those tenants holding land on the adjoining shore, and thus mearing stones were placed on the foreshore, as there was a requirement to provide an unambiguous demarcation (McErlean 2007). Harvesting of the stripes may have occurred within some families for multiple generations. In Ireland, as in Japan, the principle of equality and reciprocity (Lida 1998) is evident amongst harvesters in the face of a lack of regulation.

The self-imposition of sustainable harvesting practices by local harvester communities is commendable and has played an important role in maintaining continuous, sustainable harvesting of natural seaweed beds worldwide. It is vitally important that coastal communities effectively manage those natural resources (Kraan 2020).

3.12 Employment

The seaweed industry provides significant income and support to coastal and remote rural communities worldwide (Guiry and Morrison, 2013, Hart et al. 2014), particularly those classified as historically populated by disadvantaged persons, such as in southern Africa (Amosu et al. 2013). Employment figures for those in the wild harvest seaweed industry are notoriously difficult to decipher, with only a small fraction of those who work gathering seaweeds employed in a full-time role. The first and most direct economic benefit of gathering wild species is connected to subsistence (Salo et al. 2014). Harvesting seaweed rarely accounts for the main income of the household. Rather it is an additional income for members of coastal communities, and seaweed collection can be a good alternative to fishing in over-exploited fisheries or where terrestrial resources are limited (Rebours et al. 2014). The selling of locally derived products helps rural communities earn supplementary income where limited revenue sources may be available (Salo et al. 2014). A study of kelp harvests at two experimental sites in British Columbia indicated that the small-scale harvest of *Macrocystis pyrifera* (Linnaeus) C.Agardh had minimal impact on the seaweed and the local fish populations (Krumhansl et al. 2016). These results suggest that these benign activities could support economic growth and local livelihoods without having a negative impact on biodiversity of the associated ecosystem benefits (services) (Krumhansl et al. 2016). Seasonal and part-time employment is common for those working in the seaweed collecting industry. For example, in Brittany (France), half of the harvesting fleet then turns their attention to alternative fishing activities once the seaweed harvesting season ends (Alban and Boncoeur, 2004). The onset of winter prevents any commercial seaweed harvesting in Norway, and it forces reduced efforts in Canada, resulting in a shorter harvesting season (generally May–October), after which harvesters return to lobster fishing and processing (Sharp 1987, Rebours et al. 2014). However, in France and Spain, seaweed harvesting is an occupation that can be practised year-round, and harvesters supplement their income from fishing or farming with small-scale harvesting and, as such, is compatible with the subsistence of many coastal areas' communities (Alban and Boncoeur, 2004). In Portugal, for example, six different harvesting areas were defined, and annual licenses issued to enable harvesting for commercial purposes (Santos and Duarte, 1991). The maximum number of boats and divers per boat was fixed per harvesting area. The harvesting period was also restricted to a defined period each year. However, the harvesting of seaweeds for non-commercial purposes is not subject to Portuguese government regulations, but the collection of macroalgal biomass from beach-cast using tractors is subject to authorisation from local authorities.

In Ireland, seaweed harvesters, *buainteoir feamainne*, cut *A. nodosum* (rockweed) in an ad hoc fashion throughout the year, particularly when duties relating to their main source of income (e.g., fishing, farming, and building construction) slow down (Irish rockweed harvester, personal communication). Therefore, seaweed harvesters are informally regarded as sole traders, harvesting as they choose and independently selling the fruits of their labour. The annual Irish landings of rockweed were reported as 28 000 t (FAO 2014), although landings are said to have peaked during the mid-2000s, coinciding with the worldwide economic recession (Guiry and Morrison, 2013). In some locations, a history of hardship and a lack of available work options inevitably leads to coastal dwellers counting on the security of the resource that has served their communities for centuries, especially in times of economic distress. This is clearly expressed by a quote from Donal Hickey, then director of a seaweed factory in Connemara, Ireland, in Mouritsen's (2013) informative book on seaweeds. Hickey's words, as he described the relationship the local harvesters have with the seaweed, resonate with a deeply rooted attachment to the one thing that could be relied upon historically for survival when all else failed: 'The seaweeds have to be there if the children return home'.

3.13 The occupation of seaweed harvesting

Due to space and resource limitations, competition between harvesters (and sometimes within families) can be fierce: 'The harvest is like a war' (Lida 1998). Harvester communities have collective and often unwritten rules and customs (Becker 2001). The legal status of seaweed harvesters or *crofters* (Scottish term) differs around the world. In France, those who harvest from boats are considered fishers, and as such, receive health insurance and access to social security funds. Harvesters in Norway and Spain are given a similar status. Many countries, including Ireland, do not recognise harvesters in this way. Generally, those who harvest by hand, on foot, are not granted the same rights as those on-board vessels. Hand harvesting of seaweeds is far less controlled by authorities and is often unregulated (Baweja et al. 2016).

Seaweed harvesting is physically demanding, repetitive, seasonal, and weather-dependent, and recruitment to the sector is very low. Studies showed that one of the main concerns for the vitality of the wild seaweed harvesting industry was related to the age of its current workforce, e.g., in Brittany, one study found that the average age of fishers was 43, with 25% of the total over 50 and only 8% under 30 (Alban et al. 2004). Similarly, in Ireland, a study on the age profile of harvesters in the Connemara region found that only 3% of harvesters were under 30, and 31% were 51–60 years of age (Kelly et al. 2001). The movement of young people from rural, coastal areas into the urban centres and the difficulty in attracting young harvesters highlights a potential issue that confronts the seaweed industry worldwide (Alban et al. 2004).

Innovations in technology (resulting in increased income per unit effort) may hold the key to recruiting younger harvesters, and it would seem that mechanisation may be an inevitable consequence of an inability to attract this demographic into the industry. Shortages of supply of resources are often met through mechanisation. Where hand-harvesting practices have historically been in place, however, there may be a reluctance to introduce mechanisation, born of a sense of historical ownership and fear of a loss of traditional customs and income.

3.14 Poor harvesting practices and the importance of sustainable techniques

For a viable industry to exist, sustainable and ethical harvesting activities must be carried out to avoid undue stress placed on the resource (Hafting et al. 2012). Some factors have directly influenced the ecological impacts of seaweed harvesting operations (Vasquez 1995). Harvest impact is not only directly related to the magnitude and the frequency of the harvests, but also timing (seasonality), species identity and obviously, the local climatic conditions.

Natural seaweed resources are vulnerable to poor harvesting practices, which predatory or inexperienced harvesters sometimes carry out. Overharvesting of *Gracilaria* from wild seaweed beds occurred in central Chile in the 1970s as a consequence of a high market price for the agarophyte and a poor economic situation in the country at that time (Lindstrom and Chapman, 1996). Poorly managing resources, such as opportunistic harvesting, excessive removal of holdfast material (reducing regeneration), trampling and enhanced grazing by herbivores all place additional stresses on the resource, while near denudation of a seaweed bed is perhaps the most extreme case of a direct impact on the community (Sharp et al. 2006, Thompson et al. 2010, Araújo et al. 2012, Phillippi et al. 2014). Unregulated predatory harvesting resulted in over-exploitation of Brazilian agarophytes in the 2000s, which led to a declining population and a significant and prolonged decrease in productivity (Marinho-Soriano et al. 2006, FAO 2014). Ultimately this was then associated with a decrease in the quality of the raw material. Today, the type of *Gracilaria* that predominates in that region is popularly known as '*cisco'* (trash), considered commercially worthless when it washes up on shore (Marinho-Soriano, 2016).

Incorporation of comprehensive, sustainable harvesting techniques such as those laid out in Ugarte and Sharp (2001) and Nelson and Conroy (1989) for the harvesting of *A. nodosum* and *Porphyra*, respectively, are required. Successful collaborations between the scientific and harvester communities are important to help mitigate the impact of intensive harvesting and ensure sustainability.

In implementing best-practice harvesting guidelines, limitations of the exploitation rates of the two most economically important brown seaweeds in Chile, i.e., *Macrocystis* sp. and *Lessonia* sp., were applied only after an agreed consensus was reached between fishermen, industry, government, and scientists (Buschmann et al. 2014). The guidelines focused on the selective harvesting of sporophytes in order to allow maintenance of the reproductive stock. This important collaborative effort helped to protect and sustain Chile's northern kelp beds, estimated to be worth US$540 million (Vásquez et al. 2013).

The effective, sustainable harvesting of wild stocks is important as it relates to the ability of harvested beds and their associated ecologies to persist over time. There is a need to consider both the recovery of the harvested resource and acknowledge the potential ‘knock-on’ effects of harvesting from monospecific seaweed beds. It is necessary to consider the biodiversity principle of ‘ensure (ing) that the activity does not cause an unacceptable reduction in biodiversity’ while echoing the 1987 World Commission on Environment and Development (WCED) declaration on sustainable development. This definition, formalised in the report ‘Our Common Future’, identified sustainable development as ‘development that meets the needs of the present without compromising the ability of future generations to meet their own needs’ (Brundtland 1987, Jacquin et al. 2014).

Historically, the importance of seaweeds for sustenance has driven local-level sustainable harvesting practices. Today, there is an industry-led approach to the sustainable, self-imposed management of wild resources due to seaweeds' high commercial value. There are numerous examples of harvesting restrictions imposed by governments working jointly with industry. In the Canadian Maritimes, New Brunswick operated a 17% exploitation rate for the harvesting of wild *A. nodosum* beds, while in Nova Scotia, a strict 25% exploitation rate has been in place since 1999 (Ugarte and Sharp, 2012). A 5-year (in some cases 4) rotational management plan for *Laminaria* spp. was implemented in Norway in 1992, with the Ministry of Fisheries and Coastal Affairs – the FKD, regulating the harvest of *L. hyperborea* with local county authorities responsible for regional management of kelp resources (Meland and Rebours, 2011, Vea and Ask, 2011).

Although successfully implemented in several countries, precautionary objections have been raised regarding the sustainability of harvesting wild beds. Some critics of the harvest may feel management plans do not address the wider ecological impact associated with harvesting (Halat et al. 2015). This supposition, however, does not address the broader definition of sustainability as outlined in the Brundtland Report (1987) for the WCED, which affirmed the necessity for the inter-dependence of economic spheres with the social and environmental facets of our common global future (Jacquin et al. 2014).

Cremades Ugarte et al. (2016) developed a series of sustainability indicators, including environmental, socio-territorial, and economic, to exploit seaweeds, some of the most relevant are briefly outlined; i) the importance of acquiring a comprehensive level of biological knowledge about the resource, including the biology and ecology of the specie to be exploited, ii) to identify the suitability of resource exploitation to the characteristics of the ecosystem to protect the environment as a whole, iii) to protect seaweed resources by evaluating the effects of exploitation on the resource, iv) understand the ecological footprint derived from the exploitation of seaweed, v) the development of mandatory laws and regulation to ensure the sustainability of seaweed resources and ensure compliance to specific regulation, vi) to promote training to all actors at all levels of seaweed exploitation while guaranteeing adequate working conditions in the sector vii) the recoding of accurate statistical data relating to resource exploitation and finally viii) to promote the productive development of the sector by assessing the annual growth rate in %.

3.15 Management plans

Although seaweeds have been harvested since ancient times, in the face of growing commercial interests and pressures, specific management tools must be developed and implemented to help maintain the health and integrity of not only seaweeds but of all resources. The current increasing demand for seaweed biomass must be compatible with sustainable management practices of these resources (Borges et al. 2020). There should be a concomitant vigilance with respect to global resource science, management, and accountability. There is definite potential for mismanagement of these important resources. A clear distinction must be made between harvesting wild stocks for personal and artisanal use and the exploitation of seaweed biomass on an industrial, commercial scale.

Robust, scientific monitoring of harvesting activities is essential to assure a commensal relationship between the spheres of human economic and social needs and the seaweed resource sphere. A rigorous management system and accountability will lead to the long-term and continued conservation of a persistent and valuable natural resource. Ethical and sustainable harvesting practices are imperative, and they need careful consideration alongside economic evaluations when resource exploitation is considered. It is important also to consider the various seaweed species case by case and which harvesting technique is best employed for the crop and the location. Fortunately, some tools help regulate the harvest, including licences, quotas, and rotation systems (Baweja et al. 2016), which may need periodic enforcement.

It is imperative to develop and implement ecosystem-based management models while ensuring that long-term management studies are put into place. Potential ecosystem-based management approaches may include (but are not limited to) maintaining high canopy biomass, recovery potential, habitat structure and connectivity, limiting bycatch and discards while incorporating seasonal closures and harvest-exclusion zones into spatial management plans (Lotze et al. 2019). It is also essential that regulators are proactive and vigilant in the stewardship of seaweed resources. It is crucial also that cooperation between the relevant stakeholders in developing new sustainability initiatives is ensured (Potting et al. 2021).

Non-traditional seaweeds (those not commonly used to date) may soon enjoy a boom in popularity as the next ‘superfood’, as seedstock for cultivation or even as an eco-friendly insecticide (Tay et al. 2017). However, as research and markets highlight their economic value, availability and accessibility, vulnerable seaweed resources may be subjected to increased harvesting pressures. To exploit resources fully and mitigate against a shrinking and ageing workforce, active consideration of mechanisation may also need to be carefully examined.

Important management strategies are being implemented in many countries as the significance of caring for and sharing our coastal resources' various components becomes increasingly evident. When an appropriate harvesting plan was in place for (rockweed) harvesting, studies showed no evidence of negative impacts on invertebrate populations (Phillippi et al. 2014). The sustainable harvesting of natural *Sargassum* beds in the Philippines has been achieved by incorporating practical management practices (Marquez et al. 2014). Beds of *Sargassum* are harvested before most plants become fertile (<50% of the population), allowing the species to regenerate and proceed to the reproductive and recruitment phases. A gradual move away from unregulated, opportunistic harvesting is becoming more widespread; in 2014, the Department of Agriculture in the Philippines imposed a ban on the harvesting and gathering of all brown seaweeds in response to blatant over-exploitation of wild stocks as a consequence of high demands for ‘sea vegetables’. A breach of the ban was reported to be punishable by a 2–10-year prison sentence (Valencia 2014). In Vietnam, the high price of free-floating *Sargassum* spp. has driven non-selective, opportunistic harvesting of the seaweeds in Ninh Van and Ninh Phuoc, resulting in a sharp decline of overall Sargassum biomass in that region (Khanh Hoa News, 2012).

There is an obvious requirement for regulators to be proactive and close collaborations within a strict code of ethical conduct between local indigenous communities, fisheries, industry, and government. Increasing stakeholder interests and demands may result in unforeseen harvesting stresses placed on the wild resources of any new species entering the market. Science must first identify an appropriate and sustainable method compatible with biomass regrowth, productivity, and environmental responsibilities; in some cases, species should only be cultivated from seed stock carefully selected from wild populations. Without adequate regulation and rules provisioning for the ethical and sustainable use of wild resources, they are at risk.

3.16 Ownership of the resource

Possibly the most contentious issue surrounding the expansion of wild harvesting operations in some regions is the issue of access and ownership of the actual resource. Ambiguity surrounds the question of ownership, and different rules apply in different countries (Higgins 2017). In the majority of Atlantic European countries (i.e., Ireland, France, Spain, Portugal), ownership of seaweed resources belongs mostly to the State and the foreshore, generally from high to low water mark, and in some cases, the seabed out to 8–12 nautical miles, is under the jurisdiction of the State. As is the case in large swathes of Norway and Scotland, private ownership of the foreshore results in the need to acquire permissions from coastal communities and pay a fee to local landowners prior to any commercial commencement of harvesting operations. In Galicia, harvesters may exploit the natural resource within an allocated territory if justified requests are presented to the regional authorities and approved (Baweja et al. 2016). In some countries, seaweed rights, or ‘wrack rights’, are granted to those who have historically gathered seaweed in the region (EHS 2007). These are informal rights recognised legally and based on historical precedence relating to harvesting activities which allowed for removing small quantities of seaweed from the shore for personal use.

In many areas, people also harvested for commercial use. As an example, kelps were harvested and burned in the northwest of Ireland, broken up into manageable sizes and exported out of Mullaghmore Harbour to Scotland. It was a valued income for coastal families who had rights to the shore. In Northern Ireland, informal wrack rights were recognized if an individual had been harvesting seaweed consistently for more than 20 years (EHS 2007), whereas in the Republic of Ireland, 99% of the foreshore is a State-owned asset under the 1933 Foreshore Act, with the Department of the Marine being responsible for granting harvesting licences. In the Republic of Ireland, traditional rights[1] originated from the legal framework that existed before independence.

There exists appurtenant to coastal property ownership, the right to ‘cut, gather and remove’ seaweed from familial stripes. Many coastal householders have the right to harvest unattached, storm-cast seaweed from above the high-water mark and harvest attached seaweed material from below high water, along the boundary of their property for fertilizer, food, and extracts for both personal and commercial purposes. However, the issue of seaweed ownership and harvesting rights in Ireland is equivocal. Numerous complex cultural, historical, and familial issues, rights, and definitions need to be clarified before substantial progress is made. At the time of writing, this process had already commenced with the Attorney General examining the issue from the various viewpoints of investors, developers, Government, local seaweed harvesters, licence

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[1] Taken from Irish traditional rights agreement: ‘There is also appurtenant to the lands a right to burn seaweed for kelp . . . there is also appurtenant to the lands the right to cut gather and remove seaweed whether growing or cast by the sea upon the foreshore and bed of the sea below high water mark of medium tides‘.

holders and prospective licence holders (Joint Committee on Environment, Culture, and the Gaeltacht, 2015).

The lack of clarity regarding ownership is considered the main obstacle in further developing the seaweed industry in Ireland, with the industry wary of fostering investment/expansion when it exerts little control over either the harvesting and/or access methods to the resource. A lack of adequate restrictions on harvesting, including robust regulations protecting the resource, the harvester, and processor behaviour, has the potential to lead to a ‘tragedy of the commons’ scenario (Hardin 1968).

Seaweeds are often considered a ‘common property resource’ or a resource for which exclusion is difficult, and joint use involves sub-tractability (Feeny et al. 1990). Traditional community systems play an essential role in the successful stewarding of common resources sustainably (Lida 1998). Some examples of good community-level resource stewardship and ecomanagement are those of the indigenous Nunavik community of northern Canada and the First Nations Peoples of the Pacific Northeast (Turner 2003, Sharp et al. 2008). These examples are situations where community-level research is used to evaluate natural resources and their supply, and the demand and deep cultural respect for the environment are kept in balance.

The lack of clarity about ownership of both intertidal and subtidal resources in some regions has led to clashes among local communities, traditional harvesters, and industry, with conflicts arising over competition for space (Baweja et al. 2016). However, as the global seaweed industry continues to grow and exert pressures on those resources, it is difficult to envisage that the supply and maintenance of those resources will be held exclusively by numerous individuals claiming historical rights and access to the seaweed. It is more likely that marine spaces and offshore seaweed farms will be utilised in areas where currently no aquaculture exists. While still relatively new in Western regions, the marine offshore cultivation sector is growing rapidly (Troell et al. 2009). However, the successful development of offshore aquaculture requires environmental and economic considerations and the ability to add value to the cultured seaweed through biorefinery approaches (see also Buschmann et al. in press).

For example, in the Macaronesian Region (the Azores, Madeira, Canaries), only the Azores have commercial activity relating to the wild harvest of agarophytes. The future development of the Macaronesian Region will likely relate to the development of an aquaculture production seaweed industry, with species such as *Pyropia* and the genera *Gracilaria* and *Caulerpa* having been identified as having potential for increased valorisation and biotechnological applications. However, as stated, the sustainable harvest of Macaronesian seaweeds likely requires new regulations and the further development of "best practise" protocols to ensure the sustainable management of exploited seaweeds (Haroun et al. 2019).

3.17 Climate change and distributional shifts in species

Throughout the last century, the average global surface seawater temperature (SST) increased by approximately 0.6°C, and it is predicted to increase by up to 3.2°C in the next century (Simkanin et al. 2005, IPCC 2013). Climate variation is a key driver in defining global distribution patterns and abundance of seaweed species and is a growing concern for all fisheries worldwide (Ugarte et al. 2010). Shifts in species' ranges have been documented for a variety of organisms over the last few decades (Forsman et al. 2016, Lehikoinen et al. 2016), including marine species (Sorte et al. 2016), amongst which are some seaweeds (Simkanin et al. 2005, Wernberg et al. 2010, Brodie et al. 2014, Yesson et al. 2015, Vergés et al. 2016, Araújo et al. 2016).

The response of seaweed species to disturbance varies with species identity, location and source of the disturbance, and there have been recently reported changes in key structuring seaweed species in response to different disturbance factors (Araújo et al. 2016). This is the case for several native European kelp species, some with important economic value, with climate changes having measurable impacts on kelp forest ecosystems, and it was reported that their distribution and abundance in parts of their ranges had drastically changed (Steneck et al. 2002). For instance, *L. digitata, L. hyperborea, L. ochroleuca, L. rodriguezii, Saccharina latissimima,* and *Saccorhiza polyschides* showed regression of their populations and/or local extinction in different areas of their distribution (Pehlke and Bartsch, 2008, Moy and Christie, 2012, Couceiro et al. 2013, Oppliger et al. 2014, Rinde et al. 2014, Araújo et al. 2016, Bartsch et al.

2016). These changes were related to a multitude of natural and anthropogenic stressors such as over-grazing by sea urchins (Rinde et al. 2014), harvesting (Lorentsen et al. 2010), decline of water quality (Raybaud et al. 2013) and frequently, SST associated with climatic change, especially at distribution limits (Assis et al. 2014). Other examples include fucoid species that were also commercially exploited in Europe and have undergone distributional changes along the latitudinal or vertical range of the limits of distribution, e.g., *Fucus vesiculosus* (Nicastro et al. 2013) and *F. serratus* (Araújo et al. 2011, Duarte et al. 2013). *Himanthalia elongata*, another structuring species of increased economic interest, suffered significant reductions in its southernmost limits (i.e., northern Spain, 116 km) and central/northern Portugal (230 km) and reduced abundance of the remaining populations, presumably related to ongoing trends of warming SST (Lima et al. 2007, Duarte et al. 2013, Araújo personal observation).

Other seaweeds, e.g., *A. nodosum,* have maintained their distributional ranges, although they too are showing evidence of differentiated population dynamics with spatial fragmentation of populations towards their southern limits of distribution (Europe: Araújo et al. 2011, 2014, eastern coast of USA: C. Yarish, pers. comm).

Modelling studies have predicted the reduction, or extinction, along stretches of the European shorelines of several structuring species such as *L. digitata* (Raybaud et al. 2013), *H. elongata* (Martinez et al. 2015), *F. vesiculosus* (Assis et al. 2014), *L. hyperborea* and *L. ochroleuca* (Assis et al. 2016). In Tasmania, Australia, researchers have warned that several seaweed species face extinction due to reaching their ‘upper thermal limit’ for SST, with standing crops of *M. pyrifera* facing rapid decline (Johnson et al. 2011, Mathiesen 2017). Recent studies show that warming SST may affect kelp recovery post-harvest and that warming seawater temperatures may also threaten the viability of kelp resources (Krumhansl et al. 2016). As a result of climatic changes or shipping activities, the increasing presence of invasive species is also a growing concern (Díez et al. 2012).

For most of these species, the biomass supply for commercial purposes is assured by careful harvesting from wild stocks. Some works have examined the effects of harvesting on associated habitats and organisms (Lorentsen et al. 2010, Stagnol et al.

2013, 2016), but empirical studies on this topic are still scarce and controversial for many of the commercially explored species and regions in Europe. This knowledge assumes particular importance at edge locations, where organisms might be ecophysiologically constrained, and natural population dynamics might respond differently to the sustainable harvesting practices established for other regions. A recent study has recommended that the exploitation of *A. nodosum* at its southernmost location in Europe (Viana, Portugal, 41.69107° N, 8.84881° W) should be avoided due to the vulnerability displayed by this “edge population” to harvesting (Borges et al. 2020).

Natural disasters such as tsunamis and El Niño have been associated with major losses of inter-and subtidal seaweed species in the past. For example, Chile frequently experiences powerful earthquakes (>7 MW), which can have a major impact on belt forming sub- and intertidal species, particularly seaweeds. As a consequence of the highly destructive 8.8 MW magnitude Chilean earthquake in 2010, largescale coastal co-seismic uplifts occurred around the Gulf of Arauco, Santa María Island and the Bay of Concepción. Following the earthquake, an investigation into biomarker species indicated coastal uplifts of up to 3.1 m (Castilla et al. 2010). This uplift resulted in large-scale mortality of subtidal and intertidal organisms, including seaweed species, namely the kelps and coralline algae and resulted in a period of shortages of commercial red species. Similarly, in 1985, following a 7.8 MW earthquake in central Chile, coastal uplifts of up to 60 cm were observed, which led to the extensive mortality of kelp (*Lessonia nigrescens*) near the Estacion Costera de Investigaciones Marinas, Las Cruces (Castilla 1988).

3.18 Recent initiatives

There is a recognised requirement to establish a best practice code of conduct for the successful sustainable exploitation of seaweeds (Rebours et al. 2014, Cremades Ugarte et al. 2016). Sharing information from government agencies with responsibilities to industry and education and communication at local levels is important. In France, the agency for food, environment and occupational health and safety (ANSES) integrated seaweeds into their food composition database ‘Ciqual’, which collects, assesses, and publishes nutritional composition data of seaweeds typically consumed in France.

The implementation of a global certification programme for seaweed harvesting has been proposed. The Marine Stewardship Council (MSC) and the Aquaculture Stewardship Council (ASC) hope to provide a global standard for the certification of seaweed operations that will ensure the sustainable and responsible exploitation of seaweed resources (see www.msc.org). In the Gulf of Maine, seaweed harvester apprenticeship programmes have been introduced (see www. larchhanson.com), in which apprentices are trained in sustainable harvesting of seaweeds (*P. palmata*, *C. crispus*, *Laminaria* (*Saccharina*) spp.). Other initiatives such as the ALGMARBIO project have the objective to develop a good practice guide for seaweed producers, as well as regulating the creation of an organically certified seaweed industry (Mesnildrey et al. 2012).

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4. Arsenic Speciation in a Variety of Seaweeds and Associated Food Products

i. Acronyms and Abbreviations

As_{III}	trivalent arsenic/arsenite
As_{Bet}	arsenobetaine
As_{Cho}	arsenocholine
As_{Inorg}	organic arsenic
As_{Lip}	arseno lipid
As_{O}	inorganic arsenic
As_{Sug}	arseno sugar
As_{T}	total arsenic
As_{v}	pentavalent arsenic/arsenate
DMA	dimethylarsinic acid
MMA	monomethylarsonic acid
TMAO	trimethylarsine oxide
TMAs	tetramethylarsonium ion
DMAE	diethylarsinoylethanol
DMMTAv	dimethylmonothioarsinic acid

4.1 Abstract

Seaweeds, or sea vegetables, are popularly consumed for their nutritional qualities and have been shown to have numerous health benefits to consumers being rich in a host of vitamins and minerals. A wide range of brown, red and green seaweeds are consumed globally, with around 145 species known to be directly consumed by humans worldwide. It has been reported that several popularly consumed seaweed species, including *Laminaria digitata*, *Alaria esculenta*, and *Sargassum fusiforme,* possess the ability to accumulate elevated quantities of arsenic (As) in their tissues. Some studies have highlighted concerns relating to the consumption of certain seaweed species due to their As content. The ability of seaweed to bioaccumulate high levels of As raises some concerns regarding their safety. There is evidence that elevated levels of As known in some particular species have the potential for biomagnification through successive marine food chains and ultimately onto higher trophic levels. This presents highly pertinent questions regarding the safety of seaweed consumption and its potential to contribute to increased dietary intake of As. New classes of As metabolites such as thiolated arsenicals are yet to be fully elucidated in terms of toxicity, but it is thought that these particular forms may play an important role in As metabolism and toxicity. Similarly, much is yet to be fully understood regarding the formation pathway of methylated As and As_{Sug}. This review highlights the presence and speciation of arsenic in a variety of macroalgal food and associated products.

4.2 Introduction

The focus of this review is to highlight the presence and speciation of arsenic (As) in the most common, commercially important edible seaweeds and associated products. The chapter highlights the complex and often poorly defined role which As speciation plays in human toxicity.

The increasing trend within Western societies towards the direct consumption of some of the more commonly available seaweed species (e.g., *Porphyra* sp., *Saccharina japonica* (Areschoug) C.E.Lane, C.Mayes, Druehl & G.W.Saunders, *Alaria esculenta*) has been partly driven by consumer awareness based on the widespread reporting of their benefits to human health (Mouritsen et al. 2018a, Mouritsen et al. 2018b). Consumption of seaweeds has been shown to: improve digestive health (Rajapakse and Kim, 2011), potentially benefit the management of diabetes (Sharifuddin et al. 2015), and ameliorate some risk factors associated with cardiovascular disease (Cornish et al. 2015). Many studies have also highlighted the prebiotic benefits of seaweed supplementation in the diet of animals for enhancing livestock production and health (*Ascophyllum nodosum*) (Makkar et al. 2016), thereby improving gut microflora (*Laminaria* sp.) (Bouwhuis et al. 2017, Charoensiddhi et al. 2017), or more recently as a potent natural antimethanogenic in livestock rumen (*Asparagopsis taxiformis* (Delile) Trevisan) (Kinley et al. 2016). Several commercially available seaweeds, including *Undaria pinnatifida*, *S. japonica* and *Ulva armoricana* Dion, Reviers & Coat, have been shown to contain high levels of a number of essential and beneficial dietary nutrients (Sanjeewa et al. 2018) iodine (Domínguez-González et al. 2017) and have been shown to contain high dietary fibre (33–50%) (Mabeau and Fleurence, 1993), polyunsaturated fatty acids (Kendel et al. 2015), trace elements (Astorga-España et al. 2015), carbohydrates (Cian et al. 2015), with some brown seaweeds, in particular, being notably nutritionally dense (Kumar et al. 2015, Fleurence et al. 2017).

It has been well documented that many popularly consumed seaweeds, e.g., *Laminaria digitata*, *A. esculenta*, possess the ability to accumulate elevated quantities of As in their tissues (Morrison et al. 2014, Feldmann et al. 2016, Ronan et al. 2017). These seaweeds can be readily purchased in supermarkets as packaged consumer products in many parts of the world (Brandon et al. 2014, Khan et al. 2015, Amin et al. 2018). The elevated levels of As known to occur in some of the Sargassaceae and Laminariaceae families, including *Sargassum fusiforme* (Harvey) Setchell and *L. digitata*, and the potential for its biomagnification through successive marine food chains and ultimately higher trophic levels (including livestock and humans) present highly pertinent questions regarding the safety of seaweed consumption and its potential to contribute to increased dietary intake of As and a variety of its forms.

Speciation of As can be defined as the identification of individual physio-chemical forms of As in given biomass. Le et al. (1994) reported that arsenosugars (As_{Sug}) were the most abundant As forms present in seaweed. Pioneering research was conducted into the speciation of As within marine seaweeds as early as four decades ago (Lunde 1970, Lunde 1977, Watanabe et al. 1979, Klumpp 1980). Over the last two decades, further studies have highlighted the need for accurate identification of not only total As (As_T) but the various forms which occur in some selected seaweeds. This is particularly important when evaluating the roles of As_T and its various forms in human toxicology and its consequent impacts on human health.

Improvements in analytical methodologies for the identification of As and its forms (arsenicals) (Terlecka 2005), including the use of a range of hyphenated ICP-MS and HPLC techniques (Van Hulle et al. 2002, Hsieh and Jiang, 2012), have already allowed for the more sensitive analysis of arsenicals present in several commercially available seaweed species. Recent research into some arsenicals, such as As_{Sug}, shed light on their toxicological significances of a once considered benign and relatively nontoxic As forms (Sakurai et al. 1997, Ebert et al. 2014).

There continue to be major gaps in our knowledge regarding metabolised As forms' toxicological potential (Feldmann and Krupp, 2011). For example, some methylated forms created after ingestion of inorganic As ($_i$As), including monomethylarsonic acid (MMA) and dimethylarsinic acid (DMA), were shown to be cytotoxic and potentially of concern to the public (Reis and Duarte, 2018). More recently, the cytotoxic role of some methylated forms of As, particularly thiolated derivatives of DMA and MMA (Styblo et al. 2000), has emphasised the relevance of this poorly understood topic.

4.3 The production of macroalgae for food products

Seaweed farming, whereby cultivation lines supported in the water by ropes or rafts are seeded with seaweed juveniles and used in the production of high-quality, edible seaweeds (Chung et al. 2017, Stévant et al. 2017), is the dominant method of their production. Indeed, the majority of seaweeds produced for human consumption are produced via aquaculture rather than from wild harvesting (Mac Monagail et al. 2017). Over 80% of seaweeds' total global production from both wild harvesting and cultivation is consumed either directly or indirectly (e.g., as hydrocolloids) by humans (McHugh 2003, Abreu et al. 2011, Ferdouse et al. 2018). The five leading genera, *Saccharina*, *Undaria*, *Porphyra*, *Eucheuma*/*Kappaphycus* and *Gracilaria*, represent c. 98% of the worlds cultivated seaweed production (Yarish and Pereira, 2008, Buschmann et al. 2017).

The total global production of seaweeds from aquaculture has increased over 300% in the last two decades from 7.2 million tonnes in 1996, 14.3 million tonnes in 2006, to over 30 million tonnes in 2016 (FAO 2015). This growth over the two past decades has resulted in seaweed ranking as the third-largest aquaculture crop, just after freshwater fish and molluscs (Michalak and Chojnacka, 2018).

The vast majority of this production comes from Asia, although further growth is expected, particularly in areas where seaweeds have not been cultivated traditionally (Morris et al. 2016, Stévant et al. 2017). For example, in Europe during the period 2006–16, seaweed production from aquaculture increased by 83% (from 851 tonnes to 1554 tonnes, mainly "brown seaweeds") while in Africa there has been an increase of 57% in production (from 88,530 tonnes to 139,313 tonnes, mainly *Eucheuma*) (FAO 2015). The seaweed industry is expected to continue to expand, fueled by growing global demand for high-quality, edible seaweed products, from seaweed spaghetti, seaweed snacks, seaweed flakes or consumed directly as sea vegetables.

Seaweed cultivation techniques, such as seaweed aquaculture bed (SAB) and Integrated Multi-Trophic Aquaculture (IMTA) systems, can significantly increase the sustainability of aquaculture (Troell et al. 2009) and have been proposed as a best practice management option for reducing the environmental impact of aquaculture (Ratcliff et al.

2016). Seaweeds are popularly used in IMTA systems as biofilters of fish pond effluents (Shpigel et al. 2018). These sustainable seaweed cultivation techniques utilise seaweeds, typically kelps, to remove and recycle the waste nutrient excretions of one or more organisms. The cultivation of seaweed through IMTA promotes higher productivity levels with less variability than natural seaweed beds due to higher and more constant nutrient availability (Abreu et al. 2011). The biomass produced from IMTA can provide an alternative source for seafood and raw material (Hasselström et al. 2018) as well as being used as a feed source for fish species produced in an IMTA system (Laramore et al. 2018).

The first study to carry out a comparative investigation of As (as well as other metals) in *L. digitata* from IMTA and natural stocks concluded that neither the integration of organic salmon farming nor seaweed cultivation itself influenced the metal content of *L. digitata* outside the bounds of variability found within wild populations (Ratcliff et al. 2016). The study did find As levels in *L. digitata* to be elevated (49.44 –89.58 μg g^{1}), and as such, this specific species may pose a concern for inclusion as a dietary component.

4.4 Uptake and accumulation of arsenicals by various seaweeds

Bioaccumulation is the seaweeds' ability to accumulate metals and metalloids from the surrounding water and has been well documented (Morrison et al. 2008, Henriques et al. 2015 Henriques et al. 2017). Certain seaweeds bioaccumulate metals to an exceedingly high concentration in their tissues (Wang et al. 2015). These can be many times greater than baseline levels found in the surrounding marine environment (Reis and Duarte, 2018). Dissolved As is present in seawater at the 1 μg L^{1} level in a number of chemical forms, primarily As_{III}, As_{V}, MMA and DMA (Cabon and Cabon, 2000). The main As forms present in common seaweeds are the As_{Sug}, although some seaweed species (e.g., *Laminaria*) contain significant amounts of DMA.

The concentration of metals and radionuclides has led to the use of seaweeds as biological indicators of water quality (Shibata et al. 2004, Morrison et al. 2008). However, the bioaccumulation capacity of certain seaweeds also raises concerns regarding the presence of environmental contaminants, including As, in common, edible seaweeds.

In the marine environment, As exists in many organic and inorganic forms (Avula et al. 2015). Arsenate (As_V) is the predominant form found in marine waters as it is more thermodynamically stable than arsenite (As_{III}) (Andreae 1978). It is reported (Ma et al. 2018) that arsenate is readily and actively taken up by certain seaweeds from seawater, where it is reduced to As_{III}, methylated to MMA and DMA and then excreted (Hellweger et al. 2003), although a small percentage is incorporated into the algal tissue. Early work by Sanders and Windom (1980) showed that the pentavalent form of As(As_V) was taken up from the surrounding water by seaweeds and biotransformed into less toxic arsenate forms (Farías et al. 2007).

Seaweeds, such as *A. nodosum* and *L. digitata*, have long been known to play an essential role in the metabolism of As through the marine environment (Lunde 1977, Phillips and Depledge, 1985), as well as being incorporated in various food chains (Zhao et al. 2010). Once consumed by higher trophic organisms, seaweeds provide a vector for the transfer of arsenicals to higher trophic levels feeding on the algae such as fish and crustaceans and, crucially, humans (Wrench et al. 1979, Taylor et al. 2017).

The capacity for the absorption, retention and excretion of As differs among the various seaweed groups (Zhao et al. 2014). Several particular exceptions (e.g., *S. fusiforme*) have been highlighted as being species of interest regarding the consumer's safety.
Many external and internal factors influence the ability of seaweeds to uptake and retain As in their cells. These include the distinct cell wall composition of particular species (Liu et al. 2018) and the surrounding water's pH, temperature, and nutrient content (Klumpp 1980). The complex bioaccumulation process is governed by four main processes, namely: electrostatic interaction, surface complexation, ion exchange and precipitation (Liu et al. 2018).

The taxonomy of various seaweed species also plays a key role in As storage and in the distribution of As forms (Taylor and Jackson, 2016). Seaweed identity determines not only the uptake capacity of seaweeds but also the specific arsenicals present in seaweed (Thomson et al. 2007, Besada et al. 2009, Khan et al. 2015). Large variations in both As_T

and $_i$As are seen to exist between different phylogenetic groups. For example, considerable differences are seen in As (both total and inorganic content) between brown (Phaeophyceae) and green (Ulvophyceae) groups.

Surface chemistry plays a key role in the sorption of arsenical ions on to various seaweed surfaces. The biochemical composition of seaweeds, plus the response of seaweeds to ambient environmental conditions, including salinity levels in the water, ultimately determines the availability of binding sites for elements (Stengel et al. 2004, Malea et al. 2015). For example, many of the Phaeophyceae (i.e., brown algae) are known to have a strong affinity for As uptake and contain elevated levels in their tissues. The cell walls of brown algae contain cellulose and, in addition, mannuronic, guluronic acid and other sulphated polysaccharides. The predominant polysaccharide present in the cell walls of the phaeophytes is alginic acid, which in some instances may reach up to 70% of the dry weight in brown seaweeds such as *S. japonica*, *U. pinnatifida*, and *S. fusiforme* (Zhao et al. 2014). Alginic acid has a tremendous capacity for As sorption (Sarkar et al. 2010), with differences in alginic acid compositions potentially altering the metal-binding properties of brown algae (Smidsrød and Haug, 1968). Sorption of As to seaweed surfaces contributes to the As load present with high concentrations of cell wall polysaccharides providing excellent binding sites for As (Wells et al. 2017, Intawongse et al. 2018).

Therefore, the high alginic acid content present in brown seaweed results in higher levels of As_T than both red and green seaweeds (Duinker et al. 2016). Certainly, while taxonomy is a good indicator of As concentration in seaweeds, it is not a hard and fast rule with similar As_T concentrations reported between some red and brown species, for example, *Neopyropia tenera* var. tamatsuensis (A.Miura) N.Kikuchi & Niwa (69.9 µg g^1) and *L. digitata* (65.7 µg g^1) (Kaise et al. 1992, Almela et al. 2006).

The locations from which seaweeds are harvested also play a role in the presence of arsenicals. Several authors reported on the potential use of selected seaweeds as biomonitors (Boubonari et al. 2008, Morrison et al. 2008, Medeiros et al. 2017) as a result of their ability to regulate and retain metals from contaminated coastal environments. Sources of anthropogenic pollution discharged into the marine environment can result in elevated levels of As in seaweeds (Langston 1980). Considering the ability of seaweeds to act as a vector for As transfer to humans (Cheney 2016), this, therefore, may pose a threat if consumed.

4.5 The impact of arsenicals in marine algae commonly used as food for humans

For almost 100 years, scientists have examined the As content of marine seaweeds (Jones 1922, Chapman 1926), and historically, the primary metric recorded was the total arsenic content. Total As, however, provides little significance as a toxicological indicator since arsenicals' toxicity is closely related to their chemical form (i.e., speciation) (Hughes 2002). It is particularly challenging to derive human toxicological inferences due to the ill-defined and varying toxicities of some organic forms, including As_{Sug} and arsenolipids (As_{Lip}).

The primary arsenicals generally found present in seaweed include As_{III}, As_{V}, MMA and DMA, with trimethylarsine oxide (TMAO), tetramethylarsonium ion (TMAs), diethylarsinoylethanol (DMAE), arsenobetaine (As_{Bet}), arsenocholine (As_{Cho}) and other arsenic forms, occurring in only trace amounts in most edible seaweed species (Wolle and Conklin, 2018) along with a host of dimethylarsinoylriboside derivatives (As_{Sug}) (Kohlmeyer et al. 2002).

High levels of organic As (As_{O}) may be found in commercially available seaweed, primarily in the form of As_{Sug} (Taylor et al. 2017). At least 19 organoarsenicals have been identified in commercially important edible seaweeds (Nischwitz and Pergantis, 2006), although the full suite of As toxicities to humans is yet to be fully comprehended. Speciation studies have shown that most As present in seaweed are organic and generally contain relatively low levels of iAs compared with arsenosugars (Wells et al. 2017), although a wide variation in the As content exists in commonly consumed species (Table 4.1).

Inorganic As is a known genotoxic and neurotoxic contaminant (Kaur et al. 2011) and has been classified as a Group 1 human carcinogen by the International Agency for Research on Cancer (IARC) (IARC 2012). The toxicity of As compounds are highly dependent on both the methylation status and the valence state (Cohen et al. 2006).

The most recent epidemiological case studies have highlighted that ${}_{i}$As exposure to chickens causes oxidative stress to brain tissue and was shown to significantly induce neurotoxicity in the birds (Zhao et al. 2017), with numerous historical studies also highlighting induced physiological stress in humans (Carlson-Lynch et al. 1994, Phan et al. 2010). Some of the health issues related to ${}_{i}$As toxicity have been recently reviewed (Mehta 2018).

The ${}_{i}$As fraction exists as the minor component across all seaweed taxa (Mania et al. 2015) and shows less variability than As_O (Almela et al. 2006), generally ranging from 8% to 13% of the As_T present (Díaz et al. 2012). In the case of most edible seaweeds, the inorganic concentration rarely exceeds that of 1 µg g^{1} (Almela et al. 2006, Rose et al. 2007). This is not the case for, in particular, but not exclusive to, some *Sargassum* species, most notably *S. fusiforme* (Yokoi and Konomi, 2012).

The complex characterisation and toxicology of As forms post ingestion of seaweeds have been comprehensively outlined in Vahter (1994) and Francesconi et al. (2002) and will be mentioned only briefly here. Once seaweeds are ingested and absorbed by the gastrointestinal (GI) tract, As_V is quickly reduced to its much more toxic metabolite arsenite (As_{III}), with As_{III} being six times more toxic than As_V and 100 times more toxic than mono- and demethylated metabolites (Hughes et al. 2011, Avula et al. 2015). Generally speaking, the trivalent forms of As are more toxic than their pentavalent counterparts (Mass et al. 2001). It is interesting to note what role the GI tract may play in the preabsorptive metabolism of arsenicals, potentially having a role in converting As_V and methylated As to oxo-arsenicals and thioarsenicals (Molin et al. 2015).

Following absorption, ${}_{i}$As forms are almost entirely absorbed and undergo a series of extensive methylation conversion reactions within the liver (Thomas et al. 2004, Brandon et al. 2014). A high number of secondary methylated derivatives are generated following the metabolism of ${}_{i}$As (Tam et al. 1979), with the production of these secondary methylated derivatives playing a fundamental role in the toxicity of As to humans (Molin et al. 2015).

Table 4.1 Total and inorganic arsenic concentration of commonly consumed seaweeds

			Arsenic content (μg g^{-1})	
Phylum/family	**Species**	**Common name**	**Total arsenic**	**Inorganic arsenic**
Ochrophyta/Sargassaceae	*Sargassum* sp.	Gulf weed	6.48–120.4[a,b,c,d,e]	4.83–20.8[c,d,e,s]
Ochrophyta/Sargassaceae	*Sargassum fusiforme*	Hijiki	41–131.8[f,g,h,i]	34–87.7[g,h,i]
Ochrophyta/Sargassaceae	*Cystoseira* spp.		0.8–20[a,v]	
Ochrophyta/Sargassaceae	*Cystoseira barbata*		17.6–242[a]	
Ochrophyta/Laminariaceae	*Macrocystis pyrifera*	Giant kelp	36–131[b,u]	
Ochrophyta/Laminariaceae	*Laminaria hyperborea*	Tangle	74.04.0[m]	
Ochrophyta/Laminariaceae	*Saccharina japonica*	Royal Kombu	21.9–53[d,f,I,k]	0.254–0.297[k]
Ochrophyta/Laminariaceae	*Saccharina latissima*	Sugar Tang	43–57.5[e,p]	0.16–0.8[e,p,t]
Ochrophyta/Laminariaceae	*Laminaria digitata*	Kombu	41–114[h,j,m,n,o,p,q]	0.1–62[h,m,n,o,p,q]
Ochrophyta/Alariaceae	*Undaria pinnatifida*	Wakame; Sea mustard	31.1–70[a,f,h,i,j,k,l]	0.15–36.3[h,k,l]
Ochrophyta/Alariaceae	*Alaria esculenta*	Bladderlocks	34.4613.72[o]	0.03–0.22[o,t]
Ochrophyta/Lessoniaceae	*Ecklonia radiata*	"Kelp, brown"	42.5[b]	
Ochrophyta/Lessoniaceae	*Eisenia bicyclis*	Arame	23.8–29[k]	0.17–0.185[k]
Ochrophyta/Durvillaeaceae	*Durvillaea potatorum*	Bull kelp	13[b]	
Ochrophyta/Stypocaulaceae	*Halopteris* sp.	Sea flax weed	12–26[v]	
Ochrophyta/Himanthaliaceae	*Himanthalia elongata*	Sea thong	35.3[j]	
Ochrophyta/Fucaceae	*Ascophyllum nodosum*	Knotted wrack	23.68–51[b,j,q,r]	0.05–1.3[o,q,r]
Ochrophyta/Fucaceae	*Fucus vesiculosus*		32.76–50[j,o,m,w]	0.03–1.21[k,q]
Ochrophyta/Fucaceae	*Fucus* sp.	Lady wrack	42.3–46.2[k]	1.21–1.33[k]
Ochrophyta/Fucaceae	*Fucus spiralis*	Jelly bags	16.2 - 71.4[o]	0.04 - 0.05[o]
Ochrophyta/Fucaceae	*Pelvetia canaliculata*	Cow Tang	42.72.5[m]	
Ochrophyta/Dictyotaceae	*Padina pavonica*	Peacock's tail	1.89–18.3[a,v]	

Ochrophyta/Dictyotaceae	*Padina fraseri*		5.6[b]	
Unclassified	Phaeophyceae		16.56–49.52[x]	
Unclassified	Phaeophyceae		38.11–101.24[x]	
Unclassified	Phaeophyceae		54.7–181.14[x]	
Rhodophyta/Gigartinaceae	*Gigartina*		10.18–12.69[y]	
Rhodophyta/Gigartinaceae	*Chondracanthus*		10.2–12.7[a]	
Rhodophyta/Gigartinaceae	*Chondrus crispus*	Irish Moss/Carrageen Moss	3.8–18.2[j,l,w]	
Rhodophyta/Gracilariaceae	*Gracilaria*	Hoso Kabanori	2.61–55.35[x,y]	
Rhodophyta/Gracilariaceae	*Gracilaria gracilis*	Slender Wart Weed	2.62–15.0[a,z]	
Rhodophyta/Gelidiaceae	*Gelidium* sp.	Punaleva-suku	<1–2.39[a,j]	
Rhodophyta/Palmariaceae	*Palmaria palmata*	Dillisk	<1.0–10.1[j,k]	
Rhodophyta/Bangiaceae	*Porphyra* sp.	Red laver/sloke	13.0–40.7[a,h,i,j,l]	
Rhodophyta/Rhodomelaceae	*Polysiphonia* sp.	Atlantic Siphon Weed	8.61–10.5[a,y]	
Rhodophyta/Phyllophoraceae	*Phyllophora*	Sandy Leaf Bearer	2.6[aa]	0.81[aa]
Unclassified	*Rhodophyta*		5.73–55.34[x]	
Chlorophyta/Cladophoraceae	*Cladophora* spp.	Gronslickar	3.3–13.5[a,b,y]	
Chlorophyta/Ulvaceae	*Ulva* spp.	Green laver	0.18–9.52[a,y]	
Chlorophyta/Ulvaceae	*Ulva rigida*	Glasa´n	0.1–5.8[a,l,z]	
Chlorophyta/Ulvaceae	*Ulva intestinalis*	Gutweed	1.5–1.9[a,z]	
Chlorophyta/Ulvaceae	*Ulva lactuca*	Sea lettuce	2.2–6.89[a,j,k,m]	
Chlorophyta/Ulvaceae	*Enteromorpha* sp.	Stone hair	2.15[w]	
Chlorophyta/Ulvaceae	*Ulva enteromorpha*		15.4[j]	
Chlorophyta/Codiaceae	*Codium fragile*	Sponge Tang	3.66–23[a,z]	
Chlorophyta/Codiaceae	*Codium lucasii*		8.2[b]	
Chlorophyta/Caulerpaceae	*Caulerpa racemosa*	Sea grapes	0.77[c]	0.77[c]
Chlorophyta/Caulerpaceae	*Caulerpa taxifolia*	Lukay-lukay	0.77[c]	0.26[c]
Chlorophyta/Chlorellaceae	*Chlorella pyrenoidosa*		1.3[j]	

Continued.

Unclassified	Green laver	9.19–9.36[i]

References

(a) Bonanno and Orlando-Bonaca (2018)
(b) Foster and Maher (2016)
(c) Grinham et al. (2014)
(d) Khan et al. (2015)
(e) Whyte and Englar (1983)
(f) Kaise and Fukuit (1992)
(g) Laparra et al. (2004)
(h) Marschner et al. (2018)
(i) Nam et al. (2016)
(j) Desideri et al. (2016)
(k) Almela et al. (2002)
(l) Llorente-Mirandes et al. (2011)
(m) Hansen et al. (2003)
(n) Ronan et al. (2017)
(o) Taylor and Jackson (2016)
(p) Maulvault et al. (2015)
(q) Morrison et al. (2008)
(r) Mac Monagail et al. (2018)
(s) Zhang et al. (2017)
(t) Stévant et al. (2017)
(u) Salomone et al. (2017)
(v) Squadrone et al. (2018a)
(w) Almela et al. (2006)
(x) Santos-Silva et al. (2018)
(y) Malea et al. (2014)
(z) Malea et al. (2015)
(aa) Squadrone et al. (2018b)

The first metabolites produced following the methylation of $_{i}$As are highly toxic secondary derivatives, primarily pentavalent and trivalent MMA and DMA (Zhao et al. 2014). These methylated forms are much less toxic than $_{i}$As (Dahl et al. 2010). When $_{i}$As is ingested, it is excreted in the urine, mainly in the form of pentavalent DMA_{V} and MMA_{V} (Feldmann and Krupp, 2011). Both MMA and DMA are generally only found at trace levels in seaweed (Zhao et al. 2014).

The bioaccessibility of DMA is low and ranges from 14% to 36% (Brandon et al. 2014). Methylated forms are quickly excreted in the urine, predominantly made up of DMA (75%) with smaller derivatives of MMA (9–20%) (Buchet et al. 1981, Vahter 1999). Further reduction and methylation steps lead to the formation of trivalent As forms DMA_{III} and MMA_{III}. Dimethylarsinous acid (DMA_{III}) exhibits DNA damaging activity as an indirect result of the oxidation of DMA_{III} to DMA_{v} (Nesnow et al. 2002). Both MMA_{III} and DMA_{III} are highly reactive and cytotoxic (Cohen et al. 2002), with MMA_{III} shown to be more toxic than arsenite in human hepatocytes (Petrick et al. 2000). Furthermore, both MMA_{III} and DMA_{III} are potent human clastogens, i.e., chromosome disruptors (Kligerman et al. 2003), with very low physiologically relevant doses capable of inducing levels of oxidative DNA damage in cultured human cells (Schwerdtle et al. 2003).

As mentioned, pentavalent arsenicals are significantly less cytotoxic than trivalent As forms. The pentavalent form DMA_{V} is classified as “possibly carcinogenic to humans (Group 2B) by IARC” (Cohen et al. 2006). Monomethylarsonic acid (MMA_{V}), however, lacks toxicological evidence in animal experiments to support carcinogenicity (Cullen and Reimer, 2017).

In 1977, Crecelius showed that following administration of an As-rich wine to a 30-year-old male volunteer's diet, the majority of As forms are methylated to MMA and DMA before being excreted. High levels of DMA and MMA found in urine originating from the bioconversion of $_{i}$As, and the metabolism of organoarsenicals (Molin et al. 2015) suggests that this conversion of $_{i}$As to methylated arsenicals is a detoxification step in mammals (Lynch et al. 2014). However, the formation of toxic methylated arsenicals, particularly trivalent and thiolated forms, calls into question the accuracy of this. Some studies suggest that MMA_{III} exhibits toxicity that is comparable to inorganic arsenite (As_{III}) (Styblo et al. 2000) and is more toxic than As_{III} to cultured human cells (Petrick et al. 2000). Indeed, studies by Yamamoto et al. (1997) and Wanibuchi et al. (1996) have shown methylated arsenicals' ability to magnify other compounds' carcinogenic effects.

Several in vivo studies have been performed highlighting the nature of methylated arsenical toxicity in rodents. A long-term (2-year) feeding bioassay was carried out where male and female mice and rats were administered amounts of MMA in their diets. Following the 2-year feeding bioassay, the authors concluded that no increase of tumour incidences was seen in either rodent following MMA administration, although high doses of synthetic MMA (1300 ppm) caused a high mortality rate in both male and female rats. However, the toxicity of the large intestine was only seen at concentrations of MMA well above levels to which humans are exposed. The feeding study indicated that MMAV in a non-carcinogen in both male and female rats showed no mortality or related neoplastic effects in either mice or rats (Arnold et al. 2003). However, it may be difficult to infer human toxicological inferences from studies involving rodents considering the metabolic differences between both mammals. Rodents extensively metabolise DMA at a much higher rate and are more susceptible to the toxicity of ingested DMA than are humans (Cohen et al. 2013). The result of this extensive DMA metabolism is the formation of large quantities of toxic derivatives, including DMA_{III} (Díaz et al. 2012). Some research has suggested that the trivalent DMAIII is the active carcinogenic form and that the pentavalent DMA is entirely, or largely, inactive (Kitchin 2001).

Although there is still much to be comprehended regarding DMA and MMA's role in toxicology, what is becoming clear is the significant role methylated arsenical forms play, in particular, trivalent arsenicals (Van Hulle et al. 2002, Ebert et al. 2014). As a result of continued research highlighting the role in which methylated arsenicals play in human toxicology (Rehman et al. 2014, Shen et al. 2016), these methylated forms must be considered when defining human toxicological exposure to As from seaweed consumption.

4.6 As speciation in edible seaweeds

Seaweeds, or sea vegetables as they are occasionally culinary known, are often consumed for their nutritional qualities, being rich in proteins and vitamins B and C (Besada et al. 2009). The harvesting and consumption of seaweeds have historically been a common practice of coastal populations (Mac Monagail et al. 2017); however, nowadays, seaweed products for use in flavourings, colourings and functional food and nutraceuticals are a ubiquitous presence in supermarkets and health food stores around the world (Azania Jarvis 2015).

Many popularly consumed seaweed species in both Eastern and Western societies have been shown to contain elevated As levels (Kaise and Fukuit, 1992). Many studies highlight concerns regarding elevated As levels reported in edible seaweeds (Akcali and Kucuksezgin, 2011, Garcia-Salgado et al. 2014). These elevated As levels mean that although the health-promoting benefits of seaweeds are well established, there is the specific potential for As toxicity due to elevated levels in some commercially available seaweeds. Kelps are some of the most popularly consumed seaweeds globally, with particular cultural importance in the East, and make up the most diverse group of edible seaweeds. Species such as *Laminaria digitata* (kombu), *Saccharina latissima* (ma-konbu), *L. ochroleuca* (Atlantic kombu) and *Alaria esculenta* (winged kelp) are kelp species consumed daily in soups, broths, and salads in Asia. Numerous studies have reported high levels of As present in commercially available kelps (Edmonds and Francesconi, 1983, Ronan et al. 2017), with As_T concentrations reported as high as 107 µg g^{1} dry weight and $_iAs$ as high as 7.7 µg g^{1} dry weight (Duinker et al. 2016). Details of As_T and $_iAs$ of popularly consumed seaweeds are shown in Table 4.1.

Many Rhodophytes are popularly utilised both in direct and indirect human consumption through their use in a staggering number of products (Mouritsen et al. 2013). The range of As_T present in common Rhodophytes is low, generally in the range 6.6–23.8 µg g^{1}. Some popularly consumed Rhodophytes, such as *N. tenera*, contain As concentrations of up to 49.5 µg g^{1} dw (Besada et al. 2009), although levels of As_T in *Porphyra* sp. have been reported as high as 58.3 µg g^{1} (Almela et al. 2006).

Meanwhile, chlorophytes contain comparatively low concentrations of As compared to both Rhodophytes and Phaeophytes (Morita and Shibata, 1990). Sea lettuce (genus *Ulva*) is a staple in many Eastern dishes, including miso soup, and contains As_T concentrations of 5.2 µg g^1 and $_{i}As$ concentrations of 0.36 µg g^1 (Almela et al. 2002). Levels present in other popular edible Chlorophytes, including *Cladophora* spp., and *Codium fragile* range from 3.3 to 4.2 µg g^1 (Malea et al. 2015). These low As readings result from the fast growth rate of Chlorophytes resulting in a dilution in As in the algal tissues (Villares et al. 2005).

4.6.1 Thiolated chemical forms

Although organic arsenicals are deemed harmless to humans (Francesconi 2010), having been classed as having "intermediate" toxicity (Van Hulle et al. 2002), seaweeds contain an array of poorly defined and characterised methylated arsenical forms. Less is known of the cytotoxicity of more complex methylated forms— although TMAO and tetramethylarsonium appear to be of limited toxicological concern in humans (Lynch et al. 2014).

Along with the generation of methylated arsenicals, some thiolated forms, such as thio-DMA_V, are produced from the metabolism of $_{i}As$. This new class of As metabolite suggests that the classical metabolism pathway is, in reality, more complex than previously assumed and that this class of As metabolite may play an important role in As toxicity (Sun et al. 2016). What is particularly interesting is that the thiolated forms are about 10-fold more cytotoxic than DMA (Raml et al. 2007) and more toxic than the As_{III} from which they were methylated (Van Hulle et al. 2002). One particular metabolite of the metabolisation of As_{Sug}, thio-dimethyl As (thio-DMA), has shown considerable cytotoxicity in vitro to human bladder and lung cells (Cabon and Cabon, 2000, Bartel et al. 2011), with other studies reporting that other thiolated forms, such as $DMMTA_V$, are among the most toxic As forms with a toxicity similar to DMA_{III} (Naranmandura et al. 2011). An excellent review of the occurrence, formation, and biological implications of thiolated arsenicals in As metabolism was presented by Sun et al. (2016).

4.6.2 Arsenosugars

The primary organic fraction found in most edible seaweeds is the ribose derivatives known collectively as arsenosugars (As_{Sug}) (Yu et al. 2018). Arsenosugars are highly bioaccessible and are readily absorbed in the GI tract, making up over 80% of the soluble As fraction found in seaweeds (Almela et al. 2005). Formed following a series of sequential oxidative alkylation steps (Francesconi 2010), these are the products of the biotransformation process of inorganic arsenate (Molin et al. 2015).

Prior to the turn of the 21st century and the advent of more powerful analytical instrumentation, As_{Sug} were generally deemed to be nontoxic entities to human health in much the same manner as our current view of arsenobetaine (Edmonds et al. 1977). To date, more than 20 different As_{Sug} have been identified (Almund et al. 2018) in seaweeds, with 4 forms being the most common (glycerol sugar, Gly-sug, phosphate sugar, PO_4-sug, sulphonate sugar, SO_3-sug, and sulphate sugar, SO_4-sug) (Llorente-Mirandes et al. 2011, García-Salgado et al. 2012).

Interestingly, some studies have shown that the bioaccessibility of As_{Sug} exceeds 100%, indicating that the potential conversion to different As_{Sug} or potentially additional As_{Sug} is formed during in vitro digestion (Brandon et al. 2014). Due to their abundant presence in seaweeds, As_{Sug} are therefore the main proportion of As in seaweed consumed by humans (Sakurai et al. 1997), although some exceptions certainly exist (i.e., some *Sargasso* species). Indeed, As_{Sug} are so plentiful in some seaweeds that concentrations of up to 100 μg g^{1} wet mass have been recorded in some species (Table 4.1) (Cullen and Reimer, 1989, Schmeisser et al. 2004).

Arsenosugars are naturally synthesised from the $_{i}$As taken up from seawater, with pathways proposed for the synthesis of As_{Sug} from arsenate in seaweeds (Kohlmeyer et al. 2002). Arsenosugars are considered to be of much lower toxicity to humans than inorganic forms (Oya-Ohta et al. 1996, Wang et al. 2015). The lower toxicity of As_{Sug} is true in and of itself; e.g., As_{Sug} are initially metabolised into various arsenic metabolites, including DMA as the primary intermediate produced (67%) in urine (Francesconi et al. 2002) as a result of ingestion of synthetic As_{Sug}. Further studies, meanwhile, have shown that following administration of two As_{Sug}, DMA_V—sugar-glycerol and DMA_V—sugar-sulphate, did not exert cytotoxicity to human cultured bladder cells. The same study reported cytotoxicity in human bladder cells by both DMA_V and thio-DMA_V administration at a similar concentration range (Leffers et al. 2013).

Importantly, the true role of As_{Sug} toxicity lies in its biotransformation and generation of toxic intermediates during its metabolism. Human biotransformation of As_{Sug} results in the production of at least 12 As metabolites (Raml et al. 2005). Dimethylarsinic acid, which is the primary derivative of the metabolism of $_iAs$, is also a major product of As_{Sug} metabolism (Taylor et al. 2017).

A study found that the urine of volunteers who ingested 20–25g (dry) of *Laminaria* spp. showed positive identification of DMA, MAA and DMAE as metabolites of As_{Sug} metabolism (Van Hulle et al. 2004). Similarly, Dawczynski (2007) showed an increase in DMA in human urine following ingestion of *Porphyra* sp. containing As_{Sug} only, indicating the conversion of nontoxic As_O into toxic DMA. The authors concluded that the As_{Sug} present are entirely transformed into the more toxic metabolites DMA, MMA and a range of unknown metabolites (Van Hulle et al. 2004).

A further feeding study involved volunteers consuming 10 g daily portions of seaweeds (nori, kombu and wakame) purchased from a local market. Urine samples were collected every 24 h throughout the feeding period and the arsenicals excreted were extensively characterised. Results showed increasing urinary DMA concentrations in participants more than any other As compound following seaweed consumption, with trace levels of thioDMA increasing only slightly in a few individuals (Taylor et al. 2017). Similarly, a study involving one volunteer who had their urine samples tested immediately after ingestion of 165 g of *S. fusiforme* showed peak concentrations of As compounds (As_V, As_{III}, MMA and DMA) in urine between 4 and 17.5 h following ingestion (Nakajima et al. 2006). Rather worryingly, following ingestion of one serving of *S. fusiforme*, the concentration of urinary As was similar to those levels of individuals affected by As poisoning. The authors concluded that long-term ingestion of *S. fusiforme* might result in As poisoning (Nakajima et al. 2006).

The chemistry and metabolism of As_{Sug} are highly complex, and much is yet to be elucidated. However, it should be clear that it is not adequate to characterise As_{Sug} as non-toxic to humans as it is not possible to rule out human health risks due to the likelihood of cellular toxicity (Leffers et al. 2013).

4.6.3 Arsenolipids

Seaweeds also contain lipid-soluble As (As_{Lip}), which are associated with the oil fraction of seaweed (Taylor et al. 2017), accounting for 1–25% of As_T present in some species (Almund et al. 2018). Organic arsenicals account for the majority of As in lipid-soluble fractions (Wang et al. 2015). After ingestion, As_{Lip} have been shown to be readily taken up and excreted in the urine, with around 90% excreted within 66 h (Schmeisser et al. 2006). To date, there have been over 50 unique As_{Lip} classified, with the main group identified being arsenic-containing fatty acids (As_{FAs}) (Almund et al. 2018). Arsenolipids show a high degree of cytotoxicity to cultured human bladder cell lines, comparable, in fact, to that of arsenite (Meyer et al. 2014). It is obvious then that As_{Lip} cannot be excluded from having no risk to human health and, as suggested by Meyer et al. a risk assessment of As_{Lip} is “urgently needed” to define their cytotoxicity.

4.6.4 Arsenobetaine

Arsenobetaine (As_{Bet}) is a highly abundant arsenical found in the marine environment and has long been heralded for its benign toxicology (Edmonds et al. 1977, Sanders 1978). Arsenobetaine has been referred to as “quasi-inert”(Feldmann and Krupp, 2011), “not classifiable as to their carcinogenicity to humans” (along with other organic forms) (EFSA 2014), “fail to show any toxic effects” (Irvin and Irgolic, 1988) and represents the “end point of the As cycle in the marine ecosystem” (Cullen and Reimer, 1989). Sometimes referred to as “fish arsenic” due to its abundant presence in fish, As_{Bet} is found in seaweeds, albeit only in minor concentrations (0.045–0.49 ppm) (Khan et al. 2015).

Arsenobetaine is rapidly excreted, essentially eliminated unchanged from the body within 3 or 4 days (Vahter et al. 1983) without forming any toxic secondary derivatives (Kaise et al. 1985). There is some more recent evidence to suggest, however, that As_{Bet} may be stored in the human body and released over time. For instance, studies have shown that following ingestion of a single test meal of seafood (including cod, salmon and mussel), total urinary excretion of As_{Bet} was greater than the amount ingested, suggesting the endogenous formation of As_{Bet} from either methylated As or inorganic forms (Molin et al. 2012). Further studies have reported As_{Bet} accumulation in humans after daily repeated exposure of As_{Bet} over a 2-week period (Molin et al. 2015). Arsenobetaine retention has also been documented in rabbits (Vahter et al. 1983). There is a requirement for further research into the toxicological significance of arsenobetaine retention in humans.

4.7 The bioaccessible fraction of arsenic in seaweed

Bioaccessibility relates to the fraction of As, which is soluble in the GI tract and freely available for intestinal absorption once ingested (Laparra et al. 2003, Almela et al. 2005). Seaweed arsenicals have a high bioaccessibility, meaning that they are easily and readily taken up by humans, with the bioaccessible fraction ranging from 63% to 81% (Koch et al. 2007) or 43% to 83% (Brandon et al. 2014). However, there are conflicting data relating to which form is more readily available (Lopez et al. 2018).

It is critical to define the bioaccessible fraction of As in seaweed to accurately define the toxicological effects on humans (Intawongse et al. 2018), and the relative As form present plays a key role in bioaccessibility. An array of external factors govern the bioaccessibility of As in seaweed, including the seaweed matrix in which the arsenicals are found (Moreda-Piñeiro et al. 2011), whether the seaweeds are eaten fresh or cooked (Laparra et al. 2004) and the ability of digestive enzymes to release As into the gut (Laparra et al. 2003).

Taxa also play an important role in As solubility (Garcia-Sartal et al. 2012). Due to structural and morphological differences among the taxa, the bioaccessibility of As_T is much higher in both the Phaeophyceae (43–83%) and the Rhodophyta (80%), in comparison to the Chlorophyta (32%) (Koch et al. 2007).

4.8 Health concerns of As in seaweeds

Many authors have reported on the range of As contents and forms present in a host of commercially important edible seaweeds (Smitha et al. 2010, Mouritsen et al. 2013, Roleda et al. 2019). Arsenic present in edible seaweeds, as with many marine organisms, is present usually in organic forms (Kaise et al. 1988, Fattorini et al. 2004), generally accounting for approximately 90% of the As_T fraction present in seaweeds (Díaz et al. 2012). For example, the As present in *L. hyperborea*, a favourite edible seaweed consumed in many Eastern dishes, is 97% present in its organic form (Lunde 1970). When consumed in a "normal" way (as per producers instructions), seaweeds should not deliver toxic a toxic response as a result of their consumption, and, to date, there have been no reported incidents of ${}_iAs$ poisoning resulting from consumption of seaweed (Zhao et al. 2014).

It is essential that the concentrations of As present in seaweeds for sale for direct human consumption be routinely monitored and maintained as low as possible, paying particular attention to the As forms present. However, some justified concern exists due to the presence of elevated As levels in some popularly consumed species, which may pose a toxicological threat to consumers, particularly those who regularly include large amounts of seaweeds in their diets (Borak and Hosgood, 2007). The elevated As concentrations of seaweed combined with a high dietary intake of seaweeds could result in the increased dietary intake of As due to food chain transfer (Rose et al. 2007). Considering the known toxicological effects of elevated levels of dietary ${}_iAs$, there remains a paucity of consumption data for seaweeds globally, barring Japan (Matsumura 2001, Nagataki 2008).

4.9 Consumption of seaweeds and species of particular concern

Although the consumption of edible seaweeds is considered safe and not likely to constitute a hazard to human health (Khan et al. 2015), attention has been drawn to some species (e.g., *S. fusiforme*, *L. digitata*, *Stephanocystis* spp.) as a particular potential concern to public health as a result of their elevated ${}_iAs$ contents.

In Asia, seaweed consumption has been a habitual practice since ancient times (Mouritsen et al. 2013), with Japanese daily per capita consumption of seaweed of 4–12 g (Zava and Zava, 2011). There are 21 species of *Kaiso* (or seaweed) commonly used in everyday cooking (Indergaard 1983). Seaweeds are readily available and easily harvested in the wild and require little to no processing post-harvesting, mainly drying

(Nisizawa et al. 1987). Their inclusion in Asian diets continues to play a basic role in household nutrition (Hwang et al. 2010).

The pattern of seaweed consumption in Western countries differs from that of the East, where seaweeds commercially exploited for use as phycocolloids has historically been the main industry, having first commercialised agar, alginate and furcellaran (Guiry and Morrison, 2013). Species such as Irish moss (*Mastocarpus stellatus* and *Chondrus crispus*) continue to be widely used as food additives due to their stabilising and thickening properties (Mathieson et al. 1984, Lee et al. 2017) and are used in the production of an astounding variety of edible human products including creams, cheeses, toothpaste, etc. (Abowei and Ezekiel, 2013). More recently, a market trend towards “organic” and “natural products”, or in the development of the “functional food” market (Reis and Duarte, 2018), has resulted in increased consumption patterns of seaweeds by a more health-conscious Western palate. Seaweeds are now commonly available in Western stores, either in health food stores, markets or supermarkets, available both fresh and dry and packaged either as whole or partial ingredients in products (Bouga and Combet, 2015, Hafting et al. 2015, Kulawik et al. 2018).

4.10 Effects of seaweed processing on As speciation

In order to preserve the integrity of the seaweed product, manufacturers may employ an array of preservation methods. The various treatments used to prepare seaweed may impact the arsenicals present, thereby altering the toxicological risk with respect to the product as sold (Almela et al. 2005).

Although As present in seaweeds has been shown to be stable at room temperature (García-Salgado and Quijano, 2014), they have long been known to be easily susceptible to deterioration (Jensen 1969). Arsenicals are highly reactive to light intensity (Yadav et al. 2014), temperature and pH (Conklin et al. 2008) and a whole host of other environmental influences (Wang 2002, Lockwood et al. 2014) are shown to affect the stability of a number of common As forms present in seaweed. As such, a variety of preservation techniques such as drying, freezing, pickling and fermentation are commonly employed to maintain the material's integrity (Hafting et al. 2015). While no single universal storage or treatment technique exists for all seaweed species (Pell et al.

2013), the manner in which the products are maintained, be it fresh or dry, lyophilised or kept at room temperature, has a potentially significant impact on the arsenicals present and impact on As stability in the finished product when consumed (García Sartal et al. 2012, Mania et al. 2015).

While some seaweed species such as *Ulva* (sea lettuce) and *Chaetomorpha* sp. are commonly eaten fresh, and a great deal more due to the popularity of new fashionable cuisine trends such as New Nordic Cuisine (Mouritsen et al. 2012), more still are commonly processed before consumption. The most common processing technique employed is simple air drying or sun drying or through the use of specialised drying rooms. The relatively simple processing of seaweeds is mirrored in many different cultures. In Japan, freshly harvested *Porphyra* is chopped, pressed and dried under the warmth of the sun (Pereira 2011), while in the United Kingdom and Ireland, a similar process is generally employed before the consumption of *Palmaria palmata* (*dillisk*), with the delicate fronds either hung up or laid out and dried (Rhatigan 2009).
While the drying process allows for enhanced satiating properties and improves the preservation of the product (although having an impact on the phytochemical constituents in seaweed) (Gupta et al. 2011), the application of heat to seaweeds has been suggested to increase As content (Devesa et al. 2008) with dried seaweed containing higher levels of $_i$As than fresh seaweed (Mania et al. 2015). Once dried, the As present in the seaweeds may transform or be lost (García-Salgado and Quijano, 2014) and with a change in As forms comes a change in consumer risk and the toxicological significance of consuming seaweeds. Therefore, popular seaweed preparation methods, including roasting and toasting, would appear to result in much higher $_i$As content (Almela et al. 2006).

Arsenic forms such as MMA_{III} and DMA_{III} are highly labile (Mass et al. 2001). Even when stored frozen, As are labile and can continue to transform (Devesa et al. 2008). Freezing results in losses of large amounts of As. One study reported that frozen samples of *Ericaria mediterranea* presented had As concentrations 60% lower than frozen samples (Pell et al. 2013). It is the act of defrosting, not freezing, however, which results in significant changes compared with non-frozen products (Pell et al. 2013). Le et al.

(1994) observed losses of 48% due to defrosting, suggesting that the disruption to the algal cell wall integrity (from freezing) results in As compounds leaking out of the cell and being rinsed away in the cooking and/or preparation process.

4.11 Effects of seaweed cooking on As speciation

It is estimated that of the vast number of seaweeds available, around 145 species are known to be directly consumed by humans worldwide (Pereira 2011). The preparation and cooking of seaweeds differ between countries, and depending on cultural preferences, seaweeds may be cooked in several ways, including boiling, roasting or baking before consuming (Mouritsen et al. 2013). The type of cooking method employed may have an influence on As retention in seaweeds. Cooking seaweed in water has been shown to reduce the seaweed AsT content (Ichikawa et al. 2006). Although seaweeds are usually served cold in Japan, they generally undergo some simple preblanching or soaking steps (Hafting et al. 2015). These processing steps have been shown to influence the As content of edible seaweed and can result in a considerable increase or decrease in the actual As content in seaweed meals (Devesa et al. 2008). For example, the traditional cooking of *S. fusiforme* involves a pre-soaking step in which the alga may be soaked in warm water for 20–30 min before consuming. *Sargassum fusiforme* displays some of the highest ${}_{i}$As contents of edible seaweeds (García-Sartal et al. 2013), with ${}_{i}$As concentrations regularly exceeding 60 µg g^{1}. Pre-soaking has been demonstrated to be a highly effective As elimination step, resulting in a 60% reduction in ${}_{i}$As levels (Hanaoka et al. 2001) due to solubilisation of As from the seaweed (Laparra et al. 2003). Despite this, the levels of ${}_{i}$As remaining in *S. fusiforme* even after pre-soaking still possess a toxicological risk to humans if consumed, with 90% of the remaining As present as ${}_{i}$As (Hanaoka et al. 2001).

While some other beneficial elements are also lost through soaking (Katayama and Katayama, 2007), soaking seaweed (*S. fusiforme*) in water prior to consumption can result in As_T reduction of up to 59% (and up to 92% after cooking) (Ichikawa et al. 2006). Biological soaking treatments, such as blanching in warm water for 30 min, have been shown to alter the chemical composition of both *A. esculenta* and *Saccharina latissima* (Stévant et al. 2017), two of the most popularly consumed species globally, yet two species known to contain relatively elevated As_T levels (48 and 79 µg g^1, respectively) (Raab et al. 2013, Maehre et al. 2014).

Meanwhile, boiling with water has been shown to significantly reduce both the As_T and $_iAs$ content in *S. fusiforme* (Laparra et al. 2003). It is important to note the quality of the cooking water as high levels of contaminants in the cooking water could increase the As content of seaweeds through absorption (Morgan 1999). Commercially important edible seaweeds, including kombu, wakame, nori and sea lettuce, have shown reductions in As concentrations of 69%, 50%, 71% and 34%, respectively, after boiling in water following the manufacturer’s instructions (García Sartal et al. 2012). Boiling prompts the release of arsenicals from the seaweed matrix and transfer into the cooking water. Following on from this study, the authors further reinforced that the cooking of kombu, wakame and nori in water promotes the release of As into the cooking water (García-Sartal et al. 2013).

A whole range of popular new products are entering the food market, including “nori chips” and “sea tangle snacks”, and other baked seaweed snacks, as a healthy alternative to traditional potato crisps. Although sure to contain lower levels of fried fats and cholesterol, some products may warrant consumer caution. Nori chips, for example, contain higher levels of nori than sushi (Kulawik et al. 2018) and therefore may be an unknown risk. The main ingredient of sea tangle snacks (*S. japonica*) has a low $_iAs$ content of 0.297µg g^1, though its As_T concentration is in the range 47–53 µg g^1, with arsenosugars being the primary As present. As mentioned earlier, it would not be suitable to characterise As_{Sug} as non-toxic to humans.

There are a few commonly consumed seaweeds, particularly noteworthy due to their $_iAs$ content. For instance, some species of the genus *Stephanocystis*, such as *Stephanocystis osmundacea* (formerly *Cystoseira osmundacea*), which are consumed in Japan, have been shown to have elevated $_iAs$ contents (28.4 µg g^1) (Tokida 1954, Andreae 1978). Some seaweeds of the genus *Sargassum*, for example, *S. fusiforme*, *Sargassum horneri* and *S. fulvellum* though not commonly consumed in the West, are commonly consumed both fresh and dried in Asia and some parts of South America (Yokoi and Konomi, 2012). The Sargasso genus members' propensity for $_iAs$ uptake and accumulation has long been reported (Johnson and Braman, 1975, Watanabe et al. 1979) and subsequently corroborated by more recent research (Yamashita 2014). *Sargassum* does not reduce and methylate As in the same manner as other seaweeds resulting in elevated $_{i}$As tissue levels (Zhao et al. 2014). Some *Sargassum* seaweeds (*S. fusiforme*) can contain As$_{T}$ concentrations of 124 μg g^{1} and extremely high $_{i}$As fractions up to 72% (some 96 μg g^{1}) (Almela et al. 2002). One study even citing concentrations of $_{i}$As from *S. fusiforme* purchased from local Korean markets as high as 88.6% (Ryu et al. 2009). The $_{i}$As level found in *S. fusiforme* may be 25 times that of other Phaeophyceae, 48 times that of Rhodophytes while having a 115-fold higher increase over Chlorophytes (Almela et al. 2006). A cautionary approach when consuming *Sargassum* species may be the best course of action and has resulted in some special safety designations from several countries when consuming this seaweed (discussed below). It is true that, on the one hand, the various methods of preparation and cooking may reduce $_{i}$As concentrations in edible seaweeds, and some methods may also increase the bioaccessibility of $_{i}$As present in seaweed. The bioaccessibility of seaweeds (in this case, some phaeophytes and also nori or species of *Pyropia*) ranges from 43% to 83% (Brandon et al. 2014), although cooking (boiling) has been shown to have a significant impact on increasing the bioaccessibility of $_{i}$As in edible seaweeds compared to uncooked specimens (Laparra et al. 2003). For example, according to Laparra et al. (2004), cooking *Porphyra* sp. results in a significant increase in both the As$_{T}$ and $_{i}$As contents in the bioaccessible fraction of the cooked seaweed with respect to the raw seaweed. Information on As bioaccessibility in both cooked and uncooked seaweed is shown in Table 4.2.

4.12 Seaweed supplements

Both food manufacturers and consumers place a high degree of scrutiny on product quality, particularly amid the justified concern over environmental contaminant spoilage (Phaneuf et al. 1999, García-Rodríguez et al. 2012). Manufacturers and processors of edible seaweed products recognise the economic consequences any toxicological risk would place on seaweed products' saleability (Rubio et al. 2017). Consistently high levels of $_{i}$As in seaweed will limit that species suitability and marketability as a commercial food.

Seaweeds are generally recognised as safe (GRAS) for use as functional foods (Vlachos et al. 2001, Hwang et al. 2010). Many species of seaweed, including *Laminaria*, *Saccharina*, *A. nodosum*, *C. crispus*, *Porphyra* (*Pyropia*), *Ulva*, *Sargassum*, *Gracilaria*, *P. palmata*, and *U. pinnatifida*, are rich in bioactive compounds and therefore show potential to be exploited as products in the functional food market for both human and animal application (Charoensiddhi et al. 2017, Tanna and Mishra, 2018).

Some seaweed species which are not generally consumed directly by humans, such as *Fucus* spp., are commonly used in food supplements, owing to the fact that *Fucus* spp. show anti-inflammatory (Lopes et al. 2014) and anticellulite (pro-collagen production) (Al-Bader et al. 2012) properties, while also being a good source of polyphenols (Béress et al. 1993), fucoidan (Min et al. 2012) and sulphated polysaccharides (showing antioxidant capacity) (Rupérez et al. 2002).

Nonetheless, considering that *F. vesiculosus* has been shown to contain elevated As$_{T}$ contents (50 µg g^{1}) (Almela et al. 2002), further research into seaweed supplements' effects and metabolic breakdown is required. Therefore, the daily intake of seaweed dietary supplements may contribute significantly to $_{i}$As exposure (Hedegaard et al. 2013). Similarly, several kelp species, including *U. pinnatifida* and *S. japonica*, are popularly used as food supplements. Although these species generally contain low levels of $_{i}$As of between 0.15–0.26 µg g^{1} and 0.25–30 µg g^{1} (Almela et al. 2002), respectively, the As$_{T}$ content can be found as high as 70 µg g^{1} (Kaise and Fukuit, 1992) (Table 4.1) which may pose a threat to consumers if consumed in high doses. The individual's dietary habits play a key role in potential As toxicity from seaweeds, particularly those who consume excessive amounts of seaweed. Individuals respond differently to seaweed ingestion (Taylor et al. 2017). Along with the forms of As present and the bioaccessibility of As post-cooking, the individual's metabolism plays a decisive role in As toxicity in humans. There are contrasting and independent associations of As exposure relating to each individual’s metabolism of As (Spratlen et al. 2018) and that the metabolism of the individual is intrinsically important in As metabolism (Feldmann and Krupp, 2011).

Table 4.2 Bioaccessibility (%) of arsenic associated with some common edible seaweeds (pre- and post-cooking)

		Uncooked		**Cooked**	
Phylum/family	**Seaweed species**	**Total As bioaccessible fraction (%)**	**Inorganic As bioaccessible fraction (%)**	**Total As bioaccessible fraction (%)**	**Inorganic As bioaccessible fraction (%)**
Ochrophyta/Sargassaceae	*Sargassum fusiforme*	53–84.3[a,b,c,d]	5–74.7[a,b,d,e e]	7–74.0[a,b,c,e]	20–84.4[a,b,e]
Ochrophyta/Alariaceae	*Undaria pinnatifida*	15–43[c,d,g]	36–90[d]	13.81.07[g]	
Ochrophyta/Laminariaceae	*Laminaria* sp.	706[d]	14–72[d]		
Ochrophyta/Laminariaceae	*Saccharina japonica*	14–83[d,g]	28–52[d]	13.70.8[g]	
Ochrophyta/Fucaceae	*Fucus* sp.	62–79[e,f]	457[e]		
	"Kelp powder"	12.5–69.9[c,e]		27.8–53.8[e]	
Rhodophyta/Bangiaceae	*Porphyra*	67.2–87[b,c,d,h]	30–48.6[b,d]	15.3–106[b,c,g]	72.64.7[b]
Chlorophyta/Ulvaceae	*Ulva*	17.0–32[b,g]	77.23.9[b]	7.4+0.2[g]	
Unclassified	Mixed species (*S. fusiforme*, *Porphyra* sp. and *Enteromorpha* sp. seaweed)	32.0–67.2[e]		65.7–79.9[e]	

References

(a) Laparra et al. (2004)
(b) Laparra et al. (2003)
(c) Almela et al. (2005)
(d) Brandon et al. (2014)
(e) Kim (2014)
(f) Koch et al. (2007)
(g) García-Sartal et al. (2011)
(h) Laird and Chan (2013)

4.13 Global legislation and quality control

The sale of seaweeds for direct human consumption is allowed within the EU and in most countries around the world (Capuzzo and McKie, 2016), although in Bhutan, the Bhutan Agriculture and Food Regulatory Authority (BAFRA) has placed a ban on the sale and import of all forms of seaweeds, citing high $_{i}$As content as the reason for the prohibition (BAFRA 2016).

The EU has set maximum allowable limits for As in food products derived from seaweed used as additives in the food industry (García-Sartal et al. 2013, EU 2015). While elevated As concentrations in popularly consumed seaweed products have long been established, to date, most countries globally have little or no specific regulation whatsoever regarding allowable limits of As in edible algae products for direct human consumption (Rubio et al. 2017, Chen et al. 2018).

Due, in part, to seaweeds naturally high levels of organic arsenicals, the variability as a result of the location of harvest (Larrea-Marín et al. 2010) as well as seasonal changes (Villares et al. 2002, Misheer et al. 2006), differences as a result of the age of the alga (Mouritsen 2013) and the variability observed among species (Riget et al. 1997, Roleda et al. 2019), has resulted in difficulty in setting regulations limiting levels of As in edible seaweeds. The manner in which edible seaweeds are stored and transported before consumption and numerous environmental factors all significantly impact As present in the final product, making it exceptionally difficult for food and health authorities to set appropriate limits. Specific legislation on the As contents of edible seaweeds has been instated only in a few countries. France was the first country in Europe to set specific regulations on the $_{i}$As content of seaweeds intended for human consumption, set at a maximum of 3 µg g^{1} (AFSSA 2009), while at the same time highlighting for its consumers a number of authorised seaweeds deemed safe to consume. In China, a tolerance limit of 0.3 µg g^{1} for $_{i}$As has been set for “foods intended for special dietary uses”, which contain seaweed (FAS 2018). In New Zealand and Australia, the food standards authority has established a limit of 1 µg g^{1} for $_{i}$As in edible seaweed (FSANZ 2013). Following a request from the Norwegian food safety authority (NFSA) on the potential negative health impacts from consumption of seaweed edible products, the

National Institute of Nutrition and Seafood Research (NIFES) reported that Norwegian seaweed, in particular, brown seaweed, may contain elevated levels of As, which may limit their use as a food and feed (Duinker 2014).

Some warranted caution should be advised to consumers towards some well-known hyperaccumulators of ${}_{i}$As, such as *S. fusiforme* (Brandon et al. 2014). In some countries, the consumption of this species has been warned against. In Canada in 2001, the Canadian Food Inspection Agency (CFIA) issued warnings to its citizens around the consumption of *S. fusiforme* (CFIA 2012). Following this, the UK Food Standards Agency (FSA) issued a warning about *S. fusiforme* consumption due to elevated ${}_{i}$As levels (FSA 2004, FSA 2010). Similarly, the European Commission, the Food Standards Australia-New Zealand (FSANZ), and the Hong Kong Centre for Food Safety (CFS) (EC 2004, CFS 2011, FSANZ 2013) have all warned against consumption of *S. fusiforme*. In Japan, the government has anecdotally advised not to consume “too much” *S. fusiforme* (Zhao et al. 2014).

Some existing regulation appears antiquated and unsuitable. For example, in Spain, seaweeds are regulated under the 1978 canned vegetable group legislation (RD 2420/78), setting a maximum allowable level of As in edible seaweeds of 1 µg g^{1} (Rubio et al. 2017). Considering the known high levels of As$_{O}$ in most edible seaweed products, this regulation is seen as restrictive and inappropriate (Almela et al. 2006).

It is important to include various edible seaweeds with concerning levels of arsenicals in the guidelines for consumer protection (Almela et al. 2006). Following limits for the presence of ${}_{i}$As in apple juice of 10 parts per billion (ppb) (FDA 2013) and future limits in infant rice cereal of 100 ppb (CFSAN 2016), the introduction of regulations pertaining to the allowable limits of ${}_{i}$As in edible seaweeds seems coherent. It is important going forward that a number of criteria are met, including specific legislation relating to the maximum allowable limits for As in edible seaweed products and the implementation of speciation analysis of seaweed products.

To properly protect the consumer, it is important that a shift towards the monitoring of arsenicals in commonly consumed seaweed as food needs to be implemented. This would be particularly appropriate in new and upcoming markets, such as Europe, Africa, and North America, where seaweed consumption is not a traditional practice but has become more commonplace due to the popularity of eastern dishes, for example, sushi and the consumption of seaweed salads.

4.14 Conclusions

When considering the toxicity of certain seaweed to human health, it is more relevant to focus on the exposure of inorganic arsenic forms. However, the toxicity of new classes of As metabolites such as thiolated arsenicals is yet to be fully elucidated, but it is thought that these particular forms may play important roles in total As metabolism and toxicity. Similarly, much is yet to be fully clarified regarding the formation pathway of methylated As and As_{Sug}.

Considering the low content of bioavailable inorganic arsenates in the majority of edible seaweeds, it appears that the risk to human health due to their consumption, under normal conditions, is potentially negligible. When considering the presence and speciation of As in food products, it is important to not only consider the As form present but also the bioavailability post-cooking and processing and the metabolism of the consumer.

Consumption of certain species, particularly some of the brown seaweeds, e.g., *S. fusiforme, L. digitata,* may lead to increased dietary intake of arsenicals and the possibility of potential health risks in the context of the rise of phycogastronomy.

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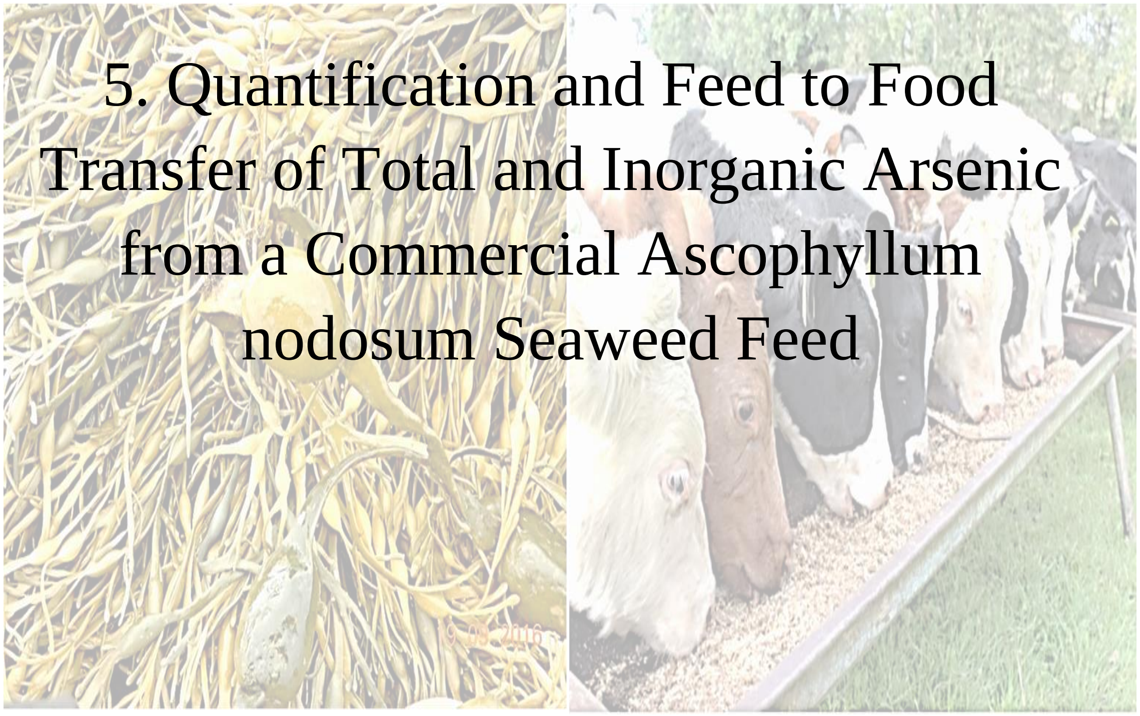

5. Quantification and Feed to Food Transfer of Total and Inorganic Arsenic from a Commercial Ascophyllum nodosum Seaweed Feed

Fig. 5.1 Graphical representation of arsenical pathway from seaweed to human

5.1 Abstract

Seaweed has a long associated history of use as a supplemented livestock feed, providing nutrients and vitamins essential to maintaining animal health. Some seaweed species, particularly the fucoids, are well-known accumulators of the metalloid arsenic (As). Arsenic toxicity to humans is well established even at low exposure levels and is considered a class 1 human carcinogen. As mankind's appetite for livestock produce continues to grow unabated, there is a concern that consumption of livestock produce reared on a diet supplemented with seaweed animal feed (SAF) may pose a threat to the human population due to potentially high levels of As present in seaweed. To address this concern and provide end-users, including industry, consumers, policymakers, and regulators, with information on the exposure associated with As in commercial seaweed animal feed, the estimated daily intake (EDI) of As was calculated to evaluate potential human exposure levels.

Using As data from a commercially available seaweed meal over a five-year period (2012–2017), a population exposure assessment was carried out. A Monte Carlo simulation model was developed to characterise the feed to food transfer of As from animal feed to animal produce such as beef, milk, chicken, and eggs. The model examined initial levels in seaweed, inclusion rate in animal feed, animal feeding rates and potential transfer to food produced from a supplemented diet of SAF. The seaweed animal feed analysis showed that inorganic As was a small fraction of the total As found in seaweed meal (80:1). Statistical analysis found significant differences in the concentration of As in seaweed animal feed depending on the grain size ($p < 0.001$), with higher As concentrations in smaller sized grain fractions. Due to several detoxification steps and subsequent rapid excretion from livestock bodies, a very low carryover rate of As compounds from seaweed animal feed into livestock produce was observed. The EDI calculated in this study for the livestock produce evaluated at the 95th confidence interval was < 0.01% of suggested safe levels of inorganic As intake. The threat to the general population resulting from the consumption of livestock products reared on a diet consisting of SAF is negligible.

5.2 Introduction

Consumption of livestock and livestock produce contributes 12.9% of global calories and 27.9% of global protein through the provision of meat, milk, eggs, and offal (FAO 2011). In response to population growth and subsequent food demand, global livestock production is forecasted to increase by 60–70% by 2050 (UN 2007, Makkar et al. 2015). It is important, therefore, that care is taken in the provision of safe animal feed. The global animal feed market is currently valued at $460 billion and equates to a total annual global production of 980 million tonnes, with 439 million and 184 million tonnes produced for poultry and cattle, respectively (Alltech 2015). The most recent surveys indicate that animal feeds' global production has surpassed 1 billion tonnes (Alltech 2016).

The global seaweed animal feed (SAF) market is worth $11.34 billion annually and accounted for roughly 2.5% of the global animal feeds market in 2016. Conservative estimates of the seaweed industry's current value are US $10.1–16.1 billion, with projections of market growth to reach US $17.6 billion by 2021 (White and Wilson, 2015, Marketsandmarkets 2016). Seaweed animal feed can play an important role in the diet of livestock as it is rich in amino acids, trace elements, antioxidants, and vitamins, while also assisting in nutrient absorption (Rey-Crespo et al. 2014). The brown seaweed *Ascophyllum nodosum* (Linnaeus) Le Jolis is the main algal species used for the production of livestock feed in Europe and North America and is exported globally to markets in Asia, Australia, and South America (Makkar et al. 2015, Mac Monagail et al. 2017).

The benefits of seaweed inclusion in the animal diet are well documented (Brown et al. 2014). However, the production of seaweeds suitable for animal feeds are not without issues; for instance, the uptake of metals from the surrounding water is a phenomenon characteristic of seaweeds (Utomo et al. 2016), and *A. nodosum* has been widely used as a biomonitor of metal contamination in the marine environment (Morrison et al. 2008). Brown seaweeds, in particular, have a tremendous capacity to accumulate As (As being enriched in *Laminaria* species by a factor 200–500 compared with As in terrestrial plant material) (Morrison et al. 2008, Ratcliff et al. 2016). Weathering of As containing rocks liberates inorganic forms of As, namely arsenic trioxide, arsenite, and arsenate, and is considered a major natural source of As distribution in the ocean (Ryan et al. 2015). The most common inorganic arsenic (As_{Inorg}) form in seawater is arsenate, with typical levels of 1.5 µg L^{-1} found (range: 1–2 µg L^{-1}) (Smedley and Kinniburgh, 2002).

Total arsenic (As_{Tot}) is the most commonly recorded As value in the scientific literature. However, having little toxicological significance due to its ill-defined toxicity, it is difficult to draw conclusions from an As_{Tot} value (Petursdottir et al. 2015). Speciation information provides defined information on the potential risks associated with the consumption of certain products. In isolation, As_{Tot} is not an adequate tool to use in the exposure assessment of As, and one cannot infer adequate information on As toxicity and bioavailability as a result. In seaweeds, over 100 major As forms, including organobetaine, organochlorine, and a number of dimethylarsinyl riboside derivatives of organosugars, have been identified (Andrewes et al. 2004, Francesconi 2010, Navas-Acien et al. 2011). Compounds of As vary in toxicity, with inorganic arsenic (As_{Inorg}) considered more toxic than organic forms (As_{Org}) (Brandon et al. 2014). Organoarsenicals present in seaweeds and other marine organisms are loosely considered nontoxic (Niegel and Matysik, 2010). However, the metabolism of arsenosugars in humans is inherently dependent upon the individual's metabolism (Feldmann and Krupp, 2011), and caution should be exercised when considering the toxicity of arsenosugars.

It was important to determine the potential human exposure to As as a result of consuming livestock meat, milk, and eggs as “any risk assessment of undesirable substances in feeds needs to consider the occurrence and exposure for consumers of these animal-derived products” (Dorne and Fink-Gremmels, 2012). Humans are routinely exposed to As in the environment via consumption of food and drinking water (Hughes et al. 2011, Morrison et al. 2016, Davis et al. 2017, McGrory et al. 2017, Monrad et al. 2017). Debate and ambiguity, however, surrounds the determination of acceptable exposure levels for various As compounds (Gentry et al. 2014). Inorganic arsenic is categorised as a Group A human carcinogen by the United States Environmental Protection Agency (USEPA) and a Class 1 carcinogen by the

International Agency for Research on Cancer (IARC) (Straif et al. 2009). The strong affinity for As uptake, coupled with the perennial growth of fucoids, may result in its accumulation at elevated concentrations, proving potentially hazardous to human health (Hwang et al. 2010). Limits on As_{Inorg} in seaweeds for human consumption vary globally. In France, the maximum allowable level of As_{Inorg} in food is < 3.0 μg g^{-1}, while in Australia and New Zealand, a limit of 1 μg g^{-1} is in place (Mabeau and Fleurence, 1993, ANZFA 2013). In animal feed, the maximum allowable concentration under European regulations is set at 40 μg g^{-1} for As_{Tot} and 2 μg g^{-1} for As_{Inorg} (Commission Regulation (EU) 2015/186) (EU 2015). Historical incidences of mycotoxin (*Fusarium*) contamination of animal feeds (Coffey et al. 2009) has drawn worldwide attention to the animal feeds industry and has resulted in increased scrutiny (Binder et al. 2007, Antonissen et al. 2014, Zachariasova et al. 2014). Although meat (beef and chicken), milk and eggs are widely consumed, to the best of the authors' knowledge, no human exposure assessment or estimation on As in seaweed animal feed has been undertaken. Therefore, this study aims to improve our understanding of the potential human exposure to As associated with livestock consumption (livestock products) raised on *A. nodosum* animal feed. The exposure to As by the studied population from consumption of bovine and poultry produce fed SAF was estimated. A Quantitative Exposure Assessment (QEA) methodology was used to assess the probability and severity of potential As transfer to humans. This exposure assessment will provide end-users, including industry, consumers, policymakers, and regulators, with information on the exposure levels associated with As in commercial seaweed animal feed and evaluate the provision of safe animal feed, addressing seaweed quality issues.

5.3 Theory - ambiguity regarding arsenic toxicity in seaweed

Much of the ambiguity regarding As toxicity in seaweed lies in the pervasiveness of naturally occurring As forms in seaweed, the high number of secondary metabolites and the vast range of toxicities displayed by As. The potential toxicity of As in SAF is a function of the concentration of As in seaweed at the time of harvesting, the inclusion rates of SAF in the diets of livestock, the subsequent transfer of As via human consumption of animal produce and finally, the chemical form As is present in (e.g., trivalent As(III) is the most toxic form of As).

A Provisional Tolerable Weekly Intake (PTWI) is often used to describe contaminants' endpoint that has cumulative properties, such as As (Nabrzyski 2006). In 1988, the Joint FAO/WHO Expert Committee on Food Additives (JECFA) established an initial PTWI value of 15 μg kg^{-1} bw week^{-1} for As$_{\text{Inorg}}$ (equivalent to 2.1 μg kg^{-1} bw day^{-1}; WHO 1988). This initial PTWI was withdrawn by JECFA in 2010, as it was deemed no longer appropriate. In its place, the JECFA proposed a Benchmark Dose Lower Confidence Limit (BMDL01) of 3 μg kg^{-1} bw day^{-1} with an associated range of 2.0–7.0 μg kg^{-1} bw day^{-1}. This BMDL was put forward as the benchmark dose for As$_{\text{Inorg}}$ for a 0.5% increase in cancer incidences of the lung, skin, and bladder (JECFA 2011). The European Food Safety Authority (EFSA) Panel on Contaminants in the Food Chain (CONTAM 2009), which provides scientific advice on contaminants in the food chain, proposed a safe BMDL01 level for As$_{\text{Inorg}}$ of between 0.3 and 8.0 μg kg^{-1} bw day^{-1} (EFSA 2010).

Arsenosugars are thought to be less toxic than As(III) and As(V) (Yu et al. 2015) and possess “limited toxicity” (EFSA 2005). Unlike terrestrial plants whose As forms occur mainly as As$_{\text{Inorg}}$ (particularly arsenite As(III) and arsenate As(V) (Quaghebeur and Rengel, 2005), marine phyta contain a much higher proportion of As$_{\text{Org}}$ (as organosugars, in the form of arsenoribosides) (Jedynak et al. 2009). As such, it was recommended by JECFA to consider As forms in seaweed differently to those found in terrestrial plants. Evidence to suggest a link between As$_{\text{Org}}$ in food and the adverse human toxicological effect appears scarce (e.g., Woods 1999, Trumbo et al. 2001, Uneyama et al. 2007, EFSA 2010). JECFA has reported no ill health effects from populations who routinely consume high levels of As_{Org} directly from their diet (> 50 μg kg^{-1} bw day^{-1}). Considering this, a $BMDL_{01}$ has not been set for As_{Org}. Nevertheless, some caution should be taken as some As_{Org} forms (i.e., monomethylarsonic) are thought to be a precursor of As_{Inorg} exposure through different demethylation processes (Feldmann et al. 2000). As such, arsenosugars should not be considered as having no potential for toxicity.

5.4 Materials and methods

5.4.1 Seaweed animal feed (SAF)

For this study's purpose, any reference made to beef, poultry, milk, or eggs refers to those commodities, which have been produced from a diet consisting of SAF. Figure 5.2 highlights the basic transport route of As into humans from SAF.

The data used in this study originated from the monthly monitoring and testing of total and inorganic As in a commercial, internationally available SAF (*A. nodosum*) between January 2012 and February 2017. During this period, total As was determined in 62 feed batches, and inorganic As in 60 batches (As_{Tot} n = 62; As_{Inorg} *n* = 60) in two different grain size fractions of the SAF (Small Grain (SG); 850–250 μg) and Large Grain (LG); 1940–850 μg).

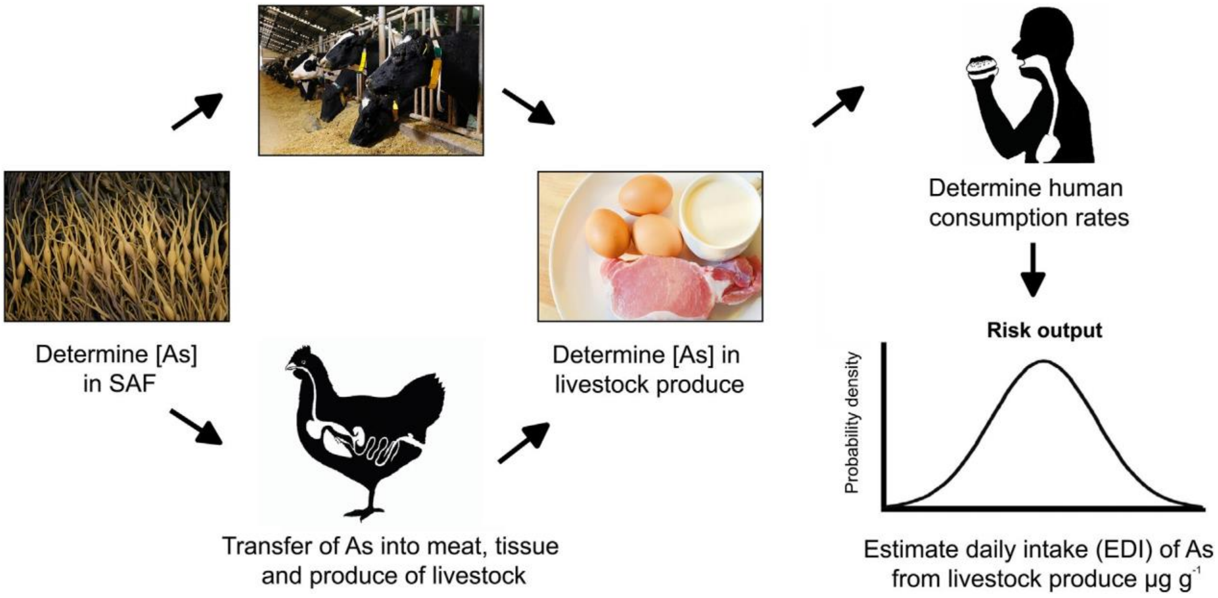

Fig. 5.2 Model schematic used to estimate the daily intake of arsenic from livestock produce consumption

5.4.2 Study area and sample preparation

The location from which *A. nodosum* was harvested for the production of SAF extends from 54° 20′ 58.8732″ N, 9° 48′ 2.592″ W to 53° 11′ 50.3772″ N, 8° 59′ 25.7244″ W over a 1000 km stretch of the Atlantic coastline of Ireland. The intertidal lithologies from these harvesting areas comprise igneous, sedimentary, and metamorphic bedrock types (Hepworth Holland and Sanders, 2009, Morrison et al. 2009, Guiry and Morrison, 2013). The study area contains a comparatively low human population density with relatively little heavy industry and subsequent low inputs of wastes into the coastal water (Morrison et al. 2008, Morrison et al. 2017, Wilkes et al. 2017).

Harvested *A. nodosum* is dried before being industrially milled via sieving through multiple screens (ranging from < 250 to 1940 μm), where it is processed into animal feed and exported worldwide.

5.4.3 Determination of total and inorganic arsenic

On a monthly basis between 2012 and 2017, dry feed samples (~0.5 kg) of LG-SAF and SG-SAF were collected at random positions from three bags of SAF product from a commercial producer in Ireland. All the samples were analysed in the GAFTA (The

Grain and Feed Trade Association) approved laboratory (TLR, Netherlands) for the determination of organic and inorganic As fulfilling the requirements of the standard NEN-EN-ISO/IEC 17025:2005. A test portion of 0.3 g of dry feed sample was treated with dilute nitric acid (CARLO ERBA, RSSuperpure for trace analysis, Cornaredo, Italy) and hydrogen peroxide (TraceSELECT® Ultra Sigma-Aldrich, USA) in a heated water bath. Hereby, the As forms are extracted into solution and As(III) is oxidized to As(V). The inorganic As is selectively separated from other As compounds using anion-exchange high-performance liquid chromatography (HPLC) (Thermo Scientific Dionex UltiMate3000) coupled online to the element-specific detector inductively coupled plasma - mass spectrometry (ICP-MS) (Thermo Scientific X Series II) for the determination of the mass fraction of inorganic As. The limit of quantification (LOQ) of the ICP-MS methods are as follows: As_{Tot}, 0.07 μg g−1 (ICP-MS) and As_{Inorg} 0.04 μg g−1 (HPLC-ICP-MS), both based on wet weight of the sample. Trueness and precision of analyses were insured by comparison with certified reference materials (Table 5.1). The measured concentrations of As were within the certified range. Both feed samples and CRMs were analysed for both inorganic and organic As. Any samples below the LOD were taken as equal to 0 μg g^{-1}. For total As in SAF, the solution, obtained by pressure digestion (ISO 13805) (CEM, MARS 6, USA), was nebulised and the aerosol transferred to a high frequency inductively coupled plasma mass spectrometer (ICP-MS). TLR uses The European Standard (EN 15763) for the determination of As in foodstuff and another method for feed which is based on EN 15763.

Table 5.1 Determination of arsenic forms in the Certified Reference Materials (CRMs) of CRM 7405a (*Hijiki*) (National Metrology Institute of Japan [NMIJ]) using HPLC-ICP-MS [μg g^{-1}]

Element	**Certified value (+SD)**	**Observed this study (+SD)**	**Recovery (%)**
As_{Tot}	35.8 ± 0.9	35.7 ± 0.9	99.7
AsIII	10.1 ± 0.05	10.2 ± 0.04	101.1

5.4.4 Data input; level of arsenic in seaweed animal feed

A summary of model inputs for estimating daily intake of As is shown in Table 5.2. To model the concentration of As_{Tot} in SAF (As_{Con}), a best-fit distribution was applied to the monitoring data (Supplementary information (SI) Appendix A; Table S1), resulting in a lognormal distribution (mean 27.87 µg g^{-1}, Standard deviation 4.99 µg g^{-1}). A Pearson distribution with alpha equal to 6.87 µg g^{-1} (shape parameter) and scale parameter beta equal to 3.23 µg g^{-1} was used to model the concentration of $As_{Inorg,}$ also based on a best-fit to monitored data (Appendix A; Table S1). Information on As concentrations in SAF are summarised in Appendix A; Figs. S1 and S2. Both figures represent the uncertainty in the levels of As in SAF and illustrate the spread of all possible concentration values based on monitoring data.

5.4.5 Data input; inclusion and feeding rates

The inclusion rate (Ir) of SAF into feed was determined from manufacturer's guidelines and are presented in Table 5.3, while information on livestock feed rates (Fr) were taken from published literature (Table 5.4).

Table 5.2 Model inputs for estimating daily intake of arsenic

Model input			Units	Reference
Seaweed animal feed	Concentration of arsenic in SAF	As_{Con}	Concentration of X or Y^{a}	Figs. S1 and S2
	SAF inclusion rate in feed	Ir	As per manufacturers guidelines	Table 5.3
	Livestock feeding rate	Fr	Feeding rate based on A, B, C, D^{a} recommendations	Table 5.4
	Level of arsenic present in total feed	Lf	$As_{Con} \times Ir$	
	Arsenic concentration in ingested feed	$Feed_{Con}$		
Biotransfer	Biotransfer factor	BTF	Species dependent	Table 5.5
	Arsenic concentration in livestock produce	LS_{As}	$Lf \times Fr$	
Human exposure	Human intake of livestock produce	HI	Based on literature	Table S3
	Body weight	BW	Based on literature	
	Exposure	EXP	$LS_{As} \times HI$	
	Estimated daily intake	EDI	$EXP \div BW$	Tables 5.6a and 5.6b

[a] Where X = As_{Tot} and Y = As_{Inorg}, A = poultry. B = eggs. C = beef. D = milk.

Table 5.3 Inclusion rate of seaweed animal feed into livestock diets and total feed of livestock

	Poultry	**Eggs**	**Beef**	**Milk**	**Units**	**References**
Recommended inclusion rate (Ir) of SAF into feed	2.5[a,1]	–	100–120[b,1]	120–150[c,1]	g/day	(1) http://www.arramara.ie/
Inclusion rate (Ir)	0.025	0.025	0.105	0.125	$kg_{seaweed}$/ kg_{feed}	As per manufacturer guidelines
Fr (feeding rate)	0.11	0.11	18–20	18–20	kg_{feed}/day	As per manufacturer guidelines

[a] Recommended feeding rate 25 kg per tonne of meal.

[b] Recommended 100–120 g per day beef cows.

[c] Recommended 120–150 g per day dairy cow

Table 5.4 Livestock feeding inputs

Livestock	Recommended total feed per day	Units
Chicken	0.113[1]	kg feed day^{-1}
	027[2]	kg feed day^{-1}
	0.125[2]	kg feed day^{-1}
	0.04[3]	kg feed day^{-1}
	0.13[3]	kg feed day^{-1}
Beef cow	6.75–15.75[4]	kg feed day^{-1}
	4.8–14.1[5,2]	kg feed day^{-1}
	6.1–17.5[6]	kg feed day^{-1}
	12.2[6]	kg feed day^{-1}
	6.9[7]	kg feed day^{-1}
	8.4–12.3[7]	kg feed day^{-1}
	8.0[7]	kg feed day^{-1}
Dairy cow	16.0–18.0[4]	kg dm day^{-1}
	0.4–15.5[5]	kg feed day^{-1}
	15.0–25.0[6]	kg feed day^{-1}
	16.9[6]	kg feed day^{-1}
	6.5[7]	kg feed day^{-1}
	11.2[7]	kg feed day^{-1}
	15.9[7]	kg feed day^{-1}
	16.0[7]	kg feed day^{-1}
Reference	(1) Jacob and Pescatore (2012) (2) NRC (1966) (3) Wiseman (1987) (4) Kavanagh (2015) (5) Hickox (2000) (6) McKone and Ryan (1989) (7) Agricultural Research Council (1965)	

5.4.6 Data input; biotransfer factors

It was possible to utilise a biotransfer factor (BTF) to estimate the transfer of As from feed to both beef and poultry meat and their co-products (Table 5.5). Biotransfer factors are defined as the ratio of the concentration of a chemical in animal tissues such as beef, poultry, milk, or eggs, to the animal's daily intake of that chemical (Dowdy et al. 1996). The carry-over rate or BTF of potentially toxic substances to livestock produce is determined via specific toxicokinetic limitations of mammalian and poultry meat (and their by-products). These specific limitations are dependent upon the absorption, distribution, metabolism, excretion rate and eventual metabolites of As once ingested (Dorne and Fink-Gremmels, 2012, Lopez-Alonso 2000). The use of BTFs is a widely used and accepted method of estimating chemical transfer from contaminated vegetation into agricultural food products (USEPA 2005). Information on the model distributions are summarised in Appendix A; Table S2 and are based on empirical data. In this study, a best-fit distribution model was applied to assess human exposure to As from the consumption of livestock produce. Although the absorption of As_{Org} and As_{Inorg} in the gastrointestinal tract of animals is variable but shown to be high (40–100% for As_{Org} and 60–100% for As_{Inorg}) (Hopenhayn-Rich et al. 1993, NRC 2005, Nabrzyski 2006, Vitousek et al. 2008), for the purpose of this study, it was assumed the bioavailability of As in livestock produce to humans was 100%.

5.4.7 Data input; human dietary intake

To assess the potential human dietary exposure to As, human dietary consumption data (kg day^{-1}) must be combined with occurrence data (i.e., As concentration in food) (Dorne et al. 2009). The dietary exposure to As is a consequence of the type and abundance of food consumed, and consumption estimates were used to determine the exposure levels to humans. A Lognormal distribution was used to characterise the consumption of different food produce based on national consumptive data from the Irish Universities Nutrition Alliance (IUNA 2001, IUNA 2011) (Appendix A; Table S3).

Table 5.5 Reported biotransfer factors used in this study

	Poultry BTF	**Egg BTF**	**Beef BTF**	**Milk BTF**
	0.02[5]	0.26[3]	0.002[9]	0.00011[1]
	0.83[3]	0.07[5]	0.002[3]	0.0009[2]
	0.03[5]	0.46[7]	0.002[5]	0.00006[3]
	0.002[6]	0.002[13]	0.0024[10]	0.00018[4]
	0.00147[15]	0.000842[15]	0.0024[11]	0.0002[4]
			0.00028[12]	0.000093[4]
			0.00136[7]	0.000052[4]
			0.0017[5]	0.000044[4]
			0.002[14]	0.00005[5]
			0.002[15]	0.00071[5]
				0.00057[2]
				0.000063[2]
				0.000062[6]
				0.00019[1]
				0.0001[7]
				0.00022[1]
				0.00016[1] 0.00014[1]
				0.00067[1]
				0.000368[8]
				0.000555[8]
				0.006[9]
				0.000062[13]
Transfer factor	Min 0.001 Max 0.83	Min 0.0008 Max 0.46	0.00085	1.46652E−05
Reference	(1) Rosas et al. (1999) (2) Stevens (1991) (3) Staven et al. (2003) (4) Pérez-Carrera and Fernández-Cirelli (2005) (5) Technical Support Document (2012) (6) Hickox (2000) (7) Cornelis et al. (2016) (8) Beni et al. (2008) (9) EPA (1998) (10) Vreman et al. (1986) (11) Ham et al. (1949) (12) Bruce et al. (2003) (13) Bureau of Land Management (1997) (14) Secil (2007) (15) Durham and York Waste (2007)			

5.4.8 Data input; bodyweight of cattle and humans

According to the Department of Agriculture, Food, and the Marine (DAFM 2015), the reported body weights of both Irish dairy cows and of beef cattle ranged from 205 kg to 527 kg for adult dairy cows and from 241 kg to 537 kg for adult beef cattle (average of summer and winter weights; type of diet not listed). These weights were used to determine the average feed requirements of cows. For human adult weight estimation, a Lognormal distribution was used, with a mean of 81 kg ± 13.1 kg based on dietary information from IUNA (2001).

5.4.9 Statistical analysis

A paired t-test was performed to assess differences in total and inorganic As concentration between the two grain sizes used for SAF. Statistical analyses were performed using the software R version 3.2.1 (R Development Core Team, 2017). In all statistical analyses, significance was set at *p*-value < 0.05 probability.

5.4.10 Model simulation

A Monte Carlo simulation model was developed to assess the estimated daily intake (EDI) of As by human adults. Monte Carlo simulation is a statistical model, which selects random values from distributions to produce multiple random scenarios of a problem while accounting for the natural uncertainty and variability in the input data (Schuhmacher et al. 2001). From the generated output, it is possible to produce a probability distribution using multiple scenarios of a problem. To develop the exposure model, the @RISK, version 4.0 (Palisade, USA), in combination with Microsoft Excel 2016 (Microsoft, USA), was used to run the simulation. The model was run for 10,000 iterations reflecting the high variability in the transfer of As to livestock products, including the inherent differences in human and animal consumption practices. The estimated level of As in livestock produce (Appendix A; Table S4) and the probability of human exposure to As (Tables 5.6a and 5.6b) were outputs of the mathematical exposure model.

5.5 Results and discussion

5.5.1 Arsenic concentration in seaweed animal feed

Statistical analysis revealed higher levels of both As_{Tot} (t-value = 6.907; p-value < 0.001) and As_{Inorg} (t-value = 5.236; p-value < 0.001) in smaller grain size fractions of the SAF (Fig. 5.3). In the larger grain size (LG-SAF), the As_{Tot} concentrations ranged from 31.1–49.1 µg g^{-1} for LG-SAF (mean 38.8 µg g^{-1}), while a concentration range of 33.8–56.3 µg g^{-1} (mean 43.1 µg g^{-1}) was observed for SG-SAF (Appendix A; Table S5). A similar trend was observed for As_{Inorg} concentrations with LG-SAF displaying an As_{Inorg} range of 0.1–1.3 µg g^{-1}, while for SG-SAF, the range was 0.1–1.4 µg g^{-1}.

These results showed that As_{Inorg} is a minor constituent of the overall As_{Tot} in SAF, which are in agreement with findings reported by the Biancarosa et al. (2017) and Morrison et al. (2014), who report the level of As_{Inorg} in feed grade *A. nodosum* to be in the range 0.1–2.4 µg g^{-1} and ~0.2 µg g^{-1}, respectively. Similarly, levels of As_{Tot} in this study (31.1–56.3 µg g^{-1}) were in the range of values published by Biancarosa et al. (2017) (Phaeophyceae; 28–107 µg g^{-1} dw) and Lunde (1970) and Morrison et al. (2014) (22–53.4 µg g^{-1}), for *A. nodosum* from Norway and Ireland.

The reasons for the higher As concentrations in the SG-SAF are not clear and may be related to a methodological bias. It is possible that the size of SG-SAF could improve the efficiency of metal extraction during the acid digestion stage of the sample processing due to the higher surface/volume ratio compared with the LG-SAF. Considering As_{Tot} concentrations are close to the European Limit of 40 µg g^{-1}, this could have important implications for SAF producers.

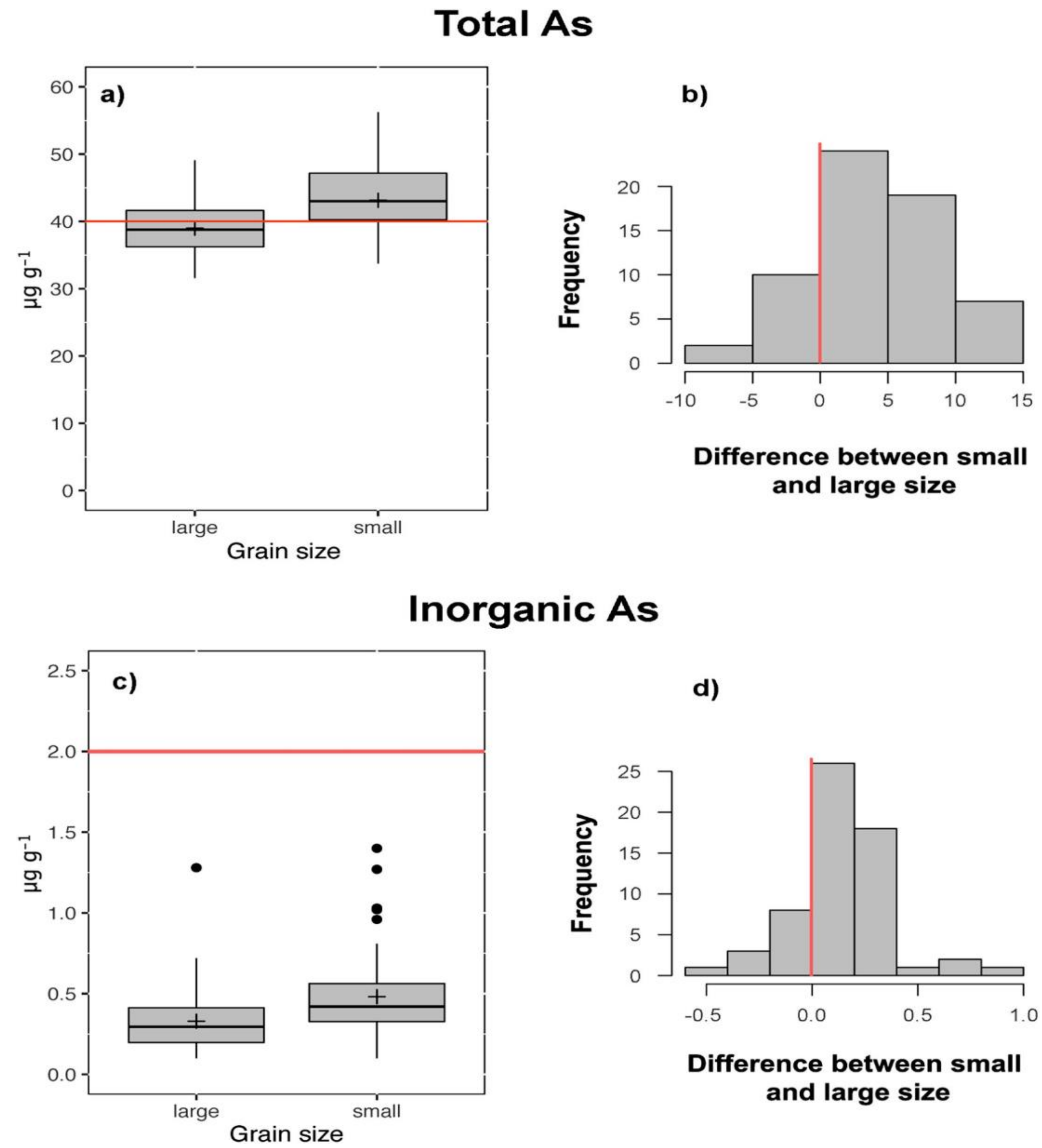

Fig. 5.3 Box plots for the total (a) (n=124) and inorganic (c) (n=120) arsenic concentrations of *Ascophyllum nodosum* seaweed animal feed according to grain size (*n* = X). Histograms showing the distribution of the difference between the small and large size for total (b) and inorganic (d) arsenic concentrations. Box plots indicate the median (bold line near the centre), the first and third quartile (the box), the mean (the cross), the extreme values whose distance from the box is at most 1.5 times the interquartile range (whiskers), and remaining outliers (dark dots). Legal limits are indicated by a horizontal red line in the box plot, and no differences (0) is indicated by a vertical red line in histograms. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article)

5.5.2 Livestock contribution to arsenic daily intake

Our results indicated that the concentration of As in livestock produce is low (Appendix A; Table S4) and, in general, agrees with previous studies (see below). Once both poultry and cattle ingest SAF, As_{Inorg} is readily transported to the liver, spleen, kidneys, and lungs (Erry et al. 2005) before being translocated to keratin-rich endpoints such as nails, hair, and eggshells (Shen et al. 2013). Biotransformation of As_{Inorg} initially reduces As(V) to the more toxic As(III) forms. Then As_{Inorg} is enzymatically methylated to methyl arsenic (MA) and subsequently dimethyl arsenic (DMA) metabolites (Ventura-Lima et al. 2011). The As_{Inorg} is excreted primarily as these metabolites (Hughes et al. 2011). Although As_{Org} is considered much less toxic than As_{Inorg} forms, methylated As_{Org} forms such as DMA and MA show intermediate acute toxicity, being classed as Group 2B "possibly carcinogenic to humans" (evidence from animal studies) (Hedegaard and Sloth, 2011, Cullen and Reimer, 2017). Once *corporis*, these metabolites are excreted mainly in the urine (Hopenhayn-Rich et al. 1993, Lopez-Alonso 2012, Mendez et al. 2016). Forms of As_{Org} are thought to be less extensively metabolised than As_{Inorg} and more rapidly excreted (Woods 1999). This detoxification step and subsequent rapid excretion results in a very low carryover rate of As compounds from SAF into the edible tissue of poultry and cattle (EFSA 2005).

Contrasting results were found by Feldmann et al. (2000) from seaweed-eating sheep of the Orkney Islands, which showed that appreciable concentrations of arsenosugars accumulated in the wool, blood, muscle, and kidneys. Bioaccumulation of As is a result of the differences between intake and excretion. In the case of intake, sheep from the Orkney Islands consumed ~4 kg of seaweed a day, mainly *Laminaria* spp., at a rate 40× higher than that of cattle in our study (~120 g). Moreover, the initial concentration of As_{Tot} in *Laminaria* is also > 2× that of *A. nodosum*. In the case of excretion, differences between poultry, cattle, and sheep are also expected. The known higher consumption rate of seaweed by sheep from the Feldmann et al. (2000) study, coupled with the unknown differences in excretion rates from sheep compared to cattle, may explain the results of the two studies. The authors of the present study wish to stress that it is important to follow producer guidelines regarding daily inclusion rates of SAF in livestock diets.

The cumulative EDI of As_{Tot} calculated in this study from consumption of poultry, eggs, beef, and milk was 0.2 μg kg^{-1} bw day^{-1} (Table 5.6a), whereas the cumulative EDI for As_{Inorg} is 2.3 × 10−3 μg kg^{-1} bw day^{-1} (Table 5.6b). The EDI calculated in this study for all livestock produced at the 95th percentile was < 0.01% of the $BMDL_{01}$ for As_{Inorg}. It was concluded that consumption of poultry, eggs, beef, and milk from livestock products fed a diet containing SAF results in a low transfer of As to humans, well below the considered safe limit suggested by CONTAM (EFSA 2010).

To date, few studies have directly quantified the potential for As transfer in humans as a result of the intake of products from livestock fed diets containing seaweed meal. Although the risks to human health due to the consumption of contaminated livestock is yet to be fully understood, this study has shown that the potential for transfer of As into the meat of livestock and the produce of these animals is extremely low. The range of intakes calculated in this study is well below the $BMDL_{01}$ range suggested by both JECFA and CONTAM. However, it should be noted that humans may be routinely exposed to As from several environmental sources, both natural and anthropogenic, and may be ingested in a number of ways. These environmental sources may contribute to the cumulative load of As in human diets and should be considered when estimating total As dietary intake by humans.

5.5.3 Chicken and eggs

As a result of chicken consumption, As_{Tot} intake distribution was in the range of 0.00–0.04 μg kg^{-1} bw day^{-1} (90% confidence) with a mean EDI of 0.01 μg kg^{-1} bw day^{-1} (Fig. 5.4a). The resulting As_{Inorg} intake distribution was in the range 0.00–4 × 10−4 μg kg^{-1} bw day^{-1} (90% confidence) with a mean EDI of 1 × 10−4 μg kg^{-1} bw day^{-1} (Fig. 5.5a). As a result of egg consumption, As_{Tot} intake distribution was in the range 0.00–2 × 10^{-4} μg kg^{-1} bw day^{-1} (90% confidence) with a mean EDI of 0.01 μg kg^{-1} bw day^{-1} (Fig. 5.4b). The resulting As_{Inorg} intake distribution was in the range 0.00–2 × 10^{-4} μg kg^{-1} bw day^{-1} (90% confidence) with a mean EDI of 1 × 10^{-4} μg kg^{-1} bw day^{-1} (Fig. 5.5b), equating to 0.003–0.005% of the JECFA and EFSA proposed BMDL for As_{Inorg}.

Important differences were found in the EDI and As concentration in chicken meat when compared with previous studies (FDA 1993, Lasky et al. 2004).

Table 5.6a Summary Table of Estimated Daily Intake (EDI) values of total arsenic due to consumption of livestock and livestock products

EDI summary table	**5th**	**Mean**	**95th**	**Units**
Poultry	6.86×10^{-4}	1.30×10^{-2}	4.30×10^{-2}	µg kg^{-1} bw day^{-1} µg
Eggs	2.62×10^{-4}	5.84×10^{-3}	1.96×10^{-2}	kg^{-1} bw day^{-1}
Beef	2.75×10^{-2}	1.23×10^{-1}	2.89×10^{-1}	–
Milk	4.40×10^{-3}	9.62×10^{-2}	3.35×10^{-1}	µg kg ^{1} bw day^{-1} µg
Cumulative exposure		0.23789		kg^{-1} bw day^{-1} µg kg^{-1} bw day^{-1}

Table 5.6b Summary Table of Estimated Daily Intake (EDI) values of inorganic arsenic due to consumption of livestock and livestock products

EDI summary table	**5th**	**Mean**	**95th**	**Units**
Poultry	4.55×10^{-6}	1.29×10^{-4}	4.48×10^{-4}	µg kg^{-1} bw day^{-1} µg
Eggs	1.93×10^{-6}	5.82×10^{-5}	2.16×10^{-4}	kg^{-1} bw day^{-1}
Beef	1.73×10^{-4}	1.22×10^{-3}	3.51×10^{-3}	bw day^{-1} µg kg^{-1} bw
Milk	3.05×10^{-5}	9.32×10^{-4}	3.40×10^{-3}	µg kg ^{1} bw day^{-1} µg
Cumulative exposure		0.00234		kg^{-1} bw day^{-1} µg kg^{-1} bw day^{-1}
Suggested BMDL		0.3–8.0		

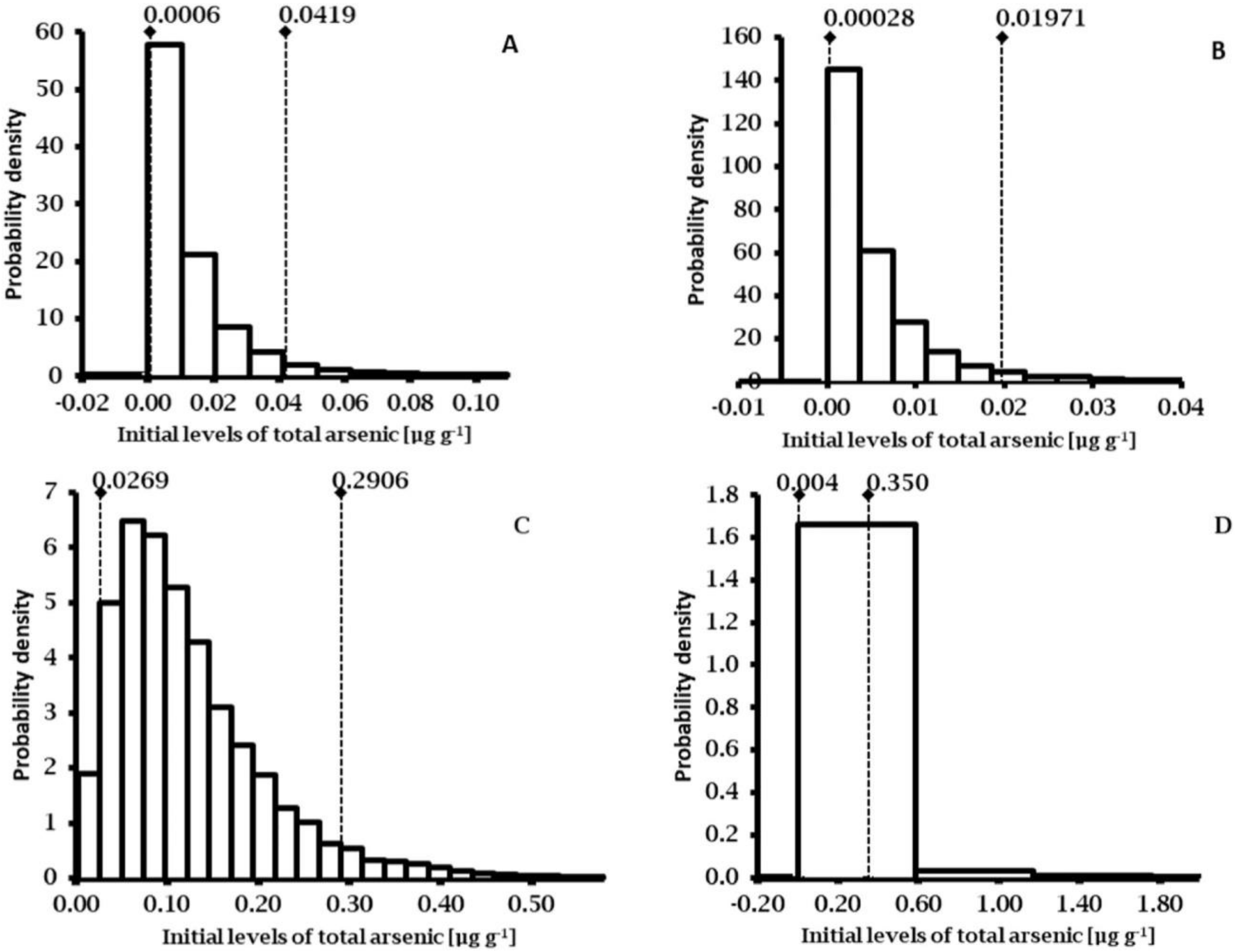

Fig. 5.4 Final exposure output of total arsenic (μg g−1) to humans from A) poultry, B) eggs, C) beef and D) milk

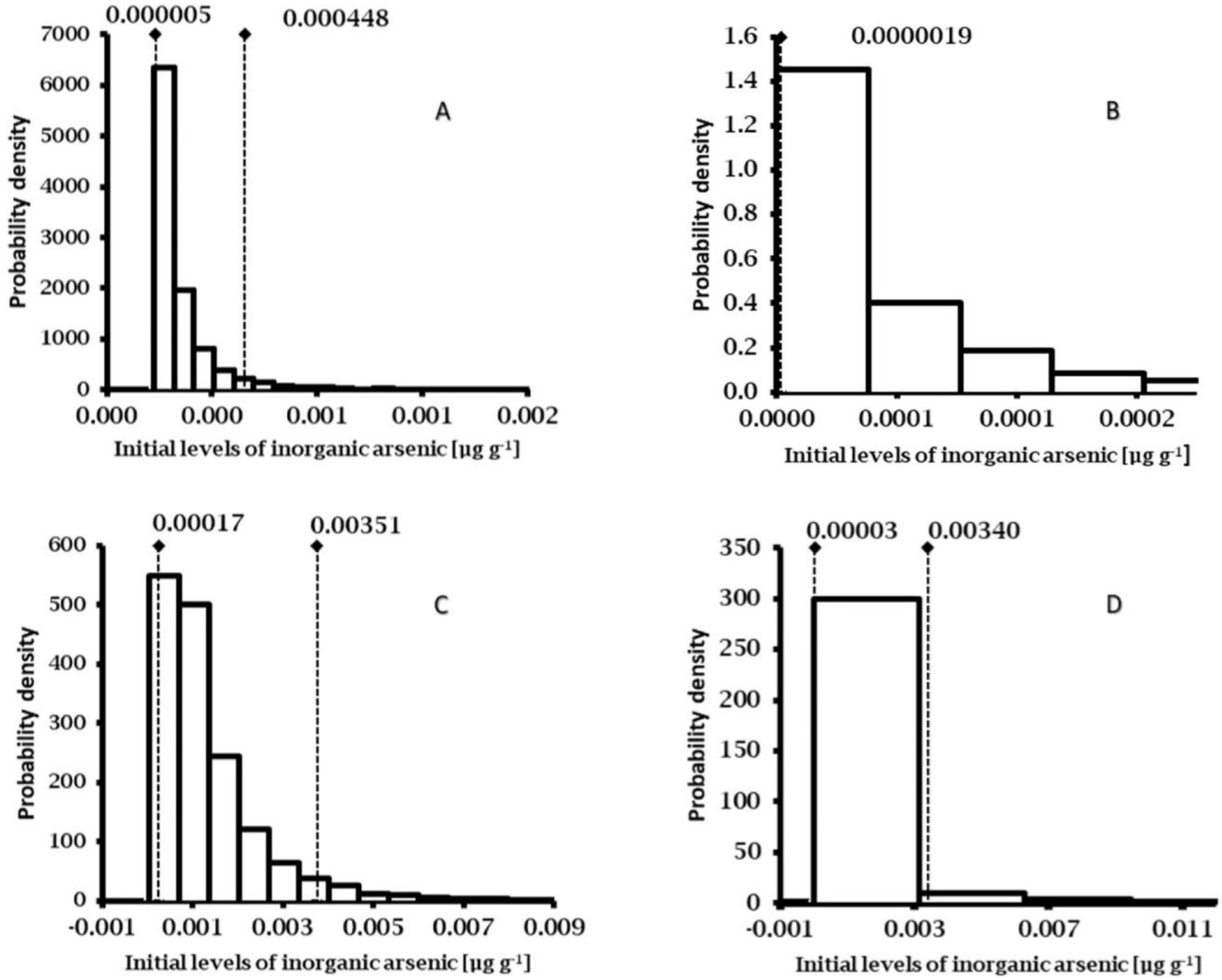

Fig. 5.5 Final exposure output of inorganic arsenic (µg g^{-1}) to humans from A) poultry, B) eggs, C) beef, and D) milk

The obtained EDI for chicken in the present study was much lower than reported As intakes from previous studies (conducted prior to the international prohibition of arsenic-based feed additives, such as roxarsone) using similar consumption rates (0.02–0.07 µg kg^{-1} bw day^{-1} for As_{Tot} and 0.08–0.12 µg kg^{-1} bw day^{-1} for As_{Inorg}, based on a body weight of 70 kg; Lasky et al. 2004). This additive was recently prohibited in many countries (2013–2016), including the EU and North America (Hu et al. 2017), which may explain these differences. Results from the current study suggested that SAF does not contribute appreciably to the final As concentration in chicken meat since As concentration is 0.00015 µg g^{-1}, three orders of magnitude lower than that previously reported by Lasky et al. (2004). Dorne and Fink-Gremmels (2012) have stated that as a result of presystemic and systemic eliminations, the concentration of As that remains present in poultry tissue and eggs is much lower than the original concentration in SAF.

Our results agree with previous studies, which state that the biological transmission of As into the meat and produce of poultry and eggs is unlikely to be high, and foodstuffs from these animals are unlikely to contribute appreciably to any form of human harm (Khalafalla et al. 2011, Ghosh et al. 2012, Mandal 2017).

5.5.4 Beef and milk

Due to the high consumption rates of bovine livestock coupled with cattle's own high dietary requirements, the highest EDIs for As_{Tot} and As_{Inorg} are found in beef. The intake distribution of As_{Tot} was in the range 0.03–0.29 μg kg^{-1} bw day^{-1} (90% confidence) with a mean EDI of 0.1 μg kg^{-1} bw day^{-1} (Fig. 5.4c). In the case of As_{Inorg} intake, the distribution ranged between 0.00 and 3.5×10^{-3} μg kg^{-1} bw day^{-1} (90% confidence) with a mean EDI of 1.2×10^{-3} μg kg^{-1} bw day^{-1} (Fig. 5.5c). Consequently, this results in an approximate intake 0.04–0.06% of the proposed $BMDL_{01}$ for As_{Inorg} (EFSA 2010, JECFA 2011). The resulting distribution model used for milk produced an EDI range of As_{Tot} 0.00–0.35 μg kg^{-1} bw day^{-1} (90% confidence) with a mean EDI of 0.1 μg kg^{-1} bw day^{-1} (Fig. 5.4d). The calculated As_{Inorg} intake distribution was in the range 0.0–3.4 × 10−3 μg kg^{-1} bw day^{-1} (90% confidence) with a mean EDI of 9 × 10−4 μg kg^{-1} bw day^{-1} (Fig. 5.5d). Numerous studies have previously examined the transfer of As into dairy milk and beef, obtaining similar As concentrations to those found in the present study (Vreman et al. 1986, Crout et al. 2004, Pérez-Carrera and Fernández-Cirelli, 2005). According to Lopez-Alonso et al. (2000), As concentrations in beef in some European and North American countries are in the same order of magnitude as those reported here (average range 0.004–0.02 μg g^{-1}; our study 0.002 μg g^{-1}). In the case of milk, Cervera et al. (1994) calculated the As the content of milk to be 0.0001–0.0008 μg g^{-1}, also in agreement with the findings of the present study (0.00035 μg g^{-1}; Appendix A; Table S4). These results suggest that the transfer of As from SAF to milk and beef are negligible and do not contribute substantially to the daily As_{Inorg} BMDL of 3 μg kg^{-1} bw day^{-1} (JECFA 2011), highlighted by a low EDI (Table 5.6b). In this sense, our results of human exposure to As (i.e., EDI) reinforce the idea that “food derived from terrestrial animals contributes only insignificantly to human exposure, due mainly to the low transfer rate of As_{Inorg} to edible tissue of mammals and poultry” as stated by the European Food Safety Authority (EFSA 2005).

5.6 Conclusions

Over the 5-year study, both As_{Tot} and As_{Inorg} concentrations were predominately significantly higher in the finer grade *A. nodosum* animal feed. In addition, As_{Tot} levels from finer grade *A. nodosum* animal feed were also predominately at or above the limit of 40 $\mu g\ g^{-1}$ set under EC Regulation 2015/186 (EU 2015). In general, As_{Tot} concentrations in the larger grade material were below the regulated limit ($< 40\ \mu g\ g^{-1}$). The concentrations of As_{Inorg} in the *A. nodosum* animal feed over the duration of the study never exceeded the EC Regulation limit of 2 $\mu g\ g^{-1}$, an important finding considering the greater toxicity of As_{Inorg}. Arsenic toxicity is species-specific, and therefore speciation analysis is critical when assessing the feed to food transfer and potential human exposure to arsenic from SAF. Moreover, this study considered only seaweed's contribution to the As load in animal diets and has not considered the compounding effects of cofactors. For example, though it has been reported that “forage crops, in general, do not need high priority in monitoring programs … although grass meal still needs attention” (Adamse et al. 2017), As uptake by grasses and fodder can differ widely (Dradrach et al. 2020) particularly in soils with a high concentration of As because of biotransference from soil to vegetation (Pérez-Carrera and Fernandez-Cirelli, 2014). Considering that the bulk of animal feed comes from vegetation crops (grass, alfalfa, hay, soyabean), these feed materials will likely further contribute to the overall As load in animal diets.

Oral ingestion of food and feed is one of the primary routes for As_{Inorg} entry into mammalian and poultry systems. The current study found EDI levels to be within the adequate range set by EFSA and JECFA for the safe use of *A. nodosum* as a raw ingredient in the diets of animals reared for human consumption. This study indicated that the EDI of As as a result of the consumption of livestock fed *A. nodosum* animal feed is negligible. When compared with the established $BMDL_{01}$ of 3 $\mu g\ kg^{-1}$ bw day^{-1}

for As_{Inorg}, all exposure outputs (chicken, eggs, beef, and milk) fell below exposure values calculated at the 95th percentile, and it can be concluded that As transfer does not constitute a hazard to human health. The EDI calculated in this study, however, should be considered alongside other human dietary intakes of As, which follow consumption of a fully balanced diet. Results from this study should be thought of as part of a cumulative intake effort of As in our diet. Consequently, a total diet exposure assessment would be relevant. It should be noted that the models used in this study are applicable only to the scenarios considered. Should new knowledge emerge, specifically regarding toxicity endpoints or biotransfer rates, the assessment should be re-evaluated.

5.7 Bibliography

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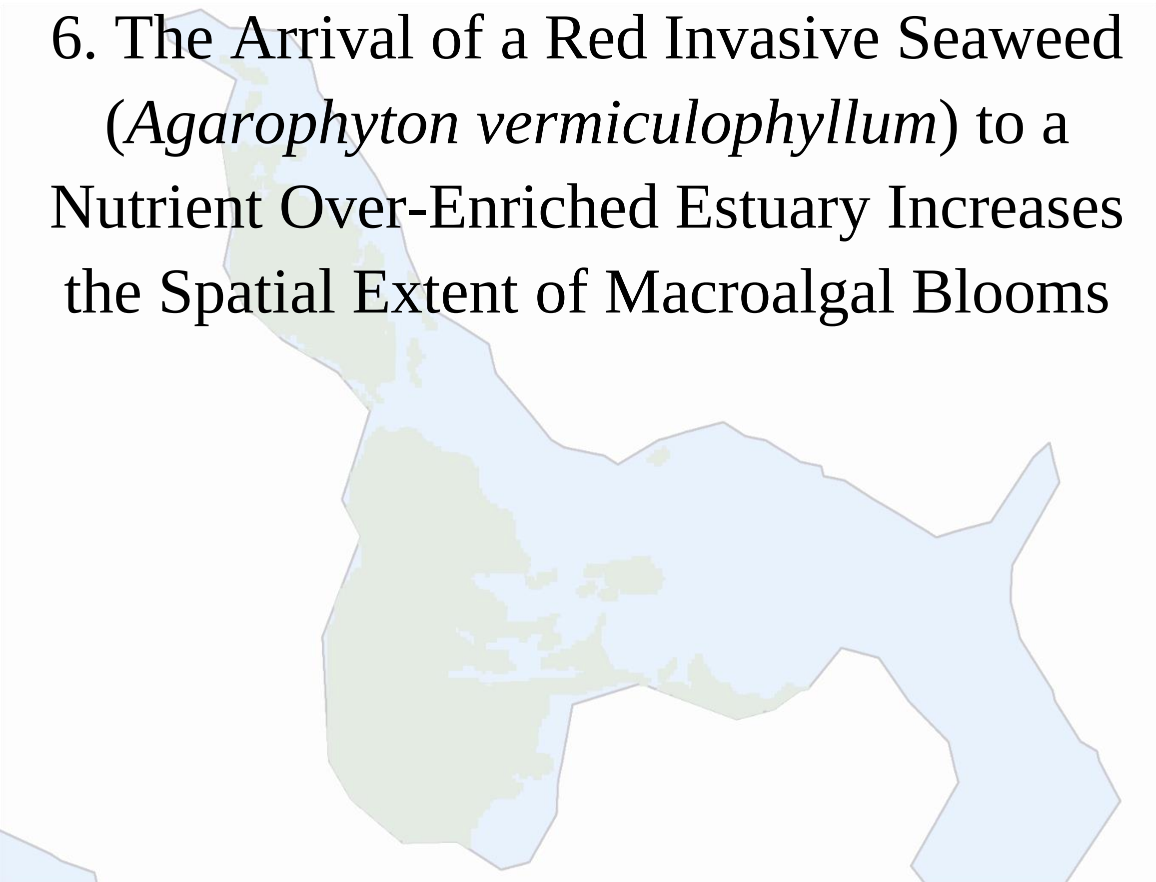
6. The Arrival of a Red Invasive Seaweed (*Agarophyton vermiculophyllum*) to a Nutrient Over-Enriched Estuary Increases the Spatial Extent of Macroalgal Blooms



6.1 Abstract

The red seaweed *Agarophyton vermiculophyllum* is an invasive species native to the northwest Pacific, which has proliferated in temperate estuaries of Europe, North America, and Africa. Combining molecular identification tools, historical satellite imagery and one-year seasonal monitoring of biomass and environmental conditions, the presence of *Agarophyton* was confirmed, and the invasion was assessed and reconstructed. The analysis of satellite imagery identified the first bloom in 2014 and revealed that *Agarophyton* is capable of thriving in areas where native bloom-forming species cannot, increasing bloom size (ca. 10%). The high biomass found during the peak bloom (>2 kg m^{-2}) and the observation of anoxic events indicated deleterious effects. The monitoring of environmental conditions and biomass variability suggests an essential role of light, temperature and phosphorous in bloom development. The introduction of this species could be considered a threat to local biodiversity and ecosystem functioning in a global change context.

6.2 Introduction

Estuarine environments harbour a great variety of habitats (e.g., seagrass meadows, salt marshes, oyster beds, mudflats) and are highly productive, providing valuable ecosystem goods and services (Costanza et al. 1997). Despite this variety of habitats and high biological productivity, species richness is relatively low due to the environmental fluctuations occurring over short spatial and temporal scales, which present a physiological challenge for the organisms inhabiting these areas (Jaspers et al. 2011, Cardoso et al. 2012, Bermejo et al. 2019). In the case of macroalgae, the scarcity of hard substrates for the settlement of its propagules poses an additional constraint precluding the development of diverse seaweed assemblages. This absence of a suitable substratum is one of the main reasons why these environments have been traditionally less studied by phycologists (Krueger-Hadfield et al. 2017b, 2018).

Coastal ecosystems have been under strong and diverse anthropogenic pressures (e.g., nutrient enrichment, the introduction of alien species, inputs of organic or inorganic contaminants) as human populations have historically been concentrated in these areas (Lotze et al. 2006, Airoldi and Beck, 2007). These pressures can change the aquatic conditions producing different forms of pollution (e.g., dystrophy caused by an excess of eutrophication, biological invasions, and pollution by organic compounds and organic matter) that degrade the environment. Estuarine environments are more susceptible to over-enrichment of nutrients and other pollutants derived from human activity as a consequence of their hydrological and geomorphological characteristics (i.e., relatively small water bodies with low rates of water renewal). The combination of strong anthropogenic pressures and low species richness make these areas prone to successful biological invasions (Occhipinti-Ambrogi 2001).

One of the most evident signs of nutrient enrichment in estuaries is the development of opportunistic macroalgal blooms (Teichberg et al. 2010). These blooms are not toxic in and of themselves, but the accumulation and subsequent degradation of large amounts of seaweed biomass can produce deleterious consequences for the ecosystem and shore-based human activities (Sfriso et al. 2003, Smetacek and Zingone, 2013). The development of macroalgal blooms has been traditionally attributed to nutrient over-enrichment of affected areas (Valiela et al. 1997, Smetacek and Zingone, 2013). Although nutrient over-enrichment is a necessary requisite for the occurrence of seaweed blooms, other factors, such as temperature, light and salinity, are also crucial in explaining the development of these blooms (e.g., Malta and Verschuure, 1997, Valiela et al. 1997, Gao et al. 2016). Previous studies suggested that the number of bloom-forming species in a particular area can also stimulate or prolong the intensity, spatial extension and duration of the bloom since temporal and spatial successions can occur (Lavery et al. 1991, Nelson et al. 2008, Bermejo et al. 2019). The arrival of alien species with differing ecophysiological requirements can increase the potential for bloom occurrences in areas or periods of the year unfavourable for the blooming of native species. For instance, the arrival of non-native cryptic *Ulva* species has explained the development of seaweed blooms in two Japanese estuaries, where nutrients conditions have remained more or less constant (Yabe et al. 2009, Yoshida et al. 2015).

Due to difficulties in the identification of bloom-forming seaweeds (Steentoft et al. 1995, Malta et al. 1999, Rueness 2005) and the scarcity of phycological research in estuarine environments (Krueger-Hadfield et al. 2017b, 2018), species composition of macroalgal blooms and its importance for their development have been frequently overlooked. The development of new molecular identification tools allows researchers to overcome these taxonomic challenges, confirming the presence of seaweed blooms formed by cryptic alien species (e.g., Rueness 2005, Baamonde-López et al. 2007, Yoshida et al. 2015). In estuarine environments of North America, Europe and North Africa, such tools have verified the extensive spreading of the Asian red seaweed *Agarophyton vermiculophyllum* (Ohmi) Gurgel, J.N.Norris et Federicq (previously known as *Gracilaria vermiculophylla* (Ohmi) Papenfuss) (Kim et al. 2010, Krueger-Hadfield et al. 2017a). This gracilarioid can thrive in mudflats as it remains anchored to the substrate by the burial of its basal parts or attached to small pebbles or the shells of calcareous organisms. This species is also very resistant to different environmental stresses, such as low salinities, low light conditions or high grazing pressures, and it can bloom in areas where native seaweeds cannot, modifying native biological assemblages and biogeochemical cycles in soft-sediment habitats (Byers et al. 2012, Cacabelos et al. 2012, Ramus et al. 2017).

The use of free, open-access satellite imagery has become a useful tool in the monitoring and assessment of macroalgal blooms (Hu et al. 2019, Zhang et al. 2019). Landsat-7 Enhanced Thematic Mapper Plus (L7-ETM+) provides satellite data from 1999 to the present and has been successfully used in identifying changes in marine environments (Andréfouët et al. 2001) and in mapping cyanobacterial bloom events (Vincent et al. 2004, Kutser et al. 2006). In comparison to L7-ETM+, the more recent Sentinel-2 Multispectral Instrument (S2-MSI), launched in June 2015 by the European Space Agency (ESA), delivers higher spectral (12 bands vs 8 bands), spatial (10m vs 30m) and temporal resolution data (2-day vs 16-day revisit). These improvements have allowed the study of environmental processes occurring at smaller temporal and spatial scales and have already been successfully used in the study of seaweed blooms (Xing et al. 2017, Dogliotti et al. 2018).

The identification of the most relevant temporal and spatial scales of variability is useful for understanding the factors controlling the abundance, distribution and composition of benthic assemblages (Burrows et al. 2009, Bermejo et al. 2015, 2019). The assessment of the most relevant scales of variability is considered a necessary prerequisite before explanatory models are proposed (Andrew and Mapstone, 1987). Furthermore, the use of exploratory correlational approaches can provide a general insight to help identify the primary environmental drivers controlling biomass development in the field (e.g., Malta and Verschuure, 1997, Mac Nally 2002, Yoshida et al. 2015). The combination of both approaches improves the interpretation of the data collected.

The three objectives of this study were: to confirm the presence of *Agarophyton* in the Republic of Ireland using molecular identification tools, which has been previously reported and confirmed from Northern Ireland using molecular identification tools (Krueger-Hadfield et al. 2017b); test the capability of free satellite imagery for the reconstruction of the invasion of this red alien species and its interaction with native species; elucidate the most important factors determining the development of the *Agarophyton* bloom in the Clonakilty estuary using an assessment of the spatial and temporal scales of variation combined with correlational analysis of abiotic variables and biotic bloom conditions.

6.3 Materials and Methods

6.3.1 Study site and *Agarophyton* identification based on molecular tools

The Clonakilty estuary is located on the southwestern coast of Ireland (Fig. 6.1 a and b) and has been historically affected by large intertidal macroalgal blooms formed by native *Ulva* spp. (Wan et al. 2017, Fort et al. 2020). This estuary is shallow, sheltered, and nutrient-enriched due to diverse human activities occurring in the surrounding area (i.e., intensive dairy farming and agriculture, the presence of a wastewater treatment facility). The Clonakilty estuary covers a surface area of 2.15 km^2 and has a length of 3.5 km. The residence time is between 6 and 9 days, the median depth is 2.5 m, and the estuary has a tidal range of 3.7 m. The studied areas affected by the *Agarophyton* bloom were muddy (percentage of fine sand and clay between 65 and 97%; Lewis et al. 2002) and enriched in organic matter (between 2.5 and 7%; nitrogen content between 0.05 and 0.25%). The bay is sheltered and protected from wave exposure. The presence of other macroalgal assemblages present in the estuary, including *Cystoclonium*, *Laminaria*, *Fucus*, *Ceramium*, *Ectocarpus* and *Rhizoclonium* were recorded, although for the most part these species were found only in negligible quantities.

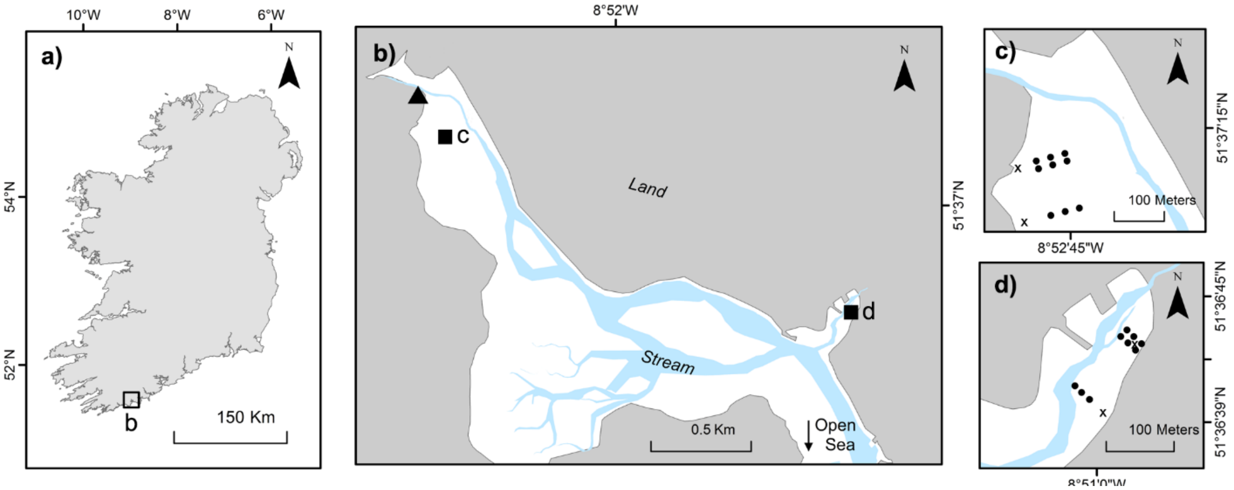


Fig. 6.1 Geographical location of the Clonakilty estuary in Ireland (a). Map of the Clonakilty showing the location of the wastewater treatment plant (black triangle) inner and outer sections (black squares) (b). Detailed maps outlining a schematic representation of the spatial sampling design in the inner (c) and outer sections (d). Black dots represent seaweed sampling station, and black "x" seawater sampling stations in subfigures c and d

6.3.2 Environmental conditions

Daily climatological data for Clonakilty (i.e., rainfall, solar radiation, maximum and minimum air temperature) were obtained from the Irish meteorological service (Met Éireann; http://www.met.ie/). Rainfall data were sourced from the closest pluviometric station in Rosscarberry (20 km). The maximum and minimum air temperature levels were linearly interpolated considering the distance from the sampling site to the two closest meteorological stations of Sherkin Island and Roche's Point, which were located 40 and 48 kms respectively from the study site. Each parameter (i.e., accumulated rainfall, solar radiation, and maximum and minimum air temperatures) was calculated considering data from the week previous to each sampling occasion.

Seawater sampling for physicochemical variables (i.e., salinity and dissolved inorganic nutrients) was conducted during the previous or subsequent high tide following the biomass sampling over six occasions (i.e., data from July 2016 were not collected due to logistical reasons). Seawater samples were collected from each sampling site at a depth of 20 cm. Salinity was determined *in situ* using a hand refractometer (ATAGO S-20E, Tokyo, Japan). Three replicate samples of water were collected for the determination of dissolved inorganic nutrients (nitrate, nitrite, ammonium, and phosphate). Replicates were filtered *in situ* using a syringe and a nylon disposable filter (pore size 0.45 μm; Sarstedt, Germany) and samples were stored at -20ºC prior to analysis. Seawater samples analysed for total oxidised N (TON) concentrations were determined on a Thermo Aquakem discrete analyser (Thermo Scientific, Vantaa, Finland), with a detection limit of 0.25 mg L^{-1} for total oxidised N. Samples were also analysed for NO_2–N, $NH4^+$-N, and dissolved reactive phosphorus (DRP) on the same instrument and Nitrate-N (NO_3-N) was calculated by subtracting NO_2–N from TON.

6.3.3 Agarophyton identification based on molecular tools

The red alga thriving on the intertidal mudflats of the Clonakilty estuary was identified at species level using a plastid-encoded marker, the large subunit of the Ribulose Bisphosphate Carboxylase-Oxygenase (RuBisCO) (*rbc*L). This marker has been widely used to unravel numerous taxonomical issues with the phylum Rhodophyta, providing enough variation for species delimitation in conflicting taxa (Wilson-Freshwater and

Rueness, 1994, Rueness 2005). In this sense, the *rbc*L allowed for the confirmation of the presence of *Agarophyton vermiculophyllum* for the first time in Europe (Rueness 2005). Algal tissue was dried with desiccated silica and whole genomic DNA was extracted with a commercial kit [NucleoSpin® Plant II, Macherey-Nagel, Düren, Germany]. Amplifications of the *rbc*L gene region in Polymerase Chain Reactions (PCRs) employed primers F8 or F57, and R1150 (Wilson-Freshwater and Rueness, 1994, Mineur et al. 2010) at an annealing temperature of 50ºC (Heesch et al. 2009). Protocols for PCR amplification, purification of the products and sequencing followed Heesch et al. (2016).

Six sequences from Clonakilty specimens were aligned with 57 published *Agarophyton* sequences from all over the world (including *G. vermiculophylla* sequences from Asia and USA, e.g., JQ407698, JQ768761, DQ095821, EU600293), using sequences of the genus *Hydropuntia* (JQ843362 and EF434914) as an outgroup. Methods for the treatment of sequences (i.e., quality control and alignment) and the analyses of data under the Maximum Likelihood (ML) criterion are given in Heesch et al. (2016). The algal nomenclature followed AlgaeBase (Guiry et al. 2014). Representative herbarium specimens were deposited at GALW under accession numbers GALW01650-GALW01652.

6.3.4 Reconstruction of Agarophyton invasion and assessment of the biotic interaction with native species using satellite imagery

In order to reconstruct the arrival of *A. vermiculophyllum* and assess the potential spatial overlapping of this invasive red alga with the native bloom-forming species *Ulva* spp. in Clonakilty Bay, two sources of free satellite data were used, namely the MultiSpectral Instrument onboard Sentinel-2 (S2-MSI) and the Landsat-7 Enhanced Thematic Mapper Plus (L7-ETM+). Suitable data scenes from 2010-2018 captured during bloom proliferation (April-September), at low tide and on cloud-free days were initially identified using Google Earth Engine (GEE; Gorelick et al. 2017). The earliest S2-MSI scenes available of the study area were from July 2015, and prior to this date, L7-ETM+ data were used. Both Level-2A and Level-1C S2-MSI scenes from 2015-2018 were downloaded from the Copernicus DataHub website (https://scihub.copernicus.eu/), and

L7-ETM+ data from 2010 – 2014 from the United States Geological Survey (USGS) website (https://earthexplorer.usgs.gov/). From 2015 – 2018, S2-MSI was used instead of L7-ETM+ because of the improved revisit time and spectral resolution, which allowed for improved identification of *Ulva* spp. and *Agarophyton*. To avoid any bias in spatial resolution and allow comparison between the datasets, both downloaded L7-ETM+ and S2-MSI scenes were resampled to 30 m spatial resolution.

Initial processing of both satellite products was carried out using the European Space Agency (ESA) Sentinel Application Platform (SNAP) toolbox (v. 6.0). Both datasets were geometrically rectified to Universal Transverse Mercator (UTM) projection and WGS 84 datum. True colour composite images of the study area were created by combining, in the case of S2-MSI, the B2: blue (490 nm), B3: green (560 nm) and B4: red (665 nm), and for L7-ETM+, the B1: blue (450 nm), B2: green (520 nm) and B3: red (630 nm). Further processing, including atmospheric and radiometric corrections using SNAP Desktop and ENVI software (v. 5.3.1; Research Systems, Boulder, CO, US). Sentinel-2 Level-1C and L7-ETM+ radiance data recorded at the top of atmosphere (TOA) were scaled to surface reflectance by applying the dark object subtraction (DOS) technique (Gilmore et al. 2015) before atmospheric correction to Level-2A bottom of atmosphere (BOA) data using Sen2Cor (Louis et al. 2016).

A pixel-based maximum likelihood classifier (MLC) was applied to individual corrected scenes to produce both *Ulva* spp. and *Agarophyton* masks. The MLC function is available in the ENVI software and calculates the average variance of the spectral training data to estimate the likelihood of a pixel belonging to each class (Foody 1992). The MLC was based on pixel training with >200 pixels per class used to train the data. Superfluous classes (water, terrestrial and saltmarsh vegetation, sand) were masked from each scene and later removed before images were refined and smoothed to improve image sharpness. The total accuracy and the kappa coefficient (Cohen 1960) of the classification were also calculated.

The annual cover, potential extension and overlapping between native and invasive bloom-forming species were estimated using QGIS (Quantum GIS Development Team 2014, Quantum GIS Geographic Information System, Open-Source Geospatial

Foundation Project, http://qgis.osgeo.org). In this study, the potential extension of both *Agarophyton* or *Ulva* spp. was defined as the entire area covered by these species at least once during the study period. A workflow showing the overall processing of the satellite imagery is shown in Figure 6.2.

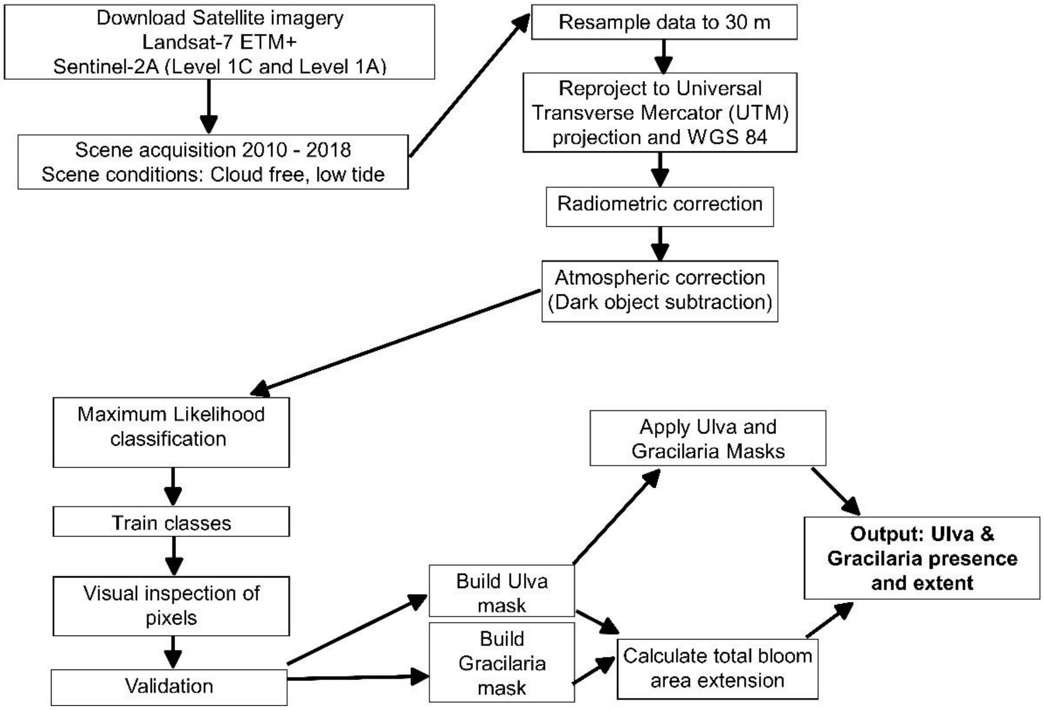


Fig. 6.2 Sentinel-2 and Landsat satellite product processing flow diagram

6.3.5 Biomass sampling and processing

To infer the most important factors influencing the development of *Agarophyton* blooms, the estuary was sampled on seven sampling occasions between July 2016 and August 2017. Biomass sampling was conducted during low water conditions of the spring tides. On each sampling occasion, a hierarchical design was followed to identify the most relevant scales of spatial variation in *Agarophyton* biomass. Two sections ("inner" and "outer") covered by large *Agarophyton* patches and separated by two kilometres were sampled (Fig. 6.1 c and d). In each section, two sites separated by one hundred meters were selected. In one site per section, two random transects perpendicular to the main channel and separated by 10 meters were sampled. In the second site, only one random transect was sampled. Along each transect, three sampling stations were positioned in the upper (between 2.4 and 2.1 m above Mean Lower-Low Water -MLLW-), middle (between 2.0 and 1.8 m above MLLW) and lower (between 1.7 and 1.4 m above MLLW) part of the intertidal covered by the bloom during their maximum extension. The maximum extension usually occurs in June or July in cold-temperate North Atlantic estuaries (e.g., Thomsen et al. 2006, Weinberger et al. 2008, Sfriso et al. 2012, Surget et al. 2017). The sampling stations were pre-determined using Sentinel-2 images of bloom events from 2015. The pre-defined sampling stations were located in the field using a Geographical Position System (GPS; Magellan Triton 400, Santa Clara, USA). Sampling stations differed in locations between sampling occasions to avoid the confounding effect of destructive resampling. At each sampling station (eighteen sampling stations per occasion), three quadrats (25 x 25 cm) were used to assess the abundance of seaweed. All seaweed material present in each quadrat was collected, placed in labelled plastic bags, and transported to the laboratory.

Once in the lab, the seaweed biomass was rinsed with fresh water to remove adherent sedimentary and particulate material, debris, and other organisms. Seaweed species were sorted, and their mass was recorded after the removal of excess water using a manually operated low-speed centrifuge (i.e., salad spinner). Three subsamples of seaweed biomass per section and sampling occasion were rinsed with deionised water, freeze-dried and stored in a desiccator until further elemental analysis (i.e., tissue N and P content). Furthermore, some specimens were washed with deionised water and stored in dry silica gel for taxonomic identification.

6.3.6 Tissue nutrient (N and P) analyses

Nitrogen and phosphorus are considered the main nutrients limiting primary production in aquatic environments. Overall, nitrogen has been traditionally considered to play a more important role in controlling maximum bloom development in coastal systems (Valiela et al. 1997). Nevertheless, phosphorus has also been identified as a limiting nutrient in cold temperate estuaries during parts of the year (Pedersen and Borum, 1996, Lyngby et al. 1999), and even different species can be limited by nitrogen or phosphorous in the same estuary (Lavery et al. 1991, Villares and Carballeira, 2003). In order to identify nitrogen or phosphorus limitation, it is necessary to estimate the tissue nitrogen and phosphorus contents and compare with the critical quota, which provides a direct measure of the nutrient status of seaweed. The critical quota is the minimum tissue nutrient content necessary to support unrestrained growth by the lack of nutrients. In the case of *Agarophyton*, the critical quota for nitrogen (2.14 % DW) and phosphorous (0.14% DW) have been previously determined by Pedersen and Johnsen (2017).

Seaweed tissue, previously freeze-dried, was ground into a homogeneous powder using a TissueLyser II (QIAGEN) and tungsten balls. The homogenised sample was divided into two subsamples; one was used for N and the other for P determination. To determine tissue N content, aliquots of the homogenised material were weighed into tin capsules that were combusted in an elemental analyser Vario ISOTOPE Cube (Elementar Analysensysteme GmbH, Hanau) connected to an isotope ratio mass spectrometer Isoprime 100 (Isoprime Ltd, Cheadle Hulm). The analytical precision was 0.15%. Analyses were carried out in duplicates. Tissue P content was determined on the same dried and ground seaweed tissue after oxidation with boiling H_2SO_4, followed by spectrophotometric analysis (Strickland and Parsons, 1968).

6.3.7 Statistical analyses

Statistical analyses were performed using the R free software environment (R Core Development Team, 2017) and PERMANOVA+ add-on PRIMER 6 (Plymouth Routines in Multivariate Ecological Research) software. In all statistical analyses, significance was set at 5% risk error, and when necessary, were based on 5999 permutations.

6.3.8 Spatial and temporal patterns of variation

To identify the relevant spatial and temporal scales of biomass distribution of *Agarophyton*, a univariate five-way permutational analysis of variance (PERMANOVA; Anderson et al. 2008) was performed based on the Euclidean distances. The five factors considered (three fixed and two random) were: Sampling occasion (fixed; seven levels: "July 16", "August 16", "October 16", "February 17", "April 17", "June 17", and "August 17"), Position in the bloom (fixed; three levels: "upper", "middle" and "lower"), Section (fixed: "Inner" and "Outer"), Site (random; two levels nested in the interaction between "Section" and "Sampling occasion"), and Sampling station (random; two levels nested in the interaction between "Site" and "Position"). In the case of significant effects of a fixed factor, a pairwise PERMANOVA test (Anderson et al. 2008) was performed in order to interpret the patterns. Biomass data complied with homoscedasticity per the Levene test but not with normality according to the Shapiro-Wilks test.

A two-way factorial ANOVA design was considered to assess the effects of "Sampling occasion" (seven levels) and "Section" (two levels) on tissue N and P content of *Agarophyton*. Tissue N and P content data can be considered normal and homoscedastic per Shapiro-Wilks and Levene's tests. A Tukey's test was used to compare levels of factors when an effect was significant.

6.3.9 Correlations between biotic and environmental variables

To interpret and visualise the relationships between environmental variables and the *Agarophyton* bloom in Clonakilty, correlations between environmental variables (i.e., dissolved inorganic nutrients, salinity, radiation, rainfall, and maximum and minimum air temperatures) and biotic variables (i.e., mean *Agarophyton* biomass, mean tissue N and P content, and mean N:P ratios) were assessed using Spearman correlations (Rho), and a principal component analysis. The principal component analysis (PCA) was based on biotic variables, and environmental variables were fitted later using the "envfit" function of the "Vegan" package in R (R Core Development Team, 2017). To perform these analyses, data from the four sampling sites and six of the seven sampling occasions were considered (n=24), as water physicochemical attributes from June 2016 were absent.

6.4 Results

6.4.1 Environmental conditions

Climatological conditions are shown in Table 6.1. Solar radiation and maximum and minimum air temperatures were highest in June and August, as expected for a temperate estuary in the Northern Hemisphere. The maximum air temperature during the week before the sampling varied from 12.3ºC (April 2017) to 26.0 (June 2017), and the minimum air temperature from 2.0ºC (April 2017) to 12.6 (August 2016). Mean daily radiation ranged from 401.2 (February 2017) to 1587.0 (June 2017) J cm^{-2}. The accumulated rainfall during the week previous to the sampling occasion was minimum in October 2016 and April 2017 and maximum in July 2016 and August 2017.

Table 6.1 Meteorological parameters for the Clonakilty estuary: Accumulated rainfall (Rain); Maximum (Max) and Minimum (Min) air temperatures during the week previous to the sampling occasion; and mean global radiation (Rad)

Sampling	Rain (mm)	Max (ºC)	Min (ºC)	Rad (J cm^{-2})
Jul 16	40.3	18.2	10.2	1587.0
Aug 16	25.7	24.6	12.6	1274.7
Oct 16	5.3	16.3	4.3	999.1
Feb 17	24.0	12.5	5.6	401.2
Apr 17	6.9	12.3	2.0	1093.6
Jun 17	16.3	26.0	5.4	1821.9
Aug 17	35.6	17.8	10.1	1487.4

The physicochemical water characteristics are presented in Table 6.2. Nitrate was the main source of DIN, followed by ammonium. Total DIN concentrations ranged from 10 (Site "Outer 2"; April 2017) to 285.71 µM DIN (Site "Inner 1"; February 2017). Overall, the maximum DIN concentrations were observed in October 2016, with the exception of Site 1. The DIP (dissolved inorganic phosphate) concentration varied between 0.16 (Site "Outer 1"; April 2017) and 1.99 µM DIP (Site "Inner 1"; August 2017). Inner sites exhibited higher nutrient concentrations than sites located in the outer part of the estuary. Regarding salinity, the value ranged between 5.0 (Site "Inner 1"; June 2017) to 33.2 (Site "Outer 2"; October 2016).

Table 6.2 Mean values of nutrient concentrations (NO_2^- - Nitrite; NO_3^- - Nitrate; NH_4^+ - ammonia; DIN - Dissolved Inorganic Nitrogen; DIP - Dissolved inorganic phosphorus) and salinity (Sal) for each Site and Sampling occasion

Site	**Sampling**	**NO_2^- (µM)**	**NO_3^- (µM)**	**NH_4^+ (µM)**	**DIN (µM)**	**DIP (µM)**	**Sal (PSU)**
Inner 1	**Aug 16**						18.2
	Oct 16	2.02	52.14	29.29	82.86	0.84	33.0
	Feb 17	2.00	140.00	7.14	148.57	0.76	12.8
	Apr 17	2.29	273.57	10.00	285.71	0.60	32.3
	Jun 17	0.55	112.86	3.57	117.14	0.65	5.0
	Aug 17	0.55	135.71	3.57	140.00	1.02	12.0
		3.86	61.43	17.14	82.14	1.99	
Inner 2	**Aug 16**						
	Oct 16	1.79	40.00	15.71	57.86	0.55	11.5
	Feb 17	2.14	187.14	10.00	199.29	1.12	30.0
	Apr 17	2.00	147.86	7.14	157.14	0.37	19.0
	Jun 17	0.52	98.57	6.43	105.00	0.64	31.0
	Aug 17	1.07	92.14	11.43	104.29	1.14	6.1
		0.74	17.14	8.57	26.43	1.63	29.0
Outer 1	**Aug 16**						24.5
	Oct 16	1.55	18.57	4.29	24.29	0.32	25.8
	Feb 17	1.60	138.57	2.86	142.86	0.37	29.0
	Apr 17	1.64	61.43	4.29	67.14	0.28	32.0
	Jun 17	0.00	26.43	1.43	28.57	0.16	10.2
	Aug 17	1.00	77.86	6.43	85.00	0.89	8.0
		0.91	96.43	1.43	99.29	0.97	
Outer 2	**Aug 16**	1.64	75.00	5.71	82.14	0.33	14.1
	Oct 16	1.74	102.86	5.00	110.00	0.31	33.2
	Feb 17	2.17	39.29	7.14	48.57	1.54	30.1
	Apr 17	0.00	10.00	0.00	10.00	0.23	33.0
	Jun 17	0.88	62.14	7.86	70.71	1.13	19.6
	Aug 17	1.29	43.57	10.00	55.00	0.75	20.0

6.4.2 Taxonomical confirmation based on molecular tools

The *rbc*L marker was amplified in six specimens of gracilarioids from the Clonakilty estuary. Sequences were included in an alignment of 1419 bases length, containing 67 sequences in total, with *Hydropuntia* Montagne species serving as an outgroup. The Irish specimens (GenBank/ENA accession numbers LR740737-LR740742) were identified as belonging to the species *Agarophyton vermiculophyllum* (order Gracilariales). Additionally, three other red algae were observed in the estuary, albeit as drift material with low biomass, which were identified based only on morphological traits: *Gracilariopsis longissima* (S.G.Gmelin) Steentoft, L.M. Irvine & Farnham, *Gracilaria gracilis* (Stackhouse) Steentoft et al. and *Cystoclonium purpureum* (Hudson) Batters.

6.4.3 Reconstructing the invasion and assessing the overlap with native bloom-forming species

The pixel-based MLC resulted in satisfactory overall accuracy with the kappa coefficient ranging from 0.7317 to 0.9617 compared with manual classification (Table 6.3).

Table 6.3 Classification accuracy, Kappa coefficient, *Ulva* and *Agarophyton* extension from 2010 to 2018, potential extension of both *Ulva* and *Agarophyton* considering this 8-year period and overlapping between *Agarophyton* and the potential extension of *Ulva*

Sensor	Year	Month	Accuracy	Kappa	***Ulva* (ha)**	***Agarophyton* (ha)**	**Overlapping (ha)**
Landsat-7 ETM+	2010	June	99.29%	0.9329	46.1	0	0
Landsat-7 ETM+	2011	-	-	-	-	-	-
Landsat-7 ETM+	2012	September	98.97%	0.9524	32.5	0	0
Landsat-7 ETM+	2013	April	98.41%	0.8643	19.6	0	0
Landsat-7 ETM+	2014	July	98.45%	0.8304	31.5	3.9	2.4
Sentinel-2	2015	August	97.42%	0.8908	50.8	3.7	0.6
Sentinel-2	2016	August	97.48%	0.8375	27.7	4.5	1.2
Sentinel-2	2017	July	87.26%	0.7317	26.7	5.5	2.4
Sentinel-2	2018	July	98.05%	0.9617	35.6	8.1	2.7
Potential extension					**63.1**	**9.9**	**3.2**

In the case of *Ulva*, the total extension of the bloom ranged from 19.6 (2013) to 50.8 (2015) ha between 2010 and 2018, although some caution should be exercised when comparing among years due to data acquisition in different months of the year. The analysis of the satellite imagery identified 2014 as the year when the *Agarophyton* bloom first appeared in Clonakilty Bay. The encroaching *Agarophyton* canopy is evident from 2014 to 2018 when the area colonised increased from 3.9 to 8.1 ha (Table 6.3). The spatial comparison between the potential extensions of *Ulva* spp. (63.1 ha) and *Agarophyton* (9.9 ha) revealed an increased overlapping from 2015 to 2018 between the native green algae and the invasive red alga due to the colonisation of *Agarophyton* in areas potentially covered by *Ulva* (Table 6.3). The results showed that *Agarophyton* colonised the northern shore, which had remained relatively bloom-free prior to 2014

(Fig. 6.3 and 6.4). The total extension of the estuary potentially covered by bloom-forming species of both *Agarophyton* and *Ulva* spp. increased by 6.7 ha after the arrival of *Agarophyton*. In this sense, the average size of macroalgal blooms during peak bloom conditions was 1.21 times larger during the period 2014-2018 (39.6 ha) than for the period from 2010-2013 (32.7 ha).

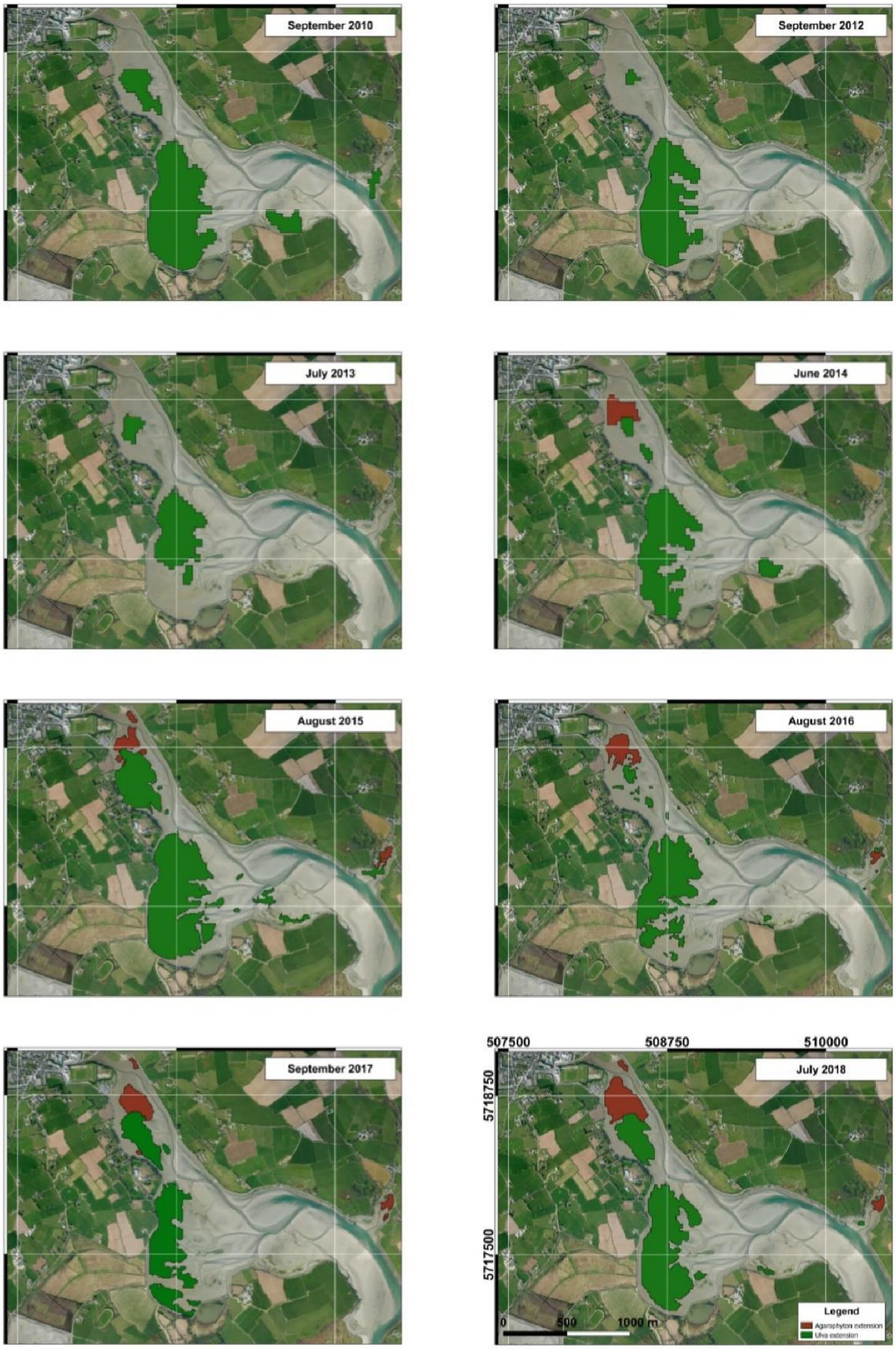


Fig. 6.3 Extension of *Agarophyton* and *Ulva* in the Clonakilty estuary based on the analysis of satellite imagery obtained from 2010 to 2018

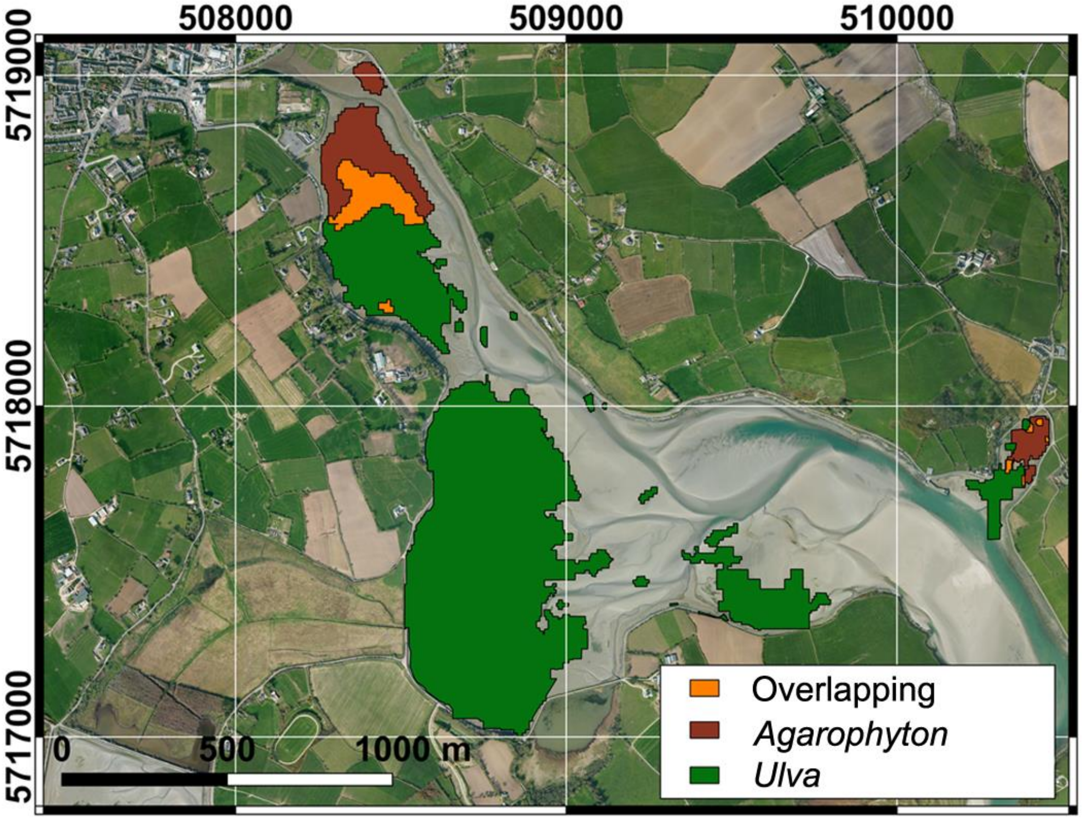


Fig. 6.4 Potential extension for *Agarophyton* and *Ulva*, and the overlapping between both, in the Clonakilty estuary based on satellite imagery collected from 2010 to 2018

6.4.4 Spatial and temporal patterns of variation

The PERMANOVA results regarding the biomass of *Agarophyton* revealed significant differences among sampling occasions, sections, and positions (Table 6.4). A common seasonal dynamic in the biomass of *Agarophyton* was observed in both inner and outer sections, with annual peaks of biomass during summer, between June and August (Fig. 6.5a), and minimum levels detected in winter (i.e., February 2017).

Table 6.4 Results of five-way PERMANOVA analysis testing the effects of the factors "Sampling Occasion" (SO - fixed, 7 levels), "Position in the bloom" (Po - fixed, 3 levels), "Area" (A - fixe, 2 levels), "Site" (Si - Random nested in "AxSO"), and "Sampling Station" (Station- Random nested in "SixPo") on the biomass of *A. vermiculophyllum* in the Clonakilty estuary. * p-value < 0.05; ** p-value < 0.01; *** p-value < 0.001

Source	**df**	**MS(x10^5)**	**Ps-F**
Sampling occasion (SO)	**6**	**204.50**	**19.59*** **
Area (A)	**1**	**112.99**	**10.83** **
Position (Po)	**2**	**61.78**	**7.01** **
SOxA	6	28.59	2.74
SOxPo	12	12.20	1.38
AxPo	**2**	**55.24**	**6.27** **
Site (Si(SOxA))	**14**	**10.44**	**2.52***
SOxAxPo	12	16.76	1.90
PoxSi(SOxA)	**28**	**8.81**	**2.13***
Station(PoxSi(SOxA))	42	4.14	1.42
Residual	252	2.91	
Total	377		

Overall, higher biomasses of *Agarophyton* were observed in the inner section than in the outer, except during April 2017, when the opposite trend was recorded. The annual peaks of biomass occurred in July 2016 and in August 2017 for both sections. The mean values observed in the inner section during July 2016 and August 2017 were 2.41 and 1.88 kg FW m^{-2}, respectively, reaching abundances higher than 5.00 kg FW m^{-2} at some sampling stations. In the outer section, the mean values observed during the peak bloom were 1.15 and 1.52 kg FW m^{-2} for July 2016 and August 2017, reaching abundances greater than 2.50 kg FW m^{-2} during this period. In contrast, during February 2017, the mean values of biomass were 229.8 g FW m^{-2} and 229.0 g FW m^{-2} for the inner and outer sections.

Regarding the shore position of the *Agarophyton* bloom, the middle position reached higher biomass abundances than the lower position (Fig. 6.5b). This pattern is dependent on the "Section" and "Site", as revealed by the significant interaction between "Position" and "Section", and also "Position" and "Site" (Table 6.4). However, this pattern was evident in the inner section, but not in the outer. Finally, at smaller spatial scales of variation, significant differences were observed between sites, but not between sampling stations (Table 6.4). The low data dispersion within sampling stations indicates homogeneity in biomass distribution at small spatial scales (Appendix B, Fig. S3).

In relation to the tissue N content, the ANOVA revealed significant differences between sampling occasions but not between sections (Table 6.5). No significant interactions between "Sampling Occasion" and "Section" were found. The tissue N content followed a seasonal pattern, opposite to the one observed for biomass abundance (Fig. 6.6a). The maximum percentage of tissue N occurred in February (4.68±0.31%; mean±SD, n =6), coinciding with minimum biomass abundance, and the minimum percentage of tissue N content was found during the summer (July 2016; 2.27±0.36%; n =6), coinciding with maximum biomass. In the case of the tissue P content, the ANOVA revealed significant differences between sampling occasions and a significant interaction between "Sampling Occasion" and "Section" (Table 6.5).

Table 6.5 Results of two-way ANOVA analyses testing the effects of the factors "Sampling Occasion" (SO - fixed, 7 levels) and "Area" (A - fixed, 2 levels) on the tissue N and P content of *A. vermiculophyllum*. * p-value < 0.05; ** p-value < 0.01; *** p-value < 0.001

		%N		**%P**	
	df	**MS**	**F**	**MS**	**F**
Area (A)	1	0.003		0.0002	0.43
Sampling occasion (SO)	6	4.753	0.02	0.0086	**13.15*** **
AxSO	6	0.101	**24.42*** **	0.0021	**3.18***
Residuals	28	0.195	0.52	0.0006	

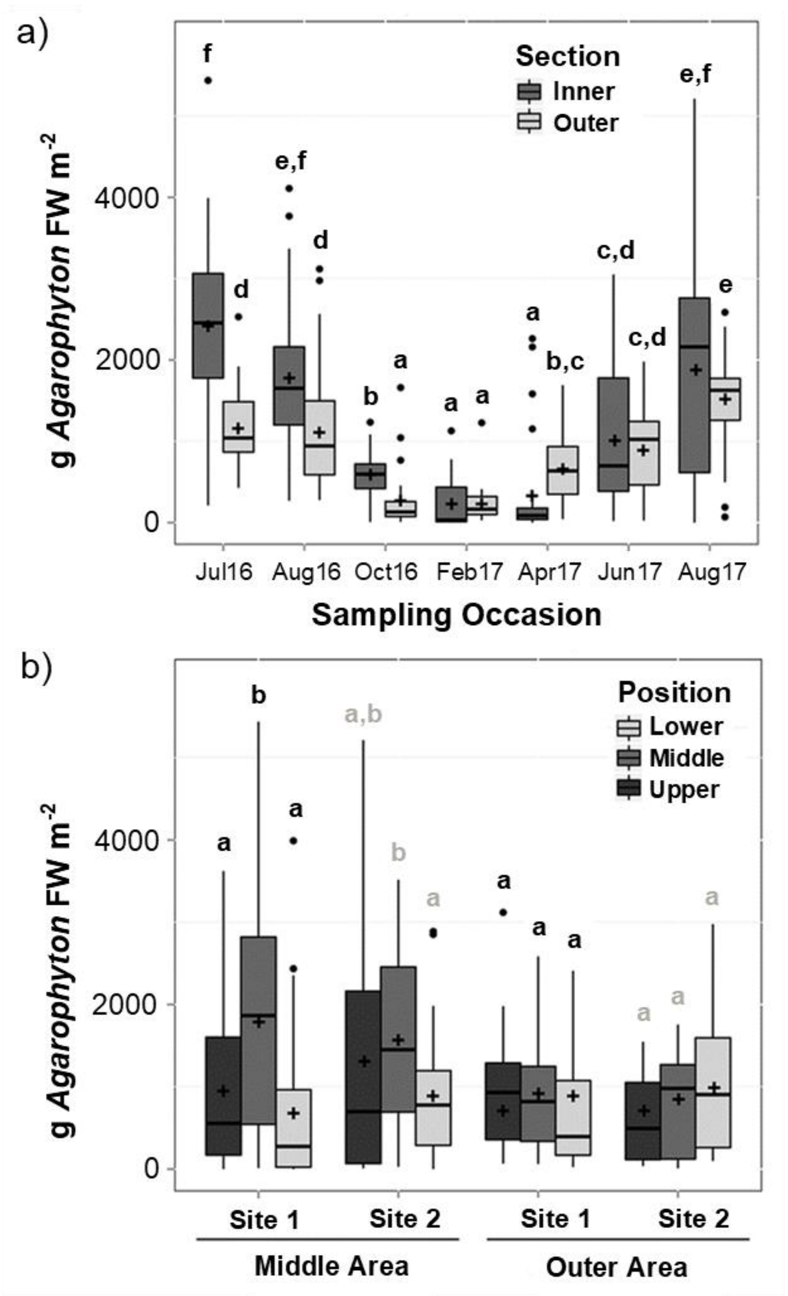


Fig. 6.5 Biomass (wet wt.) (n =54) of *A. vermiculophyllum* for each section over seven different sampling occasions (a). Biomass (wet wt.) of *A. vermiculophyllum* for each site (Sites 1 and 3, n =126; Sites 2 and 4, n =63) and position in the seaweed bloom (b). Box plots indicate the mean (bold +), the median (bold line inside the box), the first and third quartile (upper and lower lines defining the box), the extreme values whose distance from the box is at most 1.5 times the interquartile range (whiskers), and remaining outliers (dark dots). Box plots marked by the same letter are not significantly different according to post hoc analyses. In figure b, the different colours of the letters over the bars indicate that post hoc comparisons between positions were performed within each one of the four sites

Both sections displayed a relatively similar seasonal trend with maximum tissue P contents during February 2017 and minimum levels in April and June 2017 (Fig. 6.6b). In the inner section, the lowest tissue P content was observed in June 2017 (0.093±0.009 %; n=3), and the highest contents in August 2016 (0.173±0.037 %; n=3) and February 2017 (0.178±0.041 %; n=3). In the outer section, the lowest tissue P contents were observed in April (0.082±0.005 %; n=3) and June 2017 (0.087±0.006 %; n=3), and the highest contents in October 2016 (0.203±0.039 %; n=3) and February 2017 (0.193±0.026 %; n=3).

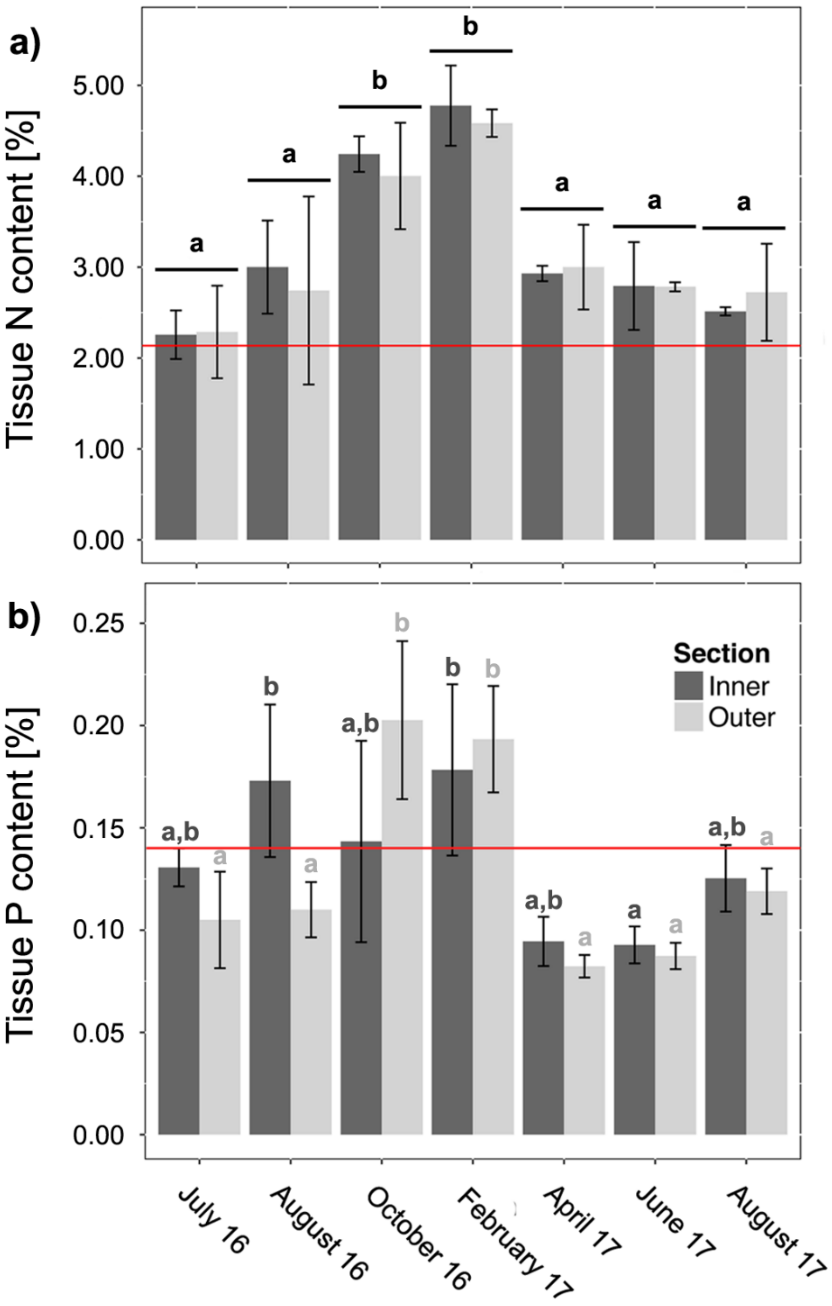


Fig. 6.6 Mean tissue N content (%N) of *A. vermiculophyllum* for each sampling occasion. Lower and Upper error bars represent standard deviation (n = 6). Bars marked by the same letter are not significantly different according to post hoc analyses. In figure b, the different colours of the letters over the bars indicate that post hoc comparisons between sampling occasions were performed within each one of the two sections

6.4.5 Correlations between biomass and environmental variables

The first two components of the PCA based on biotic variables explained over 94.2% of the total variation (Fig. 6.7). The score plot showed three main clusters, one grouping data from October 2016 and February 2017 characterised by high tissue nutrient contents and low biomasses, a second cluster including April and June 2017 with relatively high biomasses and tissue N:P ratios due to low tissue P contents, and a third cluster with samples from August 2016 and 2017, which displayed high biomass and low N:P ratios as a consequence of an increase in tissue P contents.

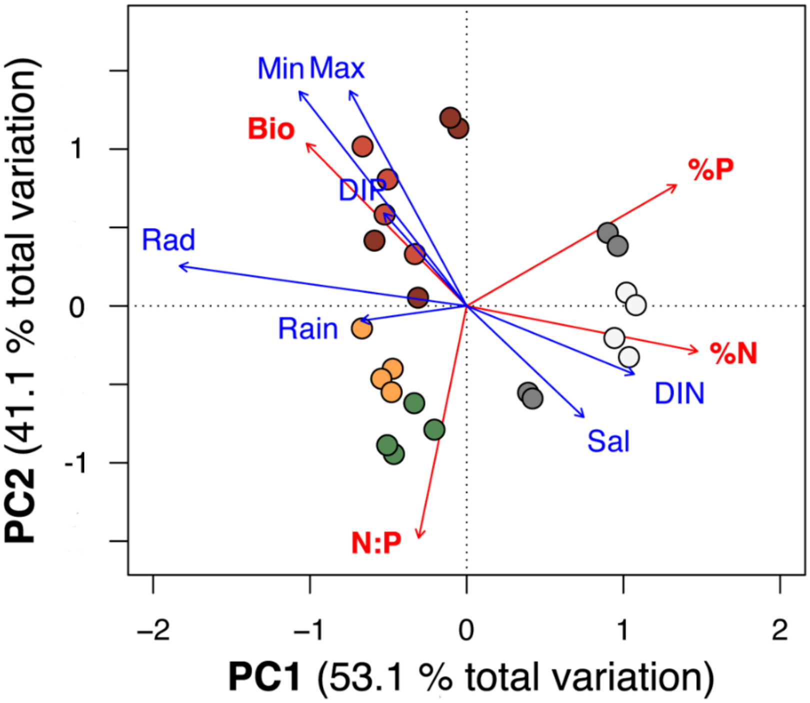


Fig. 6.7 Score biplot of the first and second principal component based on biomass (Bio), tissue N (%N) and P (%P) contents, and tissue N:P (N:P) ratio (red arrows) of *Agarophyton* bloom for the four sampling sites studied and six of the seven sampling occasions (August 2016 - light red dots; October 2016 - grey dots; February 2017 - white dots; April 2017 - green dots; June 2017 - yellow dots; August 2017 - dark red dots). Blue arrows represent environmental variables fitted using "envfit" function of the Vegan package in R (accumulated rainfall - Rain; dissolved inorganic nitrogen - DIN; dissolved inorganic phosphorous - DIP; maximum temperature - Max; minimum temperature - Min; salinity - Sal; solar radiation - Rad)

The "envfit" function and Spearman correlations between biotic and environmental variables suggested an important effect of light (i.e., solar radiation) and temperature (i.e., maximum, and minimum air temperatures) on the biological performance of *Agarophyton* (i.e., tissue N and P contents, N:P ratio and Biomass) (Table 6.6). The "envfit" found significant correlations with biotic variables for DIN (r^2 =0.283; p-value <0.05), radiation (r^2=0.727; p-value<0.001), maximum (r^2=0.517; p-value<0.01) and minimum (r^2=0.639; p-value<0.001) temperatures, and marginal correlations for Salinity (r^2=0.225; p-value<0.10).

Table 6.6 Spearman correlations (Rho) between environmental and biotic variables. DIN - Dissolved Inorganic Nitrogen; DIP - Dissolved Inorganic Phosphorous; Sal - Salinity; Rain - Accumulated rainfall; Max - Maximum Air Temperature; Min - Minimum Air Temperature; Rad - Global radiation; Bio - Biomass; %N - tissue N content; %P - tissue P content; N:P - tissue N:P ratio. * p-value < 0.05; ** p-value < 0.01; *** p-value < 0.001

	Bio	**%N**	**%P**	**N:P**
DIN	-0.39	**0.44***	0.30	0.12
DIP	0.33	-0.37	-0.04	-0.09
Sal	**-0.55****	0.37	0.09	0.27
Rain	0.24	-0.03	0.09	-0.10
Max	**0.75*****	**-0.59****	0.04	**-0.51***
Min	**0.86*****	**-0.74*****	-0.16	**-0.44***
Rad	**0.74*****	**-0.86*****	**-0.61****	-0.01

The Spearman correlations (Table 6.6) indicated that biomass was significantly and positively correlated with radiation, maximum and minimum temperatures and negatively correlated with salinity and DIN concentration (Rho=-0.39; p-value <0.10). Tissue N content was positively correlated with DIN concentration and exhibited negative and significant correlations with temperatures and solar radiation. In the case of tissue P content, only radiation showed a negative and significant correlation (Rho =-0.61; p-value <0.01). The tissue N:P ratio was significantly and negatively correlated with maximum and minimum temperatures. Biomass was significantly and negatively correlated with tissue N content (Rho =- 0.76; p-value <0.001), and tissue N:P ratio (Rho=-0.50: p-value <0.01) but did not show any correlation with tissue P content (Rho=-0.18; p-value >0.10).

6.5 Discussion

6.5.1 Presence of Agarophyton confirmed in the Republic of Ireland

Molecular genetic identification confirmed the presence of *Agarophyton* in the Republic of Ireland for the first time, which had only previously been recorded from Northern Ireland (UK) (Krueger-Hadfield et al. 2017b). In the Clonakilty estuary, the use of satellite data identified 2014 as the first year when *Agarophyton* produced a bloom and confirmed that this species can bloom in areas of the estuary devoid of native macrophytes. Evidence has suggested oyster cultures as the primary vector for the introduction and spread of this species in European and American estuaries (Krueger-Hadfield et al. 2017a). Although no oyster aquaculture facilities occur in Clonakilty Bay, oyster farming is present in other nearby estuaries, such as Oysterhaven (approx. 30 kilometres East following the coastline) and Roaringwater Bay (approx. 50 kilometres West). This species was also recorded from the adjacent Argideen estuary based on morphological identification, where this species might be present in relatively low abundance (Bermejo et al. 2019). Considering the geographical location of this record from the southernmost Irish coast (i.e., Clonakilty), along with the ubiquity of oyster cultivation throughout Ireland (https://www.agriculture.gov.ie/), the distribution of this species is likely more extended along the Irish coast than currently known. The secondary spreading of this species from estuaries, where oyster cultures are established, could explain the presence of *Agarophyton* in Clonakilty. As this red alga can survive under harsh environmental conditions (Nyberg and Wallentinus, 2009) and possesses a crucial vegetative dispersal potential (Krueger-Hadfield et al. 2016, Surget et al. 2017), it can be easily transported from one estuary to another entangled in fishing nets, boat anchors, by migrating birds or by coastal currents as drift material (Nyberg and Wallentinus, 2009, Martínez-Garrido et al. 2017).

6.5.2 A new opportunistic species blooming in areas where native opportunistic species cannot

The red seaweed *Agarophyton* is known to be more tolerant to different stresses (e.g., desiccation, extreme temperatures and salinities) and to thrive in a wide range of environmental conditions, displaying relatively fast growth rates (Abreu et al. 2011, Pedersen and Johnsen, 2017). This species is considered a euryhaline species, performing best under mesohaline conditions (optimal salinity between 10 and 20; Rueness 2005, Weinberger et al. 2008), being more competitive than *Ulva* in areas under variable salinity conditions (Sfriso et al. 2012). Moreover, *Agarophyton* also exhibits chemical defences that make it less affected by grazing and subsequently being less consumed in invaded areas than native species (Rempt et al. 2012). As a consequence of the relatively fast growth of *Agarophyton* combined with its ecological performance and probably linked to concurrent eutrophication processes, this species has outcompeted native macrophytes in some invaded estuaries (e.g., Nejrup and Pedersen, 2010, Cacabelos et al. 2012, Sfriso et al. 2012, Thomsen et al. 2013), or has bloomed in areas previously devoid of other macrophytes (Byers et al. 2012, Ramus et al. 2017, Surget et al. 2017). In this case, the analysis of the satellite images pre- (from 2010 to 2013) and post- (from 2014 to date) the *Agarophyton* bloom occurrence revealed some overlapping between *Ulva* spp. and *Agarophyton* blooms in the four years following the appearance of the first bloom (Fig. 6.3), but this invasive species has also proliferated in areas of the Clonakilty estuary devoid of native macrophytes, where salinity is usually lower and more variable as a consequence of freshwater inflows (Yokoya et al. 1999, Sotka et al. 2019). This leads to an overall more extensive area of the estuary affected by macroalgal blooms and to subsequent problems (e.g., summer anoxic events, odours), but also in a greater area capable of retaining large amounts of nutrients during late spring and summer when temperature and light conditions are favourable for the development of even more potentially harmful microalgal blooms (Sverdrup 1953).

These results have also revealed that the analysis of free open-access satellite imagery can be a useful and powerful tool to track recent biological invasions of conspicuous species in intertidal environments. The L7-ETM+ provided an interesting data record from 1999 to date and allowed the assessment of the potential area affected by macroalgal blooms and the identification of the first *Agarophyton* bloom event in 2014. This first bloom observation was supported by data from the Irish Environmental Protection Agency from the annual monitoring survey of this estuary in the context of the EU Water Framework Directive (R. Wilkes, pers. comm.). However, considerable limitations exist in the use of L7-ETM+ data as a result of the long revisit time (16-days) and excessive cloud coverage. The combination of these factors prevented any data acquisition from 2011 and precluded the comparison between years as imagery was not always available during the peak bloom period (June-August). The enhanced spatio-temporal resolution of the S2-MSI reduces these constraints. The higher revisit time of Sentinel-2 (2-days) improves the likelihood of detecting bloom events on cloud-free days. Furthermore, the higher spatial resolution of S2-MSI will improve the accuracy when studying estuarine bloom events similar in size to that found in Clonakilty.

6.5.3 Temporal variability

The assessment of the most relevant scales of variability showing explicit seasonal dynamics, with annual peaks of biomass during the summer (July-August) and minimum biomass in winter (February), as observed in other cold-temperate regions (e.g., Thomsen et al. 2006, Weinberger et al. 2008, Muangmai et al. 2014). Biomass of *Agarophyton* was present throughout the year. The highest values of biomass were observed in the inner section during July 2016 (mean±SD =1.78±1.11 kg FW m^{-2}; maximum =5.44 kg FW m^{-2}) and August 2017 (mean±SD =1.70±1.08 kg FW m^{-2}; maximum =5.21 kg FW m^{-2}). These maximum values were similar to those observed in other areas affected by *Agarophyton* blooms such as the Le Faou and Penfoul estuaries (France; 1.64 - 2.22 kg FW m^{-2} considering a 0.17 ratio dry: fresh weight; Surget et al. 2017), Mockhorn mudflat (northeast coast of USA; 1.67-2.28 kg FW m^{-2}; Gulbransen and Mcglathery, 2013), Aveiro lagoon (Portugal, 2.37 kg FW m^{-2}; Abreu et al. 2011), or Holckenhavn Fjord (Denmark; 2.73 kg FW m^{-2}; Nejrup and Pedersen, 2010), but lower than those observed in the Venice Lagoon (Italy) during conditions of peak biomass (6.53 kg FW m^{-2}; Sfriso et al. 2012).

The observed seasonal biomass dynamics was mainly explained by solar radiation and temperature, indicating that temperature and solar radiation are essential factors controlling the potential development of *Agarophyton* biomass in Irish estuaries, and the bloom size might be constrained by P rather than N limitation, as supported by the high tissue N contents observed throughout the year (above the critical quota (2.14%) proposed for this species by Pedersen and Johnsen (2017)) and the low tissue P contents (below the critical quota (0.14%)) observed during the season of active growth (from February to August; Fig. 6.5 and 6.6). The negative correlation between tissue N content and biomass (Rho =- 0.71; p-value <0.001) suggest a biomass dilution effect due to intensive growth during bloom development (Bermejo et al. 2019). On the other hand, the positive correlation between DIP and biomass, and with tissue P contents below the critical quota (Pedersen and Johnsen, 2017), supports the occurrence of P limitation during the period of intensive growth. Tissue P content seems to increase during the peak bloom (July 2016, and August 2016 and 2017; Fig. 6.5 and 6.6), likely a consequence of slower growth and a higher nutrient availability associated with an enhanced biomass degradation. The relative variation in biomass is positive and high from February to June (Fig. 6.5) as increasing temperatures and longer photoperiods promote the development of *Agarophyton*. After July, the higher temperatures might increase the stress during the desiccation period and enhance biomass degradation. In this sense, during August 2016, an anoxic event which was caused by the degradation of *Agarophyton* biomass was evident in the inner section of the Clonakilty estuary. In the outer section, the overgrowth of the bacterial community (observed as a milky liquid in the surface of the sediment or seaweeds) was not as evident or extensive. The hypoxic conditions and the release of toxic compounds (e.g., H_2S, NH_4^+, NO_2^-) associated with these events can cause stress (e.g., Vermaat and Sand-Jensen, 1987, Grazia-Corradi et al. 2006) and result in the rapid decline of the *Agarophyton* biomass (Thomsen et al. 2006, Sfriso et al. 2012). The high concentrations of ammonium observed during peak biomass in the inner section, where anoxic summer events were evident, and the positive correlations between minimum air temperature, and NO_2^- (rho =0.4; p-value <0.1) and NH_4^+ (Rho =0.53; p-value <0.01), support this hypothesis (Table 6.6).

6.5.4 Spatial variability

Unattached specimens entrained in mudflat sediments mainly comprised the *Agarophyton* bloom in the Clonakilty estuary. Nevertheless, sporophytes and gametophytes were observed, and some specimens attached to small pebbles or cockleshells were found in the outer section of the estuary, suggesting the existence of non-vegetative reproduction (Krueger-Hadfield et al. 2016). The assessment of the most relevant scales of variability (Table 6.4) indicated a homogeneous distribution at scales of meters or tens of meters, with no differences between and little data dispersion within sampling stations. The low environmental heterogeneity can explain this in these mudflats at small spatial scales and because *Agarophyton* remains somewhat anchored to the substrate by the burial of the basal part of the thallus. This has relevant implications for the biomass distribution and transport of macrophytes, determining biomass and nutrient balances in the estuary (Schories and Reise, 1993, Bermejo et al. 2019). This entrainment in the sediment could also provide access to nutrients from porewaters, as demonstrated in the case of *A. chilense* C.J.Bird, McLachlan & E.C.Oliveira (=*Gracilaria chilensis* (C.J.Bird, McLachlan & E.C.Oliveira) Gurgel, J.N.Norris & Fredericq), which is also entrained in mudflat sediments from South Pacific estuarine environments (Robertson and Savage, 2018).

At larger spatial scales, significant differences were observed in *Agarophyton* biomass distribution. Overall, higher seaweed biomass was found in the inner section, where both higher dissolved nutrient concentrations (DIN and DIP) and lower salinities were observed. This could favour the biological performance of *Agarophyton,* according to previous ecological and physiological studies (Yokoya et al. 1999, Rueness 2005, Weinberger et al. 2008). Considering the similar tissue N content found in the inner and outer sections and the high values observed during the peak bloom, both lateral transport and export from the estuary by wind and tidal currents might explain this biomass differences. Regarding the most relevant scales of spatial variability, the analysis revealed significant variability between sections, sites, and positions within the bloom, but not between sampling stations, suggesting homogeneity at small spatial scales. Different mechanisms may influence abundances in a perpendicular gradient to the main channel.

In rocky intertidal habitats, seaweed attachment combined with critical physical factors, such as emersion time and wave exposure, results in clear zonation patterns (Mangialajo et al. 2012, Chappuis et al. 2014). In mudflats, the lower slope, reduced wave exposure and weaker attachment of macrophytes to the substrate result in less evident and less consistent zonation patterns. In these areas, the distribution of macrophytes weakly anchored to the sediment such as *Ulva* spp. or *Agarophyton* might be the result of the effects of local environmental conditions on their biological performance, but also the biomass transport due to winds, wave action and tidal currents.

6.5.5 Relevance for environmental management

The arrival of *Agarophyton* to American and European estuaries has relevant impacts on the ecological functioning of mudflats. Overall, this alga acts as a habitat-forming species in areas previously devoid of vegetation for some organisms, thereby increasing habitat complexity, enhancing epibenthic diversity and altering environmental conditions (Wright et al. 2014, Davoult et al. 2017, Ramus et al. 2017). In the context of eutrophication, the decay rate is slightly lower than alternative bloom-forming *Ulva* spp., slowing down remineralisation cycling and acting as a temporal sink for nutrients (Thomsen et al. 2006, Pedersen and Johnsen, 2017). The presence of *Agarophyton* increases net denitrification rates in comparison with bare sediments, thus favouring the removal of nitrogen from the estuary (Gonzalez et al. 2013). However, this species occupies mudflats, which are protected by the European Habitat Directive (92/43/EEC; Habitat 1140). These mudflat habitats harbour their own unique and diverse biota and play a key role in the life cycle of some specialised organisms, such as shorebirds (Haram et al. 2018). Depending on the biomass density of this habitat-forming species, some of the aspects observed by previous authors may have ambiguous or deleterious effects on the environment. For instance, Gonzalez et al. (2013) pointed out that at high densities (approx. 700 gr FW m^{-2} *Agarophyton*), denitrification rates dropped, suggesting a potential biomass threshold for macroalgal enhancement of denitrification. Although the nutrient cycling may be slowed down when fast-growing species like *Ulva* spp. are replaced by *Agarophyton*, the opposite is expected when *Agarophyton* is replacing slow-growing species such as *Fucus* spp., *Ascophyllum nodosum* or seagrasses (Pedersen and Johnsen, 2017). The occurrence of summer anoxic events and associated massive mortalities of epifauna and infauna should also be considered (Ramus et al. 2017, Keller et al. 2019). Such anoxic events due to excessive input of organic matter by decomposing *Agarophyton* biomass has been described before (e.g., Thomsen et al. 2006, Weinberger et al. 2008, Sfriso et al. 2012, this study). Thus, considering: i) this species can bloom in areas previously devoid of native macrophytes, reaching high biomass densities that can lead to the occurrence of summer anoxic events; ii) the future predicted temperatures for Ireland might enhance the growth of *Agarophyton* in Irish estuaries, and iii) the expected increase in the number of estuaries affected by nutrient over-enrichment as a consequence of the intensification of agriculture in Ireland (Food Wise 2025; https://www.agriculture.gov.ie/2025strategy/); the addition of this species to Irish flora in a global change context could be considered a threat for biodiversity and ecosystem functioning, rather than an opportunity for the recovery of ecosystem functioning.

6.5.6 Potential utilisation of introduced species

Many commonly harvested seaweed species already exhibit many commercial uses in human food, feed, agricultural, pharma and cosmetics sectors (Silva et al. 2019). In this context, utilisation of bloom-forming species such as *A. vermiculophyllum* and *Ulva* may hold considerable exploitative potential. The commercial exploitation of invasive bloom-forming is a beguiling prospect, particularly as alien algal species can colonize new environments more successfully than other organisms (Marampouti et al. 2021).

The wild harvest of *A. vermiculophyllum* could provide a dietary supplementation for ruminant nutrition (Cabrita et al. 2017), while studies report on the harvesting of wild *A. vermiculophyllum* (from northwestern Portugal) to produce industrial food-grade agar (Villaneuva et al. 2010) or even as a potential source for hemagglutinin production (Kakita et al. 2020). In recent years, significant research has been invested into the use of both *Ulva* and *A. vermiculophyllum* as bioabsorbent materials for the treatment of toxic metal contamination in aqueous streams (Karthikeyan et al. 2007), to remove nutrients from fish aquaculture (Abreu et al. 2011, Shin et al. 2020) or as biofilters of toxic effluents (Msuya and Neori 2002). Increasingly novel commercial applications for species such as *A. vermiculophyllum* are coming to the fore, such as its use as functional, edible packaging material, films and coatings (Sousa et al. 2010, Baek and Song 2018, Tretiak et al. 2021) or even as an environment-friendly source of natural sunscreens (Chaves-Peña et al. 2020).

It is more likely, however, that cultivation will represent the future for obtaining raw materials for species such as *Ulva* and *A. vermiculophyllum* for commercial purposes, and it is thought that cultivation of these species would be preferable to the harvest of natural invasive populations (Calheiros et al. 2021), due in part to difficulties in the guaranteed supply of raw materials from natural stocks, natural variation in biomass yields and species abundance, As well as an inability of limited natural harvests to keep up with commercial demand (Kakita et al. 2020, Calheiros et al. 2021, Tretiak et al. 2021). For many high-value usages, the ability to monitor environmental conditions in which raw material is grown, the ability to ensure stricter control over growth conditions and water quality, and to prove traceability is crucial (Mollet et al. 1998).

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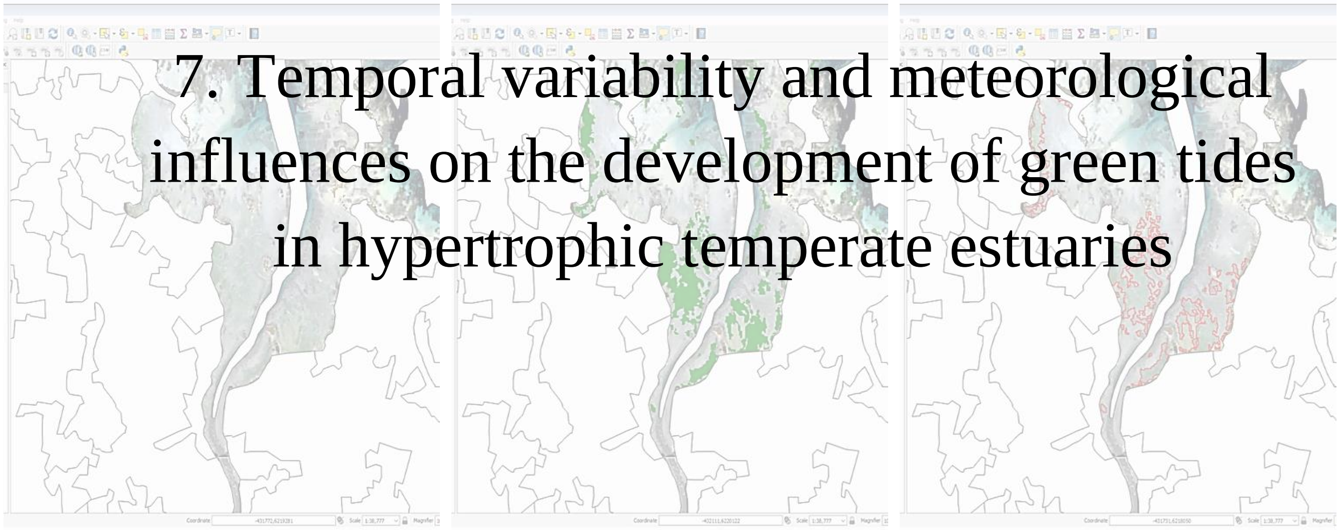
7. Temporal variability and meteorological influences on the development of green tides in hypertrophic temperate estuaries



7.1 Abstract

Estuaries are some of the most degraded habitats in Europe, with the extensive presence of green tides of the species *Ulva* blanketing a high number of these vulnerable water bodies across the North-East Atlantic. The presence of large accumulations of these “nuisance” blooms impedes the achievement of national, international, and environmental commitments set out in global legislative frameworks for the good status of water bodies. In this study, data obtained as part of the EU Water Framework Directive (WFD) on the location and magnitude of green tides in eutrophic North-East Atlantic estuaries were harmonized, and satellite imagery (Sentinel and Landsat) was used to reconstruct the occurrence of these problematic seaweeds in selected estuaries. A multivariable linear model was developed (GLS), and hierarchical partitioning (HP) was applied to a meteorological dataset (precipitation, temp, photoperiod, and UV index) to determine the contribution of each environmental variable most correlated with bloom development. Results demonstrate that green tides are present in a high number of estuaries in the North-East Atlantic, though their magnitude has remained stable since 2016. Spring and summer periods were confirmed as the most important for bloom development, with temperature and photoperiod accounting for 89% of the total variation and supporting the hypothesis that both factors are key determinants in *Ulva* seasonality in temperate hypertrophic waters. Green tides remain a pervasive presence in North-East Atlantic waters, and their presence demonstrates that these estuarine systems have shifted to systems saturated by nutrients.

7.2 Introduction

As global populations rise and affluence increases, so do the need for goods and services (Godfray et al. 2018, OECD 2018). Increased demand for agricultural land and urban space is expected to continue for the next decades (Strokal et al. 2021, Tian et al. 2021). However, the growth of land dedicated to agriculture has slowed in recent years due to finite global arable land (Blandford 2019), leading to an intensification of agricultural practices to maintain increased food production (Steffen and Stafford Smith, 2013, Steffen et al. 2015, Sturck et al. 2018). Global urbanisation has also expanded throughout the 20th century (Angel et al. 2011), with this trend expected to continue (Neumann et al. 2015); in 2017, 55% of the world's population (4.1 billion people) were living in urban areas with this proportion expected to increase to 60% by 2030 (UN 2019). Land and seascape anthropisation have been identified as powerful drivers of global change (Ren 2015, Rosa et al. 2015).

Since the “Great Acceleration” (loosely defined as the period since World War II), human activities, including fossil fuel consumption (Gaulin and Le Billon, 2020), changes in land use (Cherubini et al. 2018), the intensification of agriculture and global food systems (Clark et al. 2020, Lal 2021) and increasing urban sprawl (Elmqvist et al. 2021) have influenced global ecosystems leading to substantial responses in environmental conditions. These responses have resulted in a loss of ecosystem goods and services, undermining future human well-being and development. This loss has become especially evident in vulnerable and complex ecosystems such as estuarine environments, which have experienced profound modifications, leading to shifts from desired to less desired states (Folke et al. 2004, Lotze et al. 2006).

Estuaries and coastal lagoons are highly dynamic environments and are among the most valuable ecosystems on earth, as they provide many ecological goods and services (Costanza et al. 1997). For this reason, these environments have been focal points of settlement for human populations since the early stages of civilisation (Lotze et al. 2006, Airoldi and Beck, 2007). Located at the interface between drainage basins and the coastal ocean (Malta et al. 2017), estuarine environments are often vulnerable to receiving allochthonous inputs from urban, industrial, and agricultural effluents (Lopes et al. 2007, Wang et al. 2021). The reduced water exchange in these water bodies compared to open coastal waters makes these environments more prone to excessive nutrient enrichment, ultimately leading to eutrophication (Pang et al. 2010). Eutrophication is one of the most critical threats to biodiversity and the functioning of aquatic ecosystems and has made estuaries some of the most degraded habitats worldwide (Lotze et al. 2006, Airoldi and Beck, 2007).

One of the most evident signs of excessive nutrient enrichment in estuaries is the development of opportunistic macroalgal blooms (Valiela et al. 1997, Teichberg et al. 2010, Bermejo et al. 2019), particularly green macroalgae of the genus *Ulva* (commonly known as 'Sea Lettuce'; Ulvophyceae, Chlorophyta), referred to as “green tides”. The development of green tides is a global phenomenon impacting coastal ecosystem services and the goods they provide (Valiela et al. 1997, Ye et al. 2011, Smetacek and Zingone, 2013). As the relatively low hydrodynamics and shallowness of these areas favour the accumulation of nutrients and light availability (Valiela et al. 1997, De Casabianca et al. 2002), opportunistic algal species can proliferate and outcompete other late-successional habitat-forming species such as seagrasses and Fucales/fucoids (WFD 2014). Although these blooms are not toxic by themselves, the accumulation and degradation of large amounts of biomass can lead to dystrophic crises affecting the functioning of these ecosystems and limiting the human uses of these areas (Dominguez and Loret, 2019).

There have been records of local opportunistic *Ulva* blooms occurring in the proximity of sewage discharge points since the beginning of the 20th century (Letts and Richards, 1911), with increasing frequency and scale in industrialized countries since the early 1970s (Piriou et al. 1991, Merceron et al. 2007, Smetacek and Zingone, 2013) blanketing entire estuaries and beaches. This increase in bloom frequency and magnitude has been related to the anthropogenic increase of nutrient loads in aquatic ecosystems following the development of industrial agriculture and associated population growth (Valiela et al. 1997, Diaz and Rosenberg, 2008, Smetacek and Zingone, 2013). As with other primary producers, the development of opportunistic bloom-forming species is mainly controlled by temperature, light, nutrients, and salinity

(Floreto et al. 1993, Xiao et al. 2016). In aquatic ecosystems, nitrogen and phosphorus are the main nutrients naturally constraining the growth of primary producers (McClelland and Valiela, 1998, Elser et al. 2007). Overall, nitrogen has been identified as the limiting factor in coastal environments (Howarth and Marino, 2006), whereas phosphorus has been shown to limit primary production in freshwater ecosystems and tropical carbonate-rich marine waters (Lapointe et al. 1992, Valiela et al. 1997). Regarding pristine temperate estuaries, the proliferation of opportunistic bloom-forming species is usually limited by nitrogen during spring and summer and light and temperature during autumn and winter (Teichberg et al. 2010). Nutrient over-enrichment of these systems leads to a shift from a system limited by nitrogen inputs to a system gradually saturated by nitrogen, where light and temperature likely play a more significant role in controlling bloom development (Lyngby et al. 1999, Le Moal et al. 2019, Bermejo et al. 2020).

The continued observed environmental degradation of aquatic ecosystems has piqued concerns in the international community, leading to several important legislative initiatives to prevent further degradation (e.g., Water Framework Directive 2000/60/EC, UN Sustainable Development Goals, Marine Strategy Framework Directive). Implementing these legislative tools requires monitoring water bodies at larger scales, on many occasions comprising several countries. The increased monitoring efforts pose a challenge for environmental regulatory agencies. The use of Earth Observation (EO) technologies is becoming an affordable methodology for monitoring at broad spatial and temporal scales, providing high quality, reliable, and synoptical data. Several recent studies demonstrate the possibility of EO techniques for the monitoring of problematic macroalgal blooms of different sizes and in different environmental contexts, from large pelagic blooms covering 10,000’s of hectares of open sea (Hu 2009, Cui et al. 2012) to smaller blooms in the scale of 10’s of hectares, blanketing intertidal, coastal, and estuarine shores (Bermejo et al. 2020, Karki et al. 2021). Considering the current scenario of global warming and nutrient over-enrichment of cold temperature estuaries, a clearer understanding of the influence of climatological variability on bloom development becomes crucial for managing problematic macroalgal tides. In this context, the primary objective of this study was to assess temporal patterns of variability and the influence of meteorological factors on the development of *Ulva* blooms in cold temperate estuaries. This involved; i) using Earth Observation datasets combined with in-situ field data to reconstruct green tide events over a five-year period in selected north-Eastern Atlantic estuaries, ii) assessing the spatial and temporal distribution of intertidal blooms, and iii) investigating the impact of interannual meteorological variability on the development and magnitude of these blooms.

7.3 Materials and methods

7.3.1 Study area

The area of study comprised 217 cold-temperate estuaries, bays and beaches affected by macroalgal blooms between N 57° 29' 49.2379" and N 45° 49' 43.6773" latitude, and W 4° 46' 29.9564" and E 8° 20' 42.0444" longitude (Fig. 7.1).

In France, three recurring blooms, located at Penze (48°40'22.6"N 3°56'27.7"W) and Ty-Nod (48°38'38.4"N 3°51'37.6"W) on Brittany's northern shore on the English Channel, and also Pouldon located on the south western coast, on the Bay of Biscay (47°51'30.4"N 4°10'25.2"W) were assessed. In Ireland, four annually recurring blooms, three of which occur on Ireland's southern shore on the Celtic Sea located at Clonakilty (51°36'43.9"N 8°52'25.1"W), Argideen (51°38'22.3"N 8°43'35.7"W), Dungarvin (52°04'13.8"N 7°35'20.7"W), and one bloom occurring in the Irish Sea on Irelands eastern shore (Tolka) (53°22'05.2"N 6°09'55.9"W) were assessed. The Tyne estuary on the North Sea (56°00'18.7"N 2°35'23.0"W) was evaluated in the UK.

7.3.2 In-situ data collection

Different environmental protection agencies obtained green tide coverage as part of Water Framework Directive (WFD) surveys in transitional water bodies across the study areas (Appendix C Table S6). Due to their sensitivity to anthropogenic pressures, *Ulva* is often used as a Biological Quality Elements (BQE's) under the WFD, acting as an indicator of water quality and nutrient enrichment, allowing for the monitoring and assessment of the Ecological Status (ES) of European waters (Scanlan et al. 2007, Wells et al. 2014, Ní Longphuirt et al. 2016, Wan et al. 2017). Traditional field sampling techniques carried out at low tide were employed to determine bloom coverage, utilising low flying aircraft in British, German, and French sites and hovercraft in Irish sites. Further details about the sampling methodologies applied can be found in Ní Longphuirt et al. 2016 and Wan et al. 2017.

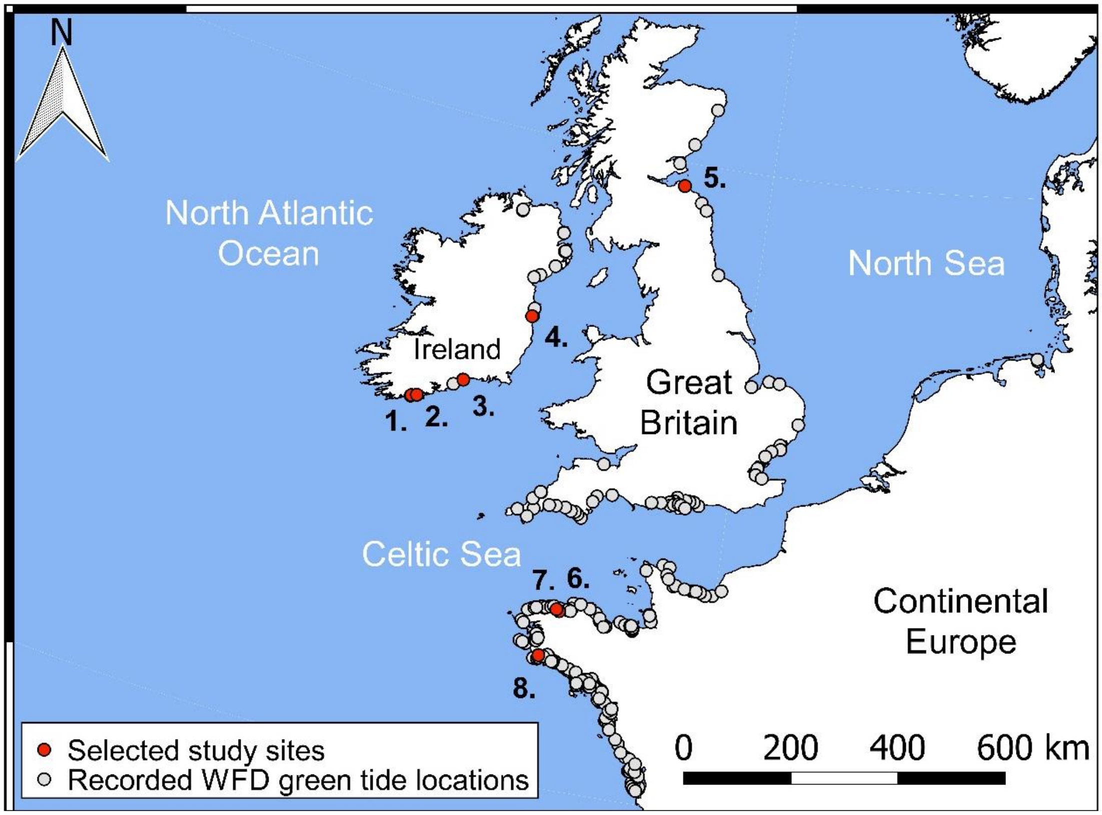


Fig. 7.1 Map highlighting the location of known macroalgal blooms across coastal North-Eastern Atlantic countries, including the location of the eight estuaries in this study, **1.** Clonakilty, **2.** Argideen, **3.** Dungarvan, **4.** Tolka, **5.** Tyne estuary, **6.** Penze, **7.** Ty Nod and, **8.** Pouldon

7.3.3 Satellite imagery

Satellite data sets from both the Landsat-8 Operational Land Imager (L8-OLI) and the MultiSpectral Instrument onboard the European Space Agency (ESA) Sentinel-2 Multispectral Instrument (S2-MSI) were used to determine green tide extensions in selected estuaries between the years 2016 and 2020 (earliest available scenes for the S2-MSI imager are from July 2015; Information on sensor and acquisition date; Appendix C, Table S7). The L8-OLI mission from the National Aeronautics and Space Administration (NASA) has been in operation since February 11, 2013 and acquires approximately 740 scenes per day on a 16-day repeat cycle. The L8-OLI provide images with a swath width of 185 km (USGS 2020). Sentinel-2, meanwhile, consists of two satellite imagers (Sentinel-2A and 2B sensors) operating on a combined 5-day revisit cycle and a swath rate of 290 km (USGS 2020).

7.3.4 Satellite imagery processing

In general, satellite imagery from S2-MSI was preferred over L8-OLI due to the former's improved spatial and temporal resolution. In the case where appropriate S2-MSI scenes were unavailable, L8-OLI scenes were used. Scenes were considered appropriate when acquired at low tide (+/- 2hrs) and with non-obstructive cloud cover. For S2-MSI data (availability: Vis. and NIR at 10 m resolution, 2015- present), both Level-2A and Level-1C S2-MSI scenes from 2015-2018 were downloaded from the Copernicus DataHub website (https://scihub.copernicus.eu/). With respect to L8-OLI, Level-1 datasets were downloaded from the United States Geological Survey (USGS) website (https://earthexplorer.usgs.gov/). Table 7.1 highlights satellite bandwidths and resolution.

The mapping and classification of green tidal events in European waters require several steps, from initial scene acquisition to atmospheric processing and applying an applicable classifier. Initial processing (resampling, scene clipping) of S2-MSI and L8-OLI scenes were carried out using the ESA Sentinel Application Platform (SNAP) toolbox (v. 6.0). Downloaded S2-MSI scenes were resampled to the resolution of 10 m bands (R, G, B or NIR), allowing coarser bands to match the 10 m resolution. Following this step, only relevant spectral bands were retained before clipping. Likewise, in the case of L8-OLI, coarser bands were resampled to 30 m resolution to allow spatial and spectral subsetting. True colour composite images (RGB) were created using ENVI software (v. 5.3.1; Research Systems, Boulder, CO, U.S.) by combining red, green, and blue colours designated as bands 4, 3 and 2, respectively, for individual S2-MSI and L8-OLI scenes. Before further processing, a visual inspection of all true colour composite scenes was carried out.

Sentinel-2 Level-1C radiance data recorded at the top of atmosphere (TOA) were scaled to surface reflectance by applying the dark object subtraction (DOS) technique (Gilmore et al. 2015) before atmospheric correction to Level-2A bottom of atmosphere (BOA) data using the Sen2Cor atmospheric correction plugin in SNAP desktop (Louis et al. 2016). According to appropriate country projections, satellite imagery was processed (Ire 29 N, UK 30 N, Brittany 30 N) and WGS 84 Datum. The ENVI software was then used to further process and classify scenes.

Table 7.1 Satellite bandwidth and resolution

Satellite imager	Band	Wavelength	Resolution
Sentinel-2	B2	443 nm	10 m
	B3	490 nm	10 m
	B4	665 nm	10 m
Landsat-8 OLI	B2	450 - 510 nm	30 m
	B3	560 – 590 nm	30 m
	B4	640 – 670 nm	30 m

7.3.5 Determining green tide coverage

Following Karki et al. (2021), an Area of Interest (AOI) was defined for each site studied using CORINE (Coordination of Information on the Environment) Land Cover (https://land.copernicus.eu/pan-european/corine-land-cover). The Corine data set is a pan-European geodatabase that provides full coverage of Europe and land uses, with each specific land use having a unique identifier. In this case, the area of interests corresponded with the tidal flats (4.2.3) and estuaries (5.2.2) labels, facilitating the removal of terrestrial vegetation and saltmarshes from the consideration.

A pixel-based supervised Maximum Likelihood (ML) classification was carried out in these AOI to determine blooms coverage as outlined in Bermejo et al. (2020). Briefly, ~10 individual classes ("Dry Sand", "Wet Sand", "Urban", "Bloom", "Vegetation", "Water", "Saltmarsh") were considered for training. The MLC was based on pixel training with >200 pixels per class used to train the data. Once pixels were classified (Foody 1992) and manually refined, superfluous classes were removed from the analysis allowing for the development of a bloom mask and the determination of bloom extent. Subsequently, a vector outline for individual blooms throughout the study period was generated, and the maximum spatial extension of each bloom was determined in ArcMap (version 10.5.1) (see Appendix C, Table S8-S15). A workflow of operations is shown in Fig. 7.2, and an example of an ML classifier output is shown in Appendix C,

Fig. S4. Satellite and WFD reference data showed a high correlation (r = 0.961, p = <0.001) and a good match (kappa; moderate -0.45- and good -0.76).

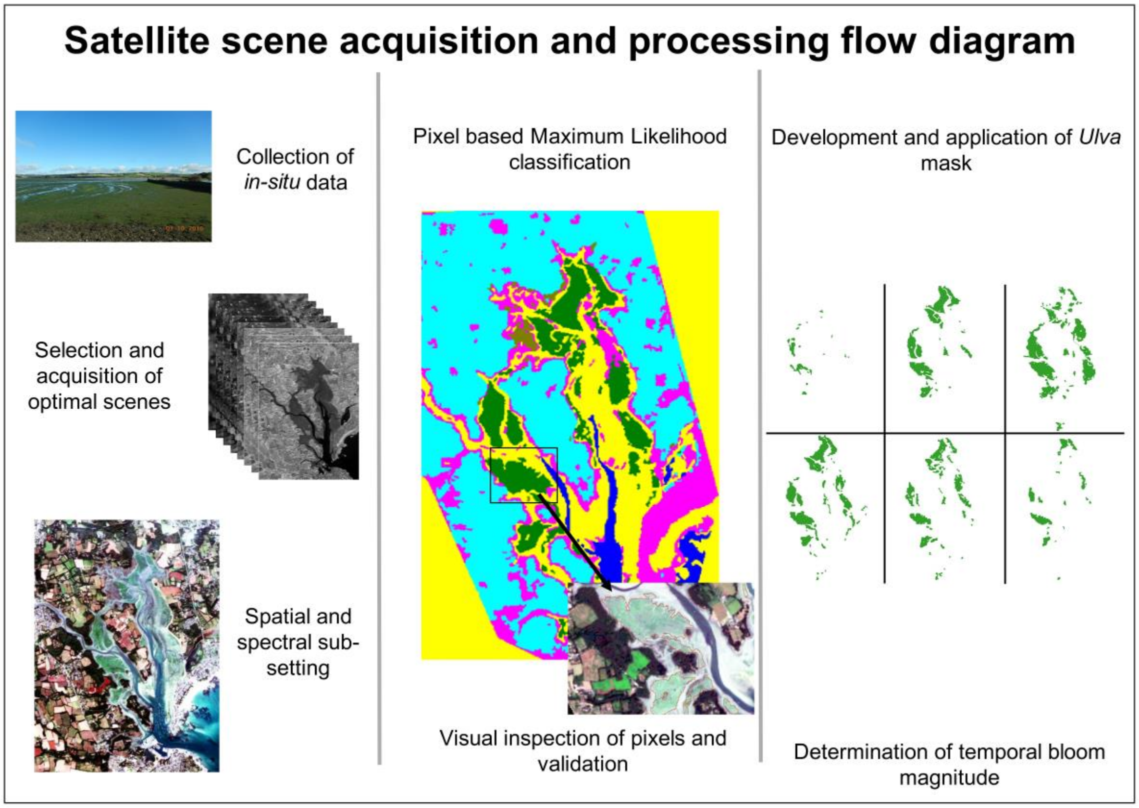


Fig. 7.2 Flow diagram showing Sentinel-2 and Landsat 8 scene processing workflow

7.3.6 Site selection

A comprehensive screening of available EO imagery matching to field survey sites was conducted to assess seasonal bloom initiation and cessation and the influence of meteorological factors in bloom development. Due to methodological and practical constraints, a subset of eight estuaries affected by nuisance green tides spread across the UK, Ireland and France were selected for further analyses. The criteria for site selection were: i) data availability; ii) the absence of conspicuous seagrass meadows; and finally, iii) the lack of significant variation in land use within the catchment in each site selected over the study period. Regarding data availability, cloud obscurity and tidal height resulted in the limited usability of an extensive number of available scenes, which constrained the number of sites with near-complete data sets (1 image per month from Jan. 2016 – December 2020; further description of each study site is found in Section 2.3). In addition, the spectral similarities of seagrass meadows and green tides at the spatial scales provided by the EO sensors renders it impossible to definitively distinguish one from another (Kutser et al. 2020, Mora-Soto et al. 2020).

7.3.7 Catchment-land use generation using the CORINE land data set

Information regarding land use in catchment areas was retrieved from CORINE Land Cover data sets. The component land use within selected catchments and the land use proportional estimates were based on vector data from the CORINE data set. Four land uses were considered for this analysis: “agricultural land”, “residential, industrial and commercial properties”, “natural vegetation and forest”, and “aquatic bodies”. The period of assessment spanned from 2012 to 2018, as no data were available for the years 2016 and 2020. Catchment areas were defined according to the European Environmental Agency (https://www.eea.europa.eu/data-and-maps/data/european-river-catchments-1).

To reduce the influence of confounding effects such as changes in pollutant loading (e.g., nitrogen, phosphorus, emergent contaminants), only estuaries that displayed little changes in land use within the catchment area were considered (<1.5% change in land use from 2012 to 2018; Appendix C, Table S16 – S20, Fig. S5-S7).

7.3.8 Meteorological conditions and photoperiod

Daily data from the nearest meteorological station for each selected estuary were extracted from the World Weather Online Data Portal (https://www.worldweatheronline.com/) over the study period (2016-2020). The meteorological variables included were air temperature (C; average, min, max), rainfall (mm), and ultraviolet (UV) index. Daily photoperiod data were retrieved from “Time and Date AS” (https://www.timeanddate.com). Each parameter (i.e., accumulated rainfall, mean photoperiod, mean UV index, and average, maximum, and minimum air temperatures) was calculated considering data from a two-week period prior to image acquisition (Appendix C, Fig. S8).

7.3.9 Assessing seasonality among estuaries

To assess seasonality and the spatial variability of *Ulva* blooms under investigation, a generalized least squares (GLS) model was fitted. Due to the heteroscedasticity of our data, a GLS model was chosen because of its ability to handle error variance. To account for heterogeneous variance in our data, we used the ‘nmle’ packages (Pinheiro et al. 2015) ‘varIdent’ variance function to test for differences between “Months” (12 levels: January through December) and “Estuaries” (8 levels: Clonakilty, Argideen, Dungarvan, Tolka, Tyne Ty Nod, Pouldon and Penze) using the software R (version 1.4.1103; R Core Team, 2009). Bloom size was previously standardized per estuary and year by dividing the bloom size by the annual maximum size for a specific estuary to remove or reduce the effect of different estuary sizes and annual variability.

7.3.10 Assessing inter-annual and spatial variability among estuaries

To identify temporal trends in maximum bloom size between estuaries and years, an Analysis of Covariance (ANCOVA) was performed. For this analysis, only bloom sizes were standardized by estuary but not year. The visual inspection of the plot of residuals versus fitted values revealed conspicuous differences in residual variance among the different “Months”. This heterogeneity in the variance between months was incorporated in the model. Its suitability was confirmed considering Akaike´s Information Criteria (AIC), comparing this model with a similar model assuming a homogeneous distribution of variability between months (Zuur et al. 2009). A Dunnett's Modified Tukey-Kramer Pairwise Multiple Comparison Test (Dunnett 1980) was used for a posteriori comparison among different levels of one or multiple factors.

7.3.11 Assessing the effects of climatological and local variability in bloom development

A multivariable linear model was developed, and hierarchical partitioning (HP) was applied to the meteorological dataset to test for collinearity and estimate each environmental variable's independent contribution most correlated with bloom development. The meteorological variables precipitation (mm), min, mean and max temp (Co), HT (number of days with temperatures exceeding 20oC during the two weeks prior to satellite image acquisition), photoperiod (hrs.) and UV index were included in the model to identify the most relevant variables and were included as random effects as they are highly correlated. We used the ‘hier.part’ package within R studio to analyse the R2 goodness-of-fit measure. Hierarchical partitioning can handle collinearity between variables and was used to distinguish redundant variables in our model. From our analysis, statistically significant environmental variables were identified using the ‘rand.hp’ function, and their contribution was assessed using z-scores obtained using 1000 randomizations of the data matrix. Non-linearity was checked by plotting the residuals versus fitted and revealed a good model fit.

Finally, to determine whether significant variation existed in our data between years (2016-2020) and considering the heteroscedasticity of the data, a Kruskal-Wallis test was performed considering year as a factor. In all statistical analyses, significance was set at p-value < 0.05 probability.

7.3.12 Verification and validation

Manual verification, subjective judgement and refinements are essential steps of the mapping workflow to assure that the bloom pixels are represented correctly. It was necessary to eliminate areas that corresponded to terrestrial vegetation in specific locations. Due to the coarse resolution of Corine land cover data sets, a few areas also included artificial structures and salt marshes.

7.4 Results

7.4.1 Spatial distribution of green tides North-Eastern Atlantic waters

Field sampled data highlighting the location and magnitude of *Ulva* blooms in the North-East Atlantic collected as part of the WFD national monitoring in Ireland, the UK, France, and Germany are shown in Fig. 7.3. In total, 217 blooms were recorded, a combined coverage of 52,133 Ha. Of these, the majority (86%) are blooms whose surface area measures below 200 ha (Table 7.2).

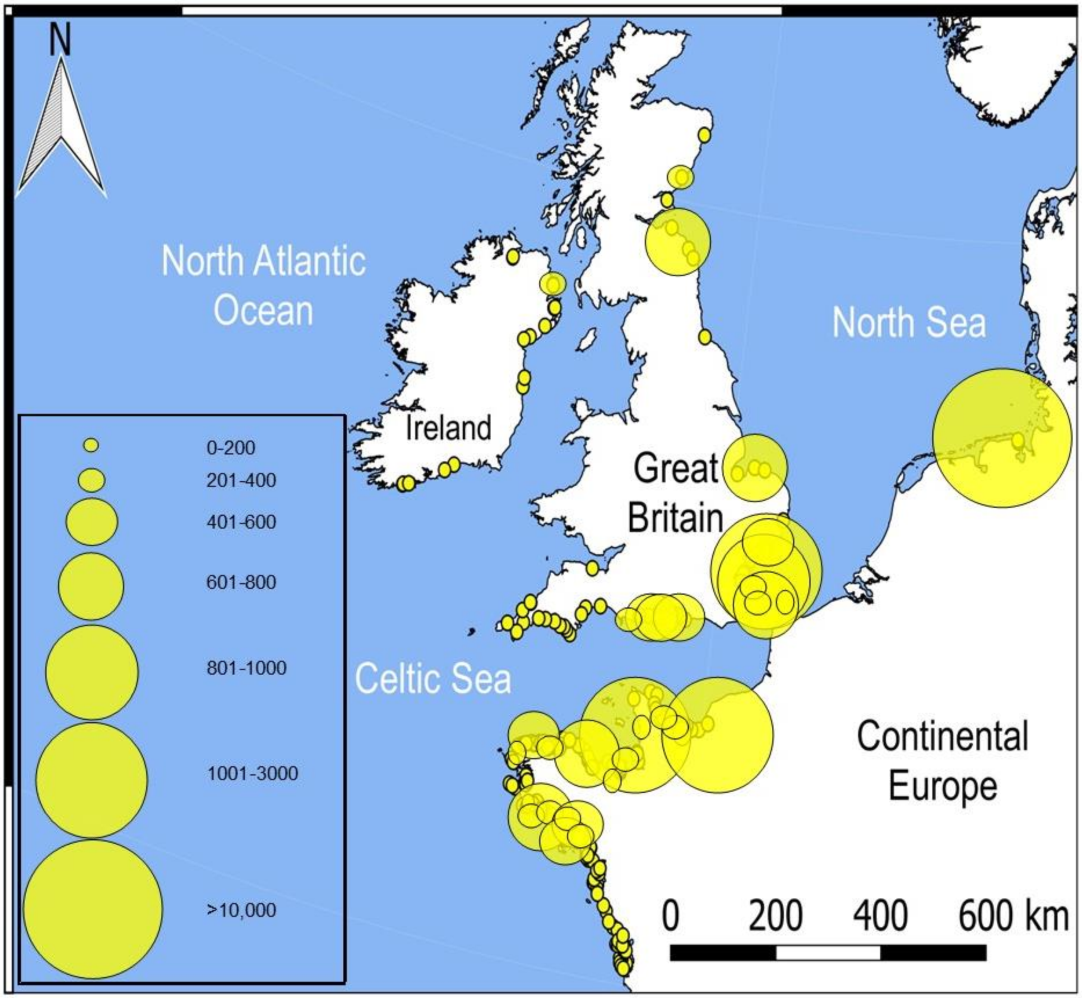


Fig. 7.3 Proportional bubble map highlighting the location and magnitude of known macroalgal blooms across North-Eastern Atlantic coastal and transitional waters collected as part of a European WFD intercalibration exercise. Area recorded in hectares.

The Wadden Sea is host to the largest *Ulva* coverage recorded in Eastern Atlantic waters, though strictly not a single bloom, rather comprised of numerous individual patches of macroalgae. Taken together, these patches measure a total surface area of 28,165 ha. Beyond the *Ulva* assemblages of the Wadden, the green tides present in the North-East Atlantic ranged from 0.1 ha. (Axe, England) to 2988.9 ha (Medway, England) (Mean: 111 ha, Median 23 ha). In France, the greatest densities of blooms occur on the Breton coast, with 157 *Ulva* blooms recorded along the northwest Brittany coast. The majority (142; 90%) of French blooms are below 200 ha. There are 15 blooms whose surface area is greater than 200 ha, with two of the largest *Ulva* blooms in north-eastern Atlantic waters (Yffiniac 1,414 ha) and Morieux (1,955 ha) measuring >1000 ha, both located on the northern Breton shore. There exist considerable *Ulva* proliferations in British waters, with four recorded off the coast of Scotland, the largest of which (285 ha) occurs in the Montrose estuary and a further 46 blooms observed via ground-truthing occurring on the south to the south-western shore of England. Of these, 34 blooms on the English coast are less than 200 ha. England has 12 blooms over 200 ha, all on the east-southeast coast, with one bloom (Medway) measuring 2,989 ha, the largest *Ulva* proliferation in UK waters. In Ireland, incidences of green tidal colonisations are particularly evident along the southern coast in the waters of the Celtic Sea, with several blooms occurring on Ireland's eastern coast along the Irish Sea. All the blooms recorded in the Republic of Ireland are between 27–176 ha. Northern Ireland, meanwhile, is host to four recurring blooms, the largest of which is located at Larne (244 ha).

Table 7.2 The magnitude of *Ulva* bloom surface extensions found in the North-East Atlantic

Country	***Ulva* surface area 0-200 (ha)**	***Ulva* surface area 201-400 (ha)**	***Ulva* surface area 401-600 (ha)**	***Ulva* surface area 601-800 (ha)**	***Ulva* surface area 801-1000 (ha)**	***Ulva* surface area 1000-3000 (ha)**	***Ulva* surface area >10,000 (ha)**	**Total surface area (ha)**
Germany	-	-	-	-	-	-	1	28,165
France	142	8	3	2	-	2	-	12,793
England	34	2	5	3	1	1	-	10,035
Scotland	3	1	-	-	-	-	-	405
Ireland	5	-	-	-	-	-	-	386
N. Ireland	3	1	-	-	-	-	-	349
Total	187	12	8	5	1	3	1	52,133

7.4.2 Seasonality of Ulva blooms in North-Eastern Atlantic waters

The GLS model indicated significant differences between months and estuaries in standardized annual cover and in the interaction between both factors (Table 7.3). Bloom cover is highly contingent on the time of year, with "Month" explaining most of the variance observed. All eight blooms show a distinct pattern of seasonal growth though differences in initial development were observed independent of latitude (Fig.

7.4). In general, blooms establish in April or May, reaching peak magnitude during June and August, for the most part during August. Over the five-year study period for the eight estuaries, 25 peaks were recorded in August, 9 in July and 6 in June. Green algal coverage remained conspicuous until October before and mostly absent from December-March. Two exceptions included the presence of a bloom all year round in Clonakilty and the earlier peaking of the bloom in the Tolka estuary in June. Data on bloom initiation, peak and cessation are displayed in Table 7.4.

Table 7.3 Values from analysis of variance, indicating the percentage variation in *Ulva* extension explained by Month, Estuary and the interaction between Month and Estuary

	numDF	**F-value**
(Intercept)	1	1787.90***
Month	11	341.75***
Estuary	7	44.62***
Month and Estuary	77	2.77***

Table 7.4 Highlighting bloom initiation, peak and end months, including mean bloom size and max bloom size, per estuary

Country	**Estuary**	**Max Bloom Size (2016-2020) (ha)**	**Mean Bloom Size (June-August; 2016-2020)) (ha)**	**Initiation month**	**Peak month**	**End month**
Ireland	Tolka	39.4±12.7	30.7±5.4	March/April	June	October
	Clonakilty	36.8±10.7	31.4±3.6	Variable	July-August	Variable
	Dungarvan	137.5±47.0	92.5±29.0	April-May	July-August	October - November
	Argideen	59.4±17.9	38.8±13.0	April-May	August	November
France	Penze	205.5±70.1	172.4±21.1	March	July	November
	Ty Nod	299.4±87.5	210.1±47.4	March	August	November
	Pouldon	158.9±57.2	134.1±25.3	March	August	October-November
Scotland	Tyne	30.8±9.6	20.1±7.0	April	August	October

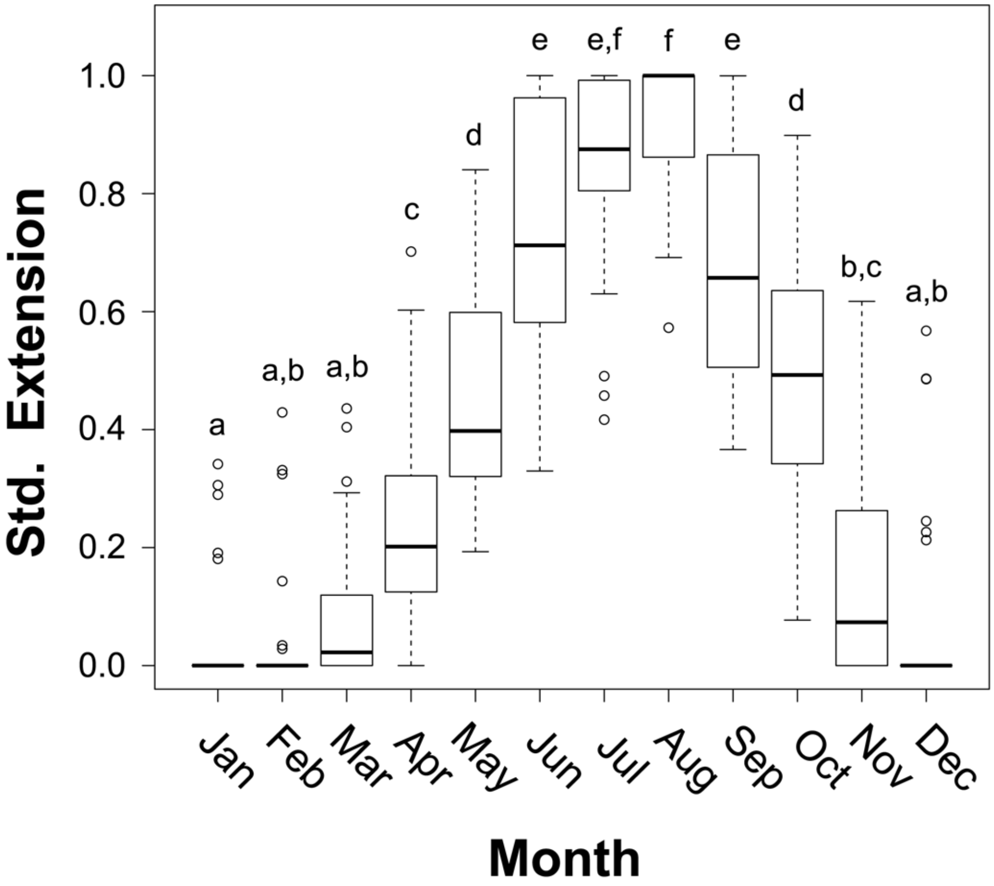


Fig. 7.4 Seasonality of standardised *Ulva* coverage. Box plots for the Standard mean extension (ha) of *Ulva* during the experimental period 2016-2020. Box plots indicate the median (bold line near the centre), the first and third quartile (the box) and the extreme values whose distance from the box is at most 1.5 times the interquartile range (whiskers), and remaining outliers (dots). Different letters above bars indicate significant differences ($p < 0.05$) between groups, as revealed by Dunnett's Modified post-hoc analysis

7.4.3 Assessing inter-annual and spatial variability

Our findings indicated that although differences were observed in the annual magnitude of *Ulva* blooms (Fig. 7.5), the blooms have remained relatively constant over the study period (2016-2020) (Kruskal-Wallis chi-squared = 5.7563, df = 4, p-value < 0.2181) and have neither significantly increased nor decreased in their magnitude, indicating continual eutrophic conditions.

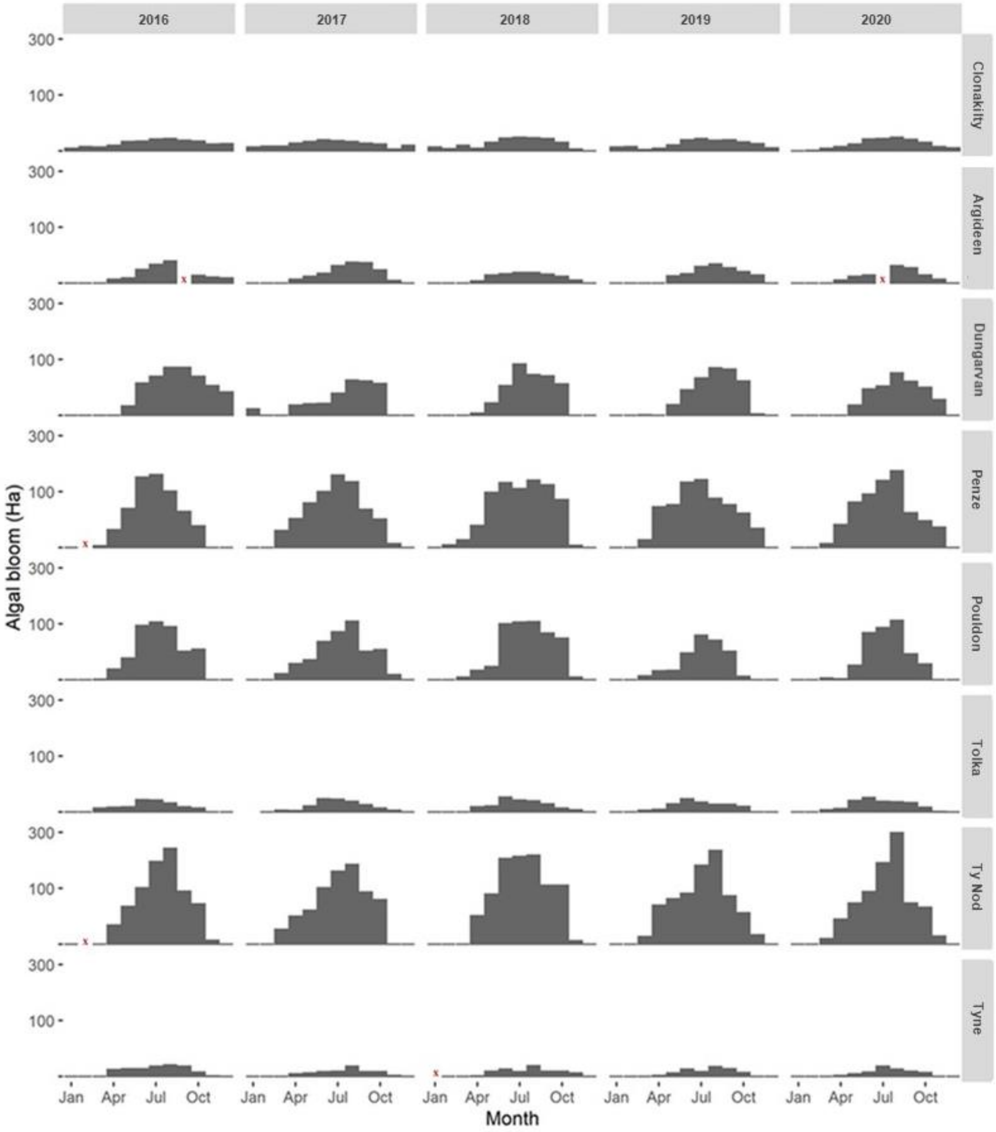


Fig. 7.5 *Ulva* bloom coverage (ha) estimated using EO data coupled with a pixel-based ML classifier for the period 2015 – 2020 (Further information in Appendix C, Tables S8 – S15)

7.4.4 Influence of environmental variables

When determining the correlation between environmental variables and *Ulva* cover, hierarchical partitioning identified “average temperature” and “photoperiod” as being the most significant environmental factors influencing *Ulva* cover (z-score = 0.33 and 0.26, respectively). Hierarchical partitioning revealed that ‘average temperature’ explained 51% of the observed variance and was the most important environmental factor for explaining bloom development in hypertrophic estuaries, and ‘photoperiod’ was another factor accounting for a further 39% of the observed variance.

7.5 Discussion

7.5.1 Ulva proliferations in the North-East Atlantic

Despite significant progress in reducing land-based nutrient pollution (EEA 2019) and preventing further environmental degradation (e.g., UN SDGs, WFD, MSFD, Nitrates Directive, Wastewater Treatment Directive), the obtained results revealed that pervasive macroalgal blooms are still blanketing a high number of estuaries across the North-East Atlantic (Fig .7.3). The monitoring of the eight studied estuaries has shown that the overall magnitude of green tide coverage has remained static over the last five years (Fig. 7.5) and confirmed spring and summer as the most problematic time of the year in terms of bloom development with a consistent and common unimodal seasonal pattern found (Fig. 7.4). The continued presence of these nuisance blooms demonstrates continual eutrophic conditions, which impedes the recovery of biodiversity and ecosystem services (Costanza et al. 1997, Lotze et al. 2006) necessary to comply with international and national environmental commitments.

The most recent OSPAR report on eutrophication indicates that the surface area in the North-East Atlantic Ocean classified as either a “potential problem area” or a “problem area” has decreased overall from 2003 to 2017 (~-59%) over the last three decades (OSPAR 2017). Stricter legislation on phosphate and nitrate use and an improvement in wastewater treatment have led to a transitory enhancement in the eutrophication status of aquatic ecosystems, particularly due to a reduction in nutrient loadings from point sources (Andersen et al. 2015, Le Moal et al. 2019). Nevertheless, this reduction in nutrient loadings has not resulted in a decline of nuisance macroalgal blooms (Bermejo et al. 2019, Schreyers et al. 2021), and an apparent second wave of eutrophication has arisen over the past decade, which has been attributed to a combination of factors including nitrogen and phosphorus loadings from diffuse sources (Beusen et al. 2016, Le Moal et al. 2019), the introduction of alien species (Gennaro et al. 2015, Bermejo et al. 2020), climate change (Smetacek and Zingone, 2013, Louime et al. 2017), and increased monitoring efforts of aquatic ecosystems (Hallegraeff et al. 2021).

Nutrient over-enrichment of aquatic ecosystems is key to explaining the occurrence of macroalgal blooms; however, once certain nutrient thresholds have been surpassed, alternative factors replace nutrients as the limiting factor controlling bloom development (Valiela et al. 1997, McGovern et al. 2019, Lotze et al. 2000). The high percentage of variability (ca. 89%) explained by photoperiod and temperature (Table 7.2) and the lack of nutrient limitation observed in several seaweed blooms affecting hypertrophic estuaries (Bermejo et al. 2020, Mateus and Neves, 2008, Bermejo et al. submitted), support the idea that this threshold has been surpassed leading to a shift from systems limited by nutrients to systems gradually saturated by nutrients. In this new scenario, light and temperature become the limiting factors of bloom development during the entire year (McGovern et al. 2019, Bermejo et al. 2020). The studied estuaries exhibited explicit and common seasonal dynamics broadly characterised by a latent winter cycle, followed by an intense growth period during May, culminating in a peak extension occurring in July-August (Table 7.4) before declining in the late autumn. This apparent phenology concurs with previously published regional data (Schories and Reise, 1993, Ménesguen and Piriou, 1995, Taylor 1999, Bermejo et al. 2019). Notably, green tides in France were much more established earlier in the year (April), with a shorter blooming season observed in Ireland and Scotland, with blooms becoming more established in May in the latter, likely as a direct result of photoperiod and temperature. Although a symmetry in annual seasonality was observed within the estuaries, temporal differences in reaching their maxima were observed between estuaries independent of latitude (Fig.7.5). These differences are likely related to local factors, namely hydrodynamic conditions, geomorphology, irradiance, grazers, species pool and propagule bank size (Lotze et al. 2000, Thornber et al. 2017, Bermejo et al. submitted).

In the current context of global change, some related aspects, including climate variability, alterations to N:P ratios of nutrient loadings or the introduction of alien species or lineages, could lead to nonlinear responses that may limit our ability to predict the occurrence and dynamics of macroalgal blooms in hypertrophic estuaries. An increase of seawater temperature in the North Atlantic Ocean of 0.49°C since the beginning of the “Great Acceleration” up to 2007 (IPCC 2013) has been observed with a predicted increase of water temperature in North-East Atlantic coastal waters between 1.2-3.6°C by the year 2100 (IPCC 2007). This increase will not be homogeneously distributed over the year and will be more apparent during the late spring and early summer (Steinthorsdottir and Wagner-Cremer, 2019), coinciding with the critical stage in green tide development in temperate estuaries (Fig. 7.4). Considering that the spring-summer temperature range within all study sites (7.62-16.35°C; Appendix C, Fig. S8) is within the optimal range for *Ulva* development (15-20°C, with tolerance up to 25-30°C; Taylor et al. 2001) and that the unimodal shape of our data suggests a lack of thermal or physical stress during the peak bloom (Fig. 7.4), it is expected that the first stages of warming will enhance bloom magnitude, as suggested by previous authors based on laboratory experiments (Gao et al. 2017). Furthermore, this non-homogeneously distributed warming will alter bloom phenology, which is anticipated to result in prolonged (Lüning 1993, Gobler et al. 2017, Ralston and Moore, 2020, Figueroa et al. 2021) and more frequent bloom events (Paerl 2006, Anderson et al. 2012, Gilbert and Burford, 2017) notably in shallow eutrophic estuaries, which are warming at a higher rate than previous climatological models' predictions (Gao et al. 2017, Scanes et al. 2020). However, increases above the thermal optimum, or the occurrence of more frequent extreme metrological events, such as heatwaves, droughts, or torrential precipitation, could lead to acute responses in bloom dynamics (Coffaro and Bocci, 1997, Román et al. 2020), resulting in a bimodal or multi-modal shape as observed in warm temperate estuaries (Flindt et al. 1997, Hernández et al. 1997, Aníbal and Sprung, 1998).

Several studies have underscored the distribution of *Ulva* blooms in temperate estuaries on a regional scale (Bermejo et al. 2019, Karki et al. 2021, Schreyers et al. 2021). However, the various international legislative frameworks for protecting marine ecosystems imply large scale monitoring of water bodies with gaps remaining between legislative requirements and actions that will ultimately yield improvements in the assessment of aquatic ecosystem health (EEA 2019). Governments have applied pressure on their regulatory agencies to develop and harmonise large monitoring programs at continental scales comprising several countries (Borja et al. 2013, Carvalho et al. 2019). Accordingly, this research is the first approach to harmonise and integrate pan-European WFD *in situ* field sampling data with historical free to access EO datasets for the continental-scale temporal reconstruction of *Ulva* blooms. Data from this study show that green tides were readily distinguished using satellite data providing improved delineation of *Ulva* cover over traditional "boots on the ground" field surveys (Appendix C, Fig. S4), allowing for assessing multiple vulnerable estuaries on a large geographic scale on a monthly basis during the last five years. Considering the high costs associated with traditional estuarine field sampling, which suppose significant logistical challenges, there is limited data on the overall extent of green tides in estuaries on a European scale which has been addressed in the current study. Accordingly, the availability of datasets that allow reconstructing macroalgal blooms at large spatial (continental) and temporal (years) scales suppose a gamechanger allowing the setting up of baselines (Pauly 1995) while avoiding sampling effort bias (Hallegraeff et al. 2021) and thus providing a powerful tool for the assessment of international legislative commitments, as demonstrated in this study.

7.5.2 The impact of bloom-forming species on commercially important native seaweeds

North Atlantic coasts and the culturally and economically important seaweed species they host are vulnerable to the adverse impacts of invasive species colonisation. Doubtless, only a minority of introduced species are likely ever to become invasive; however, it is often difficult to predict which will become pests (Pickering et al. 2007). Bloom forming seaweed colonisations, particularly from *Ulva*, *A. vermiculophyllum*, *Ectocarpus* and *S. muticum*, are becoming noticeable features of coastal ecosystems in European waters and worldwide (Thorsen et al. 2021, Andreakis and Schaffelke, 2012). Indeed the arrival of introduced species already accounts for 5-10% of European seaweeds and, based on the extent of their spread, 54 species are considered "invasive" species at this point (Colautti and MacIsaac, 2004, Mineur et al. 2015).

The impacts of invasive bloom-forming species on native macrophytes is varied. The widespread establishment of these bloom-forming species in bays and estuaries throughout the North Atlantic can be considered threats to important native species diversity, directly impacting biodiversity and being drivers of change in coastal ecosystems (Walker and Kendrick, 1998, Wikstrom and Kautsky, 2004, Mineur et al. 2015).

Generally, the primary impacts are the significant accumulations of nuisance biomass on shorelines which can inhibit the growth of fucoids (Hammann et al. 2013). Invasive species can outcompete native harvestable seaweeds due to space monopolisation and even displacement on rocky shorelines (Dayton 1971, Lubchenco and Menge, 1978, Schaffelke and Hewitt, 2007). In addition, a series of cascading effects related to invasive seaweed colonisation lead to adverse impacts on ecosystem function, impacting fish and invertebrate fauna, native biota and productivity of recipient ecological communities (Schaffelke and Hewitt, 2007, South et al. 2016).

Invasive species, such as *A. vermiculophyllum*, are a potential competitor with important intertidal harvestable species, including fucoids, and are capable of being more opportunistic than native harvestable species and outcompete these native seaweeds for light, nutrients, and other resources (Hammann et al. 2013). High growth rates (Sfriso et al. 2020), microbial "gardening" (Saha and Weinberger, 2019), and lower palatability by grazers compared with some natives (Berke et al. 2020) are several factors that can give a competitive advantage to species such as *A. vermiculophyllum* over culturally important native seaweeds. Crucially, these introduced species can negatively impact those local communities reliant on harvesting native seaweeds as a source of income. However, significant knowledge gaps exist concerning the socio-economic impacts of invasives seaweeds (Schaffelke and Hewitt, 2007).

However, concurrently, the reported impacts of some invasives on native species can be mixed. Even within a region, the effects of invasive seaweeds on native biodiversity cannot be generalised. For example, invasive species have also been reported to provide food and habitat for higher trophic levels in rocky intertidal systems (Jones and Thornber, 2010). A study examining the impacts of introduced seaweed (*S. muticum*) colonisation on epibiota diversity in different coastal systems found that *S. muticum* can enhance epibiota diversity in some sedimentary environments while having negligible impacts on epibiota diversity in rocky shore environments (Buschbaum et al. 2006). Furthermore, the effects on the composition of coastal communities following the introduction of *U. pinnatifida* in intertidal communities in New Zealand were shown to be transient while having potentially positive effects on nearshore productivity (South et al. 2016). It can be concluded that the impacts of invasive species on harvestable native species are likely to be strongly context-dependent with considerable variability in the magnitude of the impact (Thomsen et al. 2011, South et al. 2016), highlighting the importance of improving our understanding of the individual composition and structural complexities of species in native coastal environments.

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8. General Discussion and Recommendations

8.1 Summary, Recommendations and Conclusions

The key objectives, as outlined in the previous six chapters, are shown below and discussed.

- To provide a comprehensive overview of the seaweed resources of Ireland.
- To provide a synopsis of arsenic speciation in a variety of seaweeds.
- To quantify the transfer of As from a commercial seaweed animal feed and evaluate humans' consequential risk.
- To explore the applicability of using EO data to reconstruct the historical development of a macroalgal bloom in eutrophic estuaries.
- To assess the seasonality and annual variation of macroalgal blooms in eutrophic estuaries. To use appropriate modelling to determine environmental factors relating to their onset and demonstrate the applicability of free-to-access EO datasets to Europe-wide assessments.

8.2 A modern perspective on the Irish seaweed industry (Chapters 2 and 3; *See Section 1.7 Compilation of co-authored papers*)

The Irish seaweed industry has always been viewed as having “potential” (Hafting et al. 2015), and it is appropriate that Ireland takes full advantage of this enormously valuable yet hugely under-utilised national asset (Shields et al. 2005). Many of the less commercially exploited species native to Ireland, particularly some members of the Phaeophyceae and Florideophyceae, including *L. hyperborea*, *L. digitata*, *P. palmata*, *C. crispus* and *M. stellatus,* continue to play vital cultural and economic roles to many coastal populations on the west of Ireland (Chapter 2 and 3). *Ascophyllum nodosum* retains its role as the most commercially important seaweed to the Irish seaweed industry. In Chapter 2, we see that the national harvest in Ireland was 30,000 tonnes, more than 95% of which is *A. nodosum,* highlighting the considerable reliance on one species. The continued exploitation of *A. nodosum* requires a considered management approach. Ireland has the potential capacity sustainably to produce a much greater harvest (Araújo et al. 2021), yet is hampered by several immediate domestic factors, including an ageing harvester workforce, higher costs of production and localised over exploitation, making it a challenge to forecast the future of the Irish seaweed industry. An underlying impediment to a growing industry in Ireland is the lack of a guaranteed steady supply of high-quality raw material, and challenges now lie in the further development of a strategy to expand the national harvest (*See Section 1.7 Compilation of co-authored papers*). The introduction of a coherent national management plan, sustainable harvesting quotas, increased adoption of boat and rake harvesting, and industry accountability would seem prudent and long overdue measures to the continued sustainability and progressive management of the Irish seaweed industry.

Fundamentally, it is important that Ireland develops and implements a sustainable harvest plan. According to the Food and Agriculture Organization of the United Nations (FAO), sustainability can be defined as "the management and conservation of the natural resource base … to ensure the attainment and continued satisfaction of human needs for present and future generations". Presently, in view of a lack of national regulation, agreement and open conversation between industry and traditional harvesters is crucial to maintaining the industry's sustainable growth in the west of Ireland. The harvest is completely unregulated, with the onus of sustainability placed on the industry. Within Europe, countries such as Norway have implemented sustainable harvesting plans. Ireland may also look across the Atlantic to Eastern Canada, where the national *A. nodosum* harvest has been sustainably managed for almost 30 years with no significant change in biomass or plant height over that period (Lauzon-Guay et al. 2021), producing a steady annual harvest of 40,000 tonnes per annum while maintaining a strict sustainable harvesting regime.

The European seaweed industry's continued expansion will probably depend on exploiting less commonly harvested seaweed species, such as *Fucus vesiculosus*, or most likely through cultivation opportunities (*See Section 1.7 Compilation of co-authored papers*). The further expansion of the Irish seaweed industry will continue to provide employment opportunities in disadvantaged coastal communities, particularly impacted by low employment rates. However, without considered resource management or government regulations, the ever-increasing popularity of seaweed raw materials may result in poor or predatory harvesting. Unabated exploitation will likely lead to a “tragedy of the commons” scenario (Hardin 1968) if management strategies are not implemented before the decline of the population becomes evident Vásquez (2008).

8.3 Arsenic presence in seaweed-derived animal meal; important implications for animal feed producers (Chapters 4 and 5)

The purpose of this study was to bridge knowledge gaps relating to the transfer of arsenicals from seaweed-derived animal feed and to use statistical models to determine the potential for human toxicity. The topic of arsenic transfer from animal products has been addressed in only a few studies previously, focusing on evaluating the effects on milk from cows due to elevated arsenic in drinking water sources for cattle (Sigrist et al. 2010, Ghosh et al. 2013). Chapter 5 was the first study globally to investigate the potential transfer of arsenic from seaweed animal feed to livestock and ultimately human consumers.

The issue of feed safety is paramount to ensuring consumer confidence in both feed and livestock produce. Consumer perception of chemical contaminants' risks is strongly associated with negative consumer consequences (Kher et al. 2013). For example, the Irish pork debacle of 2008 showed how consumer confidence decreased significantly following the supply of dioxin-contaminated animal feed to several farms, resulting in an Irish pork product recall (Bánáti 2011). Furthermore, extensive public reporting of environmental contamination transfer, particularly in light of recent reports of microplastic transfer from marine fish (Hurt et al. 2020, Mercogliano et al. 2020), has resulted in greater public awareness and understanding of the potential hazards to human health from the transfer of environmental contaminants in the human food chain. With the well documented nutritional benefits of seaweed inclusion in animals diets (Morais et al. 2020) and human diets (Charoensiddhi et al. 2020), our research into the transfer of this naturally occurring environmental contaminant has filled significant knowledge gaps crucial to understanding the role of As transfer through the food chain.

Discussions in Chapter 4 and results from Chapter 5 have highlighted the role of arsenic (As) transfer in seaweed products and will likely have significant consequences for the Irish seaweed industry. Several important findings were reported from this work. It was shown that As_{Inorg} is consistently a minor portion of the As_{Tot} present in seaweed meal –

an important result considering the reported toxicity of As_{Inorg}. Our results showed that the estimated daily intake (EDI) levels were within the adequate range set by EFSA and JECFA for the safe use of *A. nodosum* as a raw ingredient in animals' diets reared for human consumption. Crucially, we show that the transfer of arsenicals from seaweed meal to humans is negligible and does not pose a threat to the general population.
As stated, when considering the toxicity of certain seaweeds to human health, it is more relevant to focus on As_{Inorg} forms' exposure. However, some new classes of As metabolites, such as thiolated arsenicals (As_{Thio}), are yet to be fully elucidated, though it is thought that these particular forms may play important roles in total As metabolism and toxicity. Similarly, much is yet to be clarified regarding the formation pathway of methylated As forms and $As_{Sug,}$ and care should be exercised as to the true fate of As_{Sug}, representing the most substantial portion of As present in *A. nodosum*. These arsenicals should not be thought of as non-toxic. However, considering the low content of bio-available inorganic arsenates in most edible seaweeds, it appears the risk to human health due to their consumption, under normal digestive conditions, is of no consequence. From a more general perspective, however, the specific risks to the general population from cumulative As toxicity loads are yet to be fully understood as humans are routinely exposed to multiple alternate sources of As through vectors such as drinking water (Ersbøll et al. 2018) and various foods (Anastácio et al. 2018, Maher et al. 2018, Ashmore et al. 2019, Tanabe et al. 2019).

As stated in a recent review on the toxicological effects of consuming marine seaweeds, the authors stated that “there is lack of attention toward their [seaweed] toxicity reports which might be due to toxic chemical compounds from seaweed” (Kumar and Sharma, 2021). This statement seems particularly apt, considering the prevalence of seaweed and seaweed-derived products in the food chain. Results and discussions in both Chapter 4 and Chapter 5 significantly contribute to relevant knowledge gaps.

8.4 Green tides in the Anthropocene Ocean (Chapters 6 and 7; *See Section 1.7 Compilation of co-authored papers*)

Over the past twenty years, European management of water bodies has shown mixed success, with less than half of European water bodies being considered as of Good

Ecological Status (GES). Since 2000, the E.U. Directive 200/60/EC (WFD) has endeavoured to ensure European water body health with one of the primary aims to establish a framework for the protection of European water bodies and "… to ensure that a sufficient quantity of good-quality water is available for both people's needs and the environment" (EEA 2018). Sensitive estuarine and riverine environments are vectors for nutrient loading from continued agricultural and urban inputs, which exacerbates bloom-forming seaweeds formation, ultimately impeding the WFD aims of clean water bodies and GES.

The introduction of invasive species or lineages with differing environmental requirements or higher growth rates could lead to increases in green tide mass, enhanced persistence, and more extended blooms through out competition of slower-growing lineages or species (e.g., native fucoids), and temporal and spatial successions between different taxa (Lavery et al. 1991, Bermejo et al. 2020, Fort et al. 2020).

In Chapter 6, the first arrival of an alien bloom species and the evidence of colonisation of the northern shore of Clonakilty in 2014 was successfully identified and reconstructed. Analysis of imagery from satellites (Sentinel and Landsat) showed a considerable overlapping of native *Ulva* and invasive *A. vermiculophyllum* due to the colonisation of *A. vermiculophyllum* in areas potentially covered by *Ulva*.

The results of the pixel-based ML classification of EO data in Chapters 6 and 7 and Appendix D, S.I.6, shows an effective technique in reconstructing blooms, both native and invasive, on a local and Europe-wide scale. Relevant technologies must be used in their monitoring to complement traditional field surveys. The use of both Sentinel-2 or Landsat-8 data is less restrictive than aircraft, UAV or ship monitoring and provides another technique to resource managers and is easily adaptable and applicable, as shown in Chapters 6 and 7.

Although the colonisation of *A. vermiculophyllum* in Clonakilty maybe does not pose an immediate threat to the area's local ecology, it is quite evident that this bay would benefit from annual monitoring of bloom extents. In the context of a rapidly warming Earth and considering the direct negative impacts these nuisance seaweed blooms exert on native perennial fucoids, which range from impeding the growth of fucoids to sudden community shifts and even complete canopy collapse (Edgar 1990, Salovius and Kraufvelin, 2004, Kraufvelin et al. 2006), a longer-term threat to Irish seaweed resources, and those who utilise these native species will likely become more apparent. Species-specific consideration of the best way to utilise these nuisance species will be crucial as their presence becomes more commonplace. The harvesting of nuisance seaweeds occurs on shores worldwide. For example, the commercial harvesting of 1,500 tonnes of the invasive beach-cast rhodophyte, *Mazzaella japonica,* on eastern Vancouver Island, British Columbia (Holden et al. 2018)., the harvesting of natural, free-floating populations of *Ulva* in South Africa as abalone (*Haliotis midae*) feed (Bolton et al. 2009), or more recently the forthcoming commercial harvesting of *Ulva* from Milford Haven, UK (Jessica Adams, pers. comm.).

The continued spread of *A. vermiculophyllum* in Clonakilty Bay and throughout other bays across Europe (Rueness 2005) emphasises the need for coherent research collaboration between coastal European nations and monitoring organisations to protect vulnerable coastal zone resources. Similarly, the recurring proliferation of *Ulva* blooms in vulnerable European estuaries requires a coherent European management plan, with a monitoring programme a practical step in protecting these vulnerable marine environments.

In Chapter 7, the main objectives of this study were to obtain baseline WFD information on the magnitude of green tide occurrences in the North-East Atlantic to assess temporal patterns of variability using satellite imagery. Our results filled knowledge gaps relating to environmental variables influences on bloom development in nutrient-enriched estuaries. It is expected that the seasonal window for green tide development will expand in some cases as a result of warming waters (Wells et al. 2015, Xiao et al. 2019), with recent modelling of North Atlantic SST showing that the duration of optimal growth of opportunistic macroalgal blooms has increased by 2-3 weeks since 1982 (Gobler et al. 2017, Ralston and Moore, 2020). This increase in warming, coupled with the hospitable environmental conditions in temperate North Atlantic waters (Lüning 1993, Fulton et al. 2014, Figueroa et al. 2021), are anticipated to result in prolonged and more frequent bloom events (Paerl 2006, Anderson et al. 2012, Gilbert and Burford, 2017). In this context, this research was the first study I have seen that harmonises and integrates pan-European *in situ* field sampling data obtained from the WFD and combined with historical EO datasets and environmental variable modelling for the continental-scale temporal reconstruction of *Ulva* blooms. The study addressed several meaningful knowledge gaps relating to the persistence of green tides in nutrient-enriched temperate estuaries and the meteorological factors most associated with their development. The developed generalised linear model (GLS) and Hierarchical Partitioning (HP) models identified clear seasonality of the blooms and the significant role of environmental variables, namely photoperiod and temperature paly in interannual fluctuations of blooms in European waters, accounting for 89% of the total variation and supporting the hypothesis that both factors are key determinants in *Ulva* seasonality in temperate waters.

Though no change in land use was observed between 2012 and 2018, this is likely too short an assessment period. However, this study window provides a wider understanding of the anthropogenic land-use change in the coastal environment. The continued influence of agriculture is the predominant driver in explaining the development of *Ulva* in eutrophic estuaries under investigation.

In European waters, the colonisation spread rates by invasive seaweeds have increased in the 21st century. In this context, high-quality EO data tracking the interactions of invasive species such as *A. vermiculophyllum* and native species is of importance as it is generally poorly understood, with little agreement in the literature regarding their overall effects (e.g. Ramus et al. 2017, Sotka and Byers, 2019). It has been established that *A. vermiculophyllum* is a potential competitor with important intertidal harvestable species, through direct competition for resources, and can inhibit the growth of commercially important fucoids. Reconstructing the occurrence of these events will provide fundamental information on species propagation over time and improve our understanding of native and invasive bloom species' co-occurrence.

The easy to use, pixel-based methodology offers users a low-cost and pragmatic aid to traditional field sampling. As a result of the high costs and labour-intensive nature of traditional field monitoring of estuaries, there is limited data on the extent of *Ulva* development on a European scale that has been addressed in Chapter 7. Earth Observation datasets, particularly those provided by Sentinel, provide extensive spatial coverage allowing for Europe-wide assessment, which is likely impossible using “up and coming” technologies such as UAV and is more flexible and cheaper than light aircraft (*See Section 1.7 Compilation of co-authored paper*). Another primary advantage of this technique is the ease at which data is captured and the speed at which scenes can be processed and compliment the costly and laborious, large-scale field surveys. Considering the advantages of using satellite imagery coupled with appropriate classification tools, this technique is currently being applied to *A. nodosum* resource management on the west coast of Ireland (data currently unpublished, Mac Monagail et al.).

8.5 Recommendations and further research

The commercial seaweed landscape in Ireland has improved considerably in recent years. However, fundamental gaps exist in information relating to resource location and species abundance. The continued development of Ireland's sustainable bio-economy (*See Section 1.7 Compilation of co-authored papers*) is dependent on filling these fundamental knowledge gaps relating to economically significant seaweed biomass quantities (Sánchez et al. 2018).

8.5.1 Recommendations on broadening the number of species harvested commercially

As discussions in Chapters 2 and 3 have shown, Irish shorelines are home to a diverse and underutilised seaweed flora, yet only a limited number of seaweeds are of cultural or economic significance. Several species, including *C. crispus* and *P. palmata,* are cut on a smaller "cottage industry" scale or for individual usage. There is scope to broaden the number of wild-harvested species. One evident example would be the commercial harvest of *Fucus vesiculosus*. *Fucus* would likely be the most attractive Fucoid to the commercial industry, particularly due to its abundance, ease of access and similar harvesting technique employed to that of *A. nodosum*. The drying and processing of *Fucus* are likely similar to that of *A. nodosum* (though differences may be observed in drying temperature, raw material throughput, and how quickly the harvested material deteriorates). Importantly, retraining of harvesters would likely be kept to a minimum, although training to ensure correct species identification may be required. However, as with any commercial harvesting of seaweed resources, it would be fundamental first to define the standing crop of *Fucus* on Irish shores and to ensure clear adherence to SSSI, SACs and forthcoming MPAs when harvesting.

Globally, less than 1% of harvested seaweed comes from wild stocks (Mac Monagail et al. 2017). The future development of the Irish seaweed industry likely lies in the development of the cultivated sector. The cultivation of seaweeds can support Ireland's well-established wild harvesting industry, particularly as growth markets such as the human consumption sector, nutraceuticals, and cosmetics require raw material at a standard likely only guaranteed through cultivation (Araújo et al. 2021). As of 2018, there were 17 applications submitted to the Department of Agriculture, Food and the Marine (DAFM) for seaweed licences to cultivate and process a range of native species in Ireland. Enterprises such as Allihies Seafood Ltd., Emerald Seaweed Ltd., and Dingle Bay Seaweed Ltd have applied for seaweed aquaculture licenses to cultivate a significantly varied range of species, including *A. esculenta*, *S. latissima*, *L. digitata*, *P. palmata*, *Porphyra*/*Pyropia*, *C. crispus* and *M. stellatus* while researchers at Bantry Marine Research Station (BMRS) are developing methodologies for the cultivation of the red seaweed *A. armata*. This activity is expected to grow substantially by granting additional cultivation licenses and support grants totalling €4.5 million in Irelands cultivation sector (DAFM 2021). Indeed, Ireland's National Strategic Plan for Sustainable Aquaculture Development aims to grow Irish seaweed production sustainably by providing grant aids and special incentives to new entrants to the sector. Irelands seaweed cultivation sector shows enormous potential to grow its seaweed production sustainably. With that being said, however, and despite the potential of this upcoming sector, major challenges need to be met to catch up with global cultivation pacesetters. Ireland's cultivation sector is hampered by an inefficient and complex licensing process that urgently needs reform. Delayed or lengthy licensing times have proven difficult for businesses to plan accordingly. The capital costs of setting up a cultivated-seaweed farm are high, while public acceptance of seaweed cultivation in Irish waters remains a key challenge.

8.5.2 Recommendation on potential harvest regulations

To date, the sustainability of Irish seaweed resources has been ensured through the self-imposition of good harvesting practices of harvesters and industry. This co-management between native harvesters and industry players has, thus far, ensured that the commercial harvest of seaweed resources in Ireland has been carried out sustainably. However, with the continued added pressure of new entrants to the commercial sector, it may be pertinent at some point in the near future to consider the introduction of regulations to protect vulnerable seaweed resources and to ensure the continued development of the industry. Though the harvest scale may differ between commercial and cottage industries, the same principles of co-management between relevant players exist. Ireland may take guidance from successful and sustainable harvest management plans implemented in Chile, Norway, France and Atlantic Canada. Some specific sustainable harvesting recommendations include but are not limited to the following;

i) development of baseline resource estimates for targeted species
ii) developing monitoring programmes
iii) to leave the holdfast intact and enough meristematic tissue for regrowth
v) to harvest plants selectively, choosing larger specimens (older plants; species-specific)
vi) the rotation of harvest areas
vii) establishing recess/fallow periods
viii) the implementation of quotas and harvest budgets
ix) licensing
x) the implementation of national seaweed monitoring programmes
xi) fines/bans for poor or predatory harvesting

In this context, a coherent harvest management plan is required for Ireland's seaweed resources. Annual, large-scale resource assessment is crucial to the sustainability of the Irish seaweed industry and requires comprehensive field surveys to fill knowledge gaps relating to biomass quantities. Quotas on harvested material and minimum cut heights, with sufficient regeneration time for the plants, are minimum requirements. As new entrants to the seaweed market emerge to satiate a growing demand, there has been and remains potential for over-exploitation of these resources, in my opinion.

A multidisciplinary management plan involving all stakeholders, including government, industry and harvesters, and improved data flow between these players is crucial. However, considering the scale of the Irish coastline (abundant seaweed resources available from County Donegal to Country Cork), the limited accessibility and the lack of surveillance and accountability, there remain considerable hurdles to overcome.

What is certain is that, regardless of the volume of harvested material (whether on an artisanal or commercial scale), without accurate baseline assessments, it is not possible to ensure that harvesting is undertaken within sustainable limits confidently. Biomass assessment should be seen as a minimum requirement before commercial harvesting wild seaweed biomass. For smaller cottage industries that do not have the capabilities of carrying out such surveys, several independent consultancies are available, including AquaFact and the Irish Seaweed Consultancy, which provide resource assessment.

8.5.3 Recommendations on harvesting techniques

The spectre of mechanical harvesting looms in the Irish seaweed landscape. Although mechanical harvesting is an effective technique for the harvesting of wild seaweed resources when strictly employed under sustainable harvesting principles (pre-and-post - biomass assessment, strict harvesting quotas, allowing sufficient time for regeneration) (See Phillippi et al. 2014), the major hindrance to its implementation in Irish waters may be more cultural than operational. There is a reluctance to use mechanical harvesters, both from traditional harvesters who see the introduction of mechanical harvesting as an affront to the culture of traditional hand harvesting carried out in Ireland for hundreds of years (pers. comm Traditional harvester, County Kerry). Also, the current view of the authorities is not positive, with the National Parks and Wildlife Service (NPWS) stating, "… such activities are not compatible with the conservation objectives of and should not be permitted in Natura 2000 sites". However, as the popularity of seaweed continues to grow (Phyconomy 2022), alongside an ageing harvester workforce, the mechanised harvest of seaweed may be seen as a more stable opportunity for a new generation of cutters and one which may be required to meet industry needs.

A preliminary study assessed over 18 months carried out in Counites Galway and Mayo has shown that traditional harvesting was far more effective and cost-effective than mechanical harvesting in Irish waters (Kelly et al. 2001). However, the authors recognised that the study was the first of its kind for the mechanical harvest of seaweed in Ireland. With improvements in mechanical harvester design, it could result in greater harvesting efficiency in the future. It is recommended that further long-term research be carried out.

In the intervening period, it appears the traditional hand harvesting, in conjunction with the recent success of the boat and rake harvesting method will remain the primary harvesting techniques in Irish waters.

8.5.4 Recommendations on ground-truthing

Though the use of free to use Sentinel and Landsat is an effective tool in the classification and delineation of seaweed blooms, under the current spatial and spectral limitations of the imagers, it is quite apparent that traditional ground-truthing “boots on the ground” sampling is required to ensure the precision of EO data.

Field survey data collection likely outperforms remotely sensed equivalents when defining the spatial extension of biological habitats (Rhodes et al. 2015). However, it is also true that the cost-benefit threshold between EO data and traditional “boots on the ground” surveys will be context-specific. The application of EO techniques can be an effective tool in mapping and surveying invasive species colonisation. In some cases, EO offers the potential to establish a baseline of invasive seaweed distribution and, for now, can offer targeted guidance as to where traditional fieldwork can concentrate their efforts. In others, the use of EO techniques remains advantageous over conventional monitoring. For example, considering the muddy nature of estuarine environments, traditional field monitoring can be practically extremely challenging. In these environments, ground-truthing may not be practical (although an excellent example of estuarine monitoring occurs in the southern estuaries of country Cork, where scientists aboard a small hovercraft annually survey local *Ulva* distributions). The use of EO techniques has also been put forward for the mapping of invasive kelp species, providing improved information on the areal extent of kelp beds likely impossible or at the very last prohibitive and dangerous to collect, particularly due to the location of kelp beds at the infralittoral fringe of rocky shores which can often hinder traditional monitoring efforts (Bennion et al. 2018).

Moreover, at small spatial scales, field survey data often remains the only viable option due to the coarse resolution of many satellite imagers. Although no hard and fast rule exists when considering the extent of ground-truthing required to ensure the robustness of EO data, integration of field survey data with EO survey data provides a higher resolution (Rhodes et al. 2015). Data from Chapters 6 and 7 suggest that both forms of data should be considered for future invasive seaweed colonisation studies.

8.5.5 Recommendations on the management of invasive species

Certainly, invasive species deserve significant management efforts. It would be advantageous to look to countries that historically have had tremendous successes in successfully managing invasives. For example, Australia and New Zealand have in the past taken proactive steps in dealing with the prevention, eradication and control of invasive marine organisms, with a strong emphasis on science-based management (Williams and Grosholz, 2008). Historical examples such as the eradication of *Caulerpa taxifolia* in southern California are often considered a gold standard in estuarine and marine invasive species management and rapid response (Anderson 2005, Williams and Grosholz, 2008).

Since introduced marine and estuarine species are among the top factors associated with threatening or endangering marine species with extinction (Kappel 2005, Venter et al. 2006), prevention is always the most desirable. However, prevention has been compromised, eradication and control are the two next management options (Williams and Grosholz, 2008).

Crucially, the improved collective understanding of the impacts of introduced seaweeds on native coastal environments is crucial for developing appropriate management strategies (Wright and Gribben, 2008). Some key policy efforts are needed which marry science with cohesive ecological management. When prevention has been surpassed, some efforts, such as, include but are not limited to i) early efforts to eradicate the invasive when populations are still at a low level, ii) setting early eradiation benchmarks for success, iii) desirable qualitative risk assessment and cost-benefit analyses and iv) research into the impacts of communities and ecosystems.

What is certain is that highly coordinated, decisive, and crucially fast-acting efforts between government agencies, resource managers, and experts in ecological and biological fields are crucial in developing a coherent approach to treating individual cases of alien seaweed invasion.

More vigilance is recommended to monitor both native and invasive blooming species. The research described in Chapters 6 and 7 highlighted the need for further investigations of the dynamics and spread of invasive seaweeds species around Europe, a matter that is now receiving much-warranted attention. Looking to the future, it would be pertinent to consider using EO techniques to reconstruct other invasive species known to colonise Irish waters (Kraan 2017, Bermejo et al. 2019, Schoenrock et al. 2019) and tracking potential new arrivals. The use of EO technology to monitor the impact of *A. vermiculophyllum* of native *F. vesiculosus* beds (Hammann et al. 2013) and of *Laminaria ochroleuca* with native *L. hyperborea* assemblages (Smale et al. 2015) would be appropriate. Significantly, this information provides relevant data to water authorities on alien species assessment and monitoring, ultimately providing a standardised tool that can cover the entire European continent in the context of the WFD.

The study outlined in Chapter 7 is not, as yet, an exhaustive description of the current *Ulva* macroalgal bloom status in European waters and gives only an approximate account of the situation in vulnerable estuaries and bays in Irish, Scottish and Breton waters, and south-coast lagoons of England. It would be appropriate to broaden the analysis and include several other areas with known annual blooming events, such as described in Kolbe et al. 1995, Runca et al. 1996, Tan et al. 1999 and Ménesguen et al. 2006. My co-authors and I hope to make available information to relevant EU coastal nations or incorporated into the WFD monitoring programme, with interest shown by the Irish EPA at present.

8.5.6 Recommendations on monitoring arsenic in commercial seaweed species

When considering the presence and speciation of As in food products, it is crucial to consider the As forms present and i) the bioavailability post-cooking and processing, and ii) the individual's metabolism. In the context of future or upcoming legislation relating to seaweed safety, emphasis should be placed on the presence of As_{Inorg} due to its known higher toxicity. However, further elucidation on the fate of As_{Sug} and other metabolites in the human body are crucial to deepening our understanding of As toxicity. A shift towards monitoring arsenicals in common, edible seaweeds needs to be implemented to ensure consumer protection and confidence. Due to the greater availability of sea vegetables and the seeming current lack of enforced standardised regulation regarding products sold in both shops and markets, it is vital that periodic monitoring of seaweeds is carried out. Monitoring would be particularly appropriate in new and upcoming markets throughout Europe, North America, and Africa, where their consumption is not a traditional practice but has become more common and is likely to increase with burgeoning affluence. Whole seaweed will always be a “niche” food for the affluent.

Different seaweed groups also have differing capacities for As accumulation. The Laminariales, for example, are well known to contain elevated levels of As above that of the Ulvophyceae (See Chapter 4 for more detailed description). Some kelp species are popularly used in animal feed, with several internationally recognised products available for livestock. Although many Laminariales contain nutritional qualities suitable for animal nutrition (Sweeney et al. 2017, Bruhn et al. 2019), care should be taken considering kelp has been shown to contain higher concentrations of both As_{Org} and As_{Inorg} than *A. nodosum* (Ratcliff et al. 2016, Ronan et al. 2017). Without defining firstly i) the As concentration in kelp-based seaweed animal feed, ii) the transfer capacity of As from kelp and iii) consumption patterns, it is impossible to quantify human or animal exposure accurately. What is certain is that further research is required into the metabolic fate of As from kelp- and wrack-based seaweed animal feed.

Similarly to the assessment carried out in Chapter 5, an exposure assessment using kelp and some seaweeds is gaining in popularity as a potential feed supplement such as *Ulva,* and *Palmaria palmata* (Bikker et al. 2016, Garcia-Vaquero and Hayes, 2016) would be relevant. These data would provide end-users, including industry, consumers, policymakers, and regulators, accurate data on the exposure levels associated with As in commercial kelp-based animal feed. As the “Monte Carlo” simulation model used in Chapter 5 does not define the risk of exposure, a risk assessment would be pertinent. However, this was outside the initial scope of this study but could be considered for further research.

This thesis has explored several themes important for the continued maturation of the commercial Irish seaweed landscape. The Irish seaweed industry has a long and sometimes colourful history (Mac Monagail and Morrison, 2020) and was generally regarded as having “potential” (Hafting 2015). Today, the Irish seaweed industry is approaching that potential, with a highly skilled industry workforce, with several academic research groups dedicated to algal research and a swath of exciting seaweed company start-ups operating on the Atlantic seaboard. The continued progression of the Irish seaweed industry will likely continue through less commercially exploited species native to Ireland (e.g., *Fucus* spp., kelps, together with a few red algae), the cultivation of species, and the utilisation of native seaweeds in higher-value products, including biostimulants, cosmetics and nutraceuticals. However, the industry currently relies mainly on the sustainable harvesting of *A. nodosum*. As such, an underlying impediment to the growth of the industry in Ireland is the lack of a guaranteed steady supply of high-quality raw material, and further challenges now lie in the absence of a national strategy to manage these resources. As there have been at least 60 years of commercial harvesting of *A. nodosum* in the west of Ireland without any diminution of the resource, the current industry- and harvester-led safeguarding has resulted in a well-maintained resource. Nevertheless, a coherent national management plan is a rational and reasonable objective for the continued evolution of the Irish seaweed industry in the 21st century.

8.6 Bibliography

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Appendices

Appendix A Supplementary Information Chapter 5

Appendix B Supplementary Information Chapter 6

Appendix C Supplementary Information Chapter 7

Appendix A

Supplementary Information Chapter 5

Supplementary Information Figure S1 and Figure S2

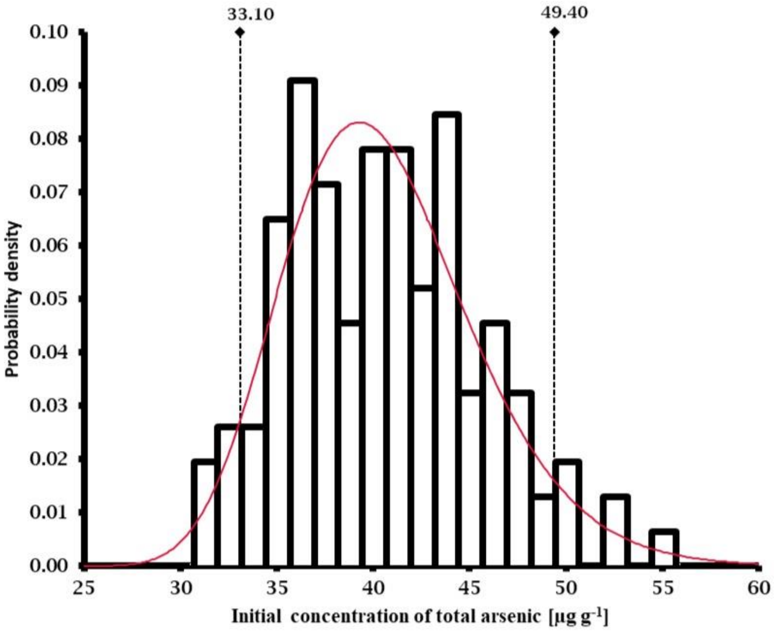

Fig. S1 Best fit distribution

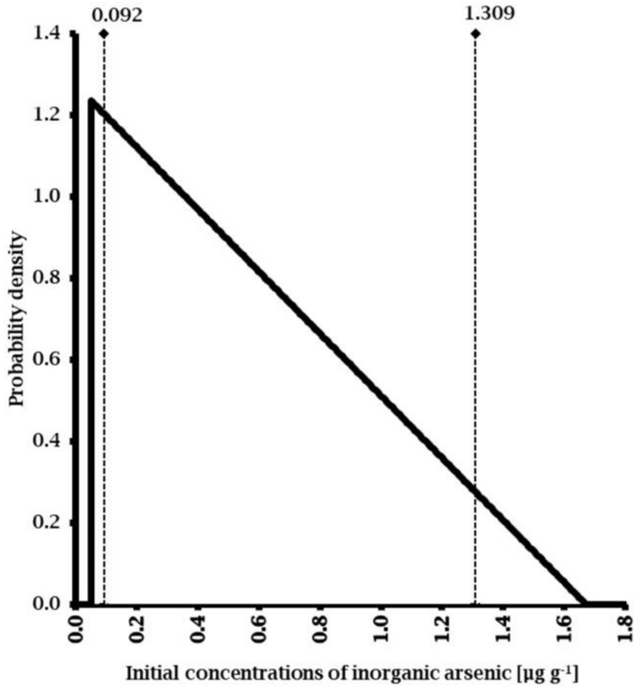

Fig. S2 Distribution model

Supplementary Information Table S1-S5

Table S1 Monthly monitoring data of Total and Inorganic arsenic in large grain (LG) and small grain (SG) seaweed animal feed (Jan 2012 - Feb 2017)

	Total arsenic		Inorganic arsenic	
Date	**LG-SAF**	**SG-SAF**	**LG-SAF**	**SG-SAF**
Feb 2017	31.05	44.97	0.35	1.27
Jan 2017	35.26	34.69	0.46	0.79
Dec 2016	35.82	36.49	0.42	0.39
Nov 2016	40.72	41.95	0.22	0.35
Oct 2016	36.69	42.57	0.39	0.67
Sep 2016	38.89	38.67	0.49	0.57
Aug 2016	36.72	38.67	0.52	0.57
Jul 2016	38.78	42.53	1.28	0.73
Jun 2016	37.31	46.83	0.31	1.03
May 2016	40.79	50.46	0.49	0.96
Apr 2016	38.81	53.52	0.41	0.52
Mar 2016	44.12	50.42	0.72	1.02
Feb 2016	44.12	47.91	0.72	0.81
Jan 2016	32.39	43.77	0.39	0.77
Dec 2015	33.42	43.99	0.32	0.59
Nov 2015	33.61	36.96	0.51	0.36
Oct 2015	43.73	47.46	0.33	0.56
Sep 2015	43.18	50.38	0.68	0.48
Aug 2015	46	52	-	-
Jul 2015	39.4	42.4	0.5	1.4
Jun 2015	44.2	56.25	0.5	0.55
May 2015	35.63	47.94	0.23	0.54
Apr 2015	36.16	45.46	0.26	0.46
Mar 2015	40.86	48.28	0.16	0.18
Feb 2015	40.47	42.03	0.27	0.53
Jan 2015	41.74	44	0.54	0.5
Dec 2014	41.34	41.61	0.34	0.51
Nov 2014	42.04	35.18	0.54	0.38
Oct 2014	39.4	45.15	0.3	0.45
Sep 2014	35.66	43.81	0.16	0.51
Aug 2014	37.97	37.14	0.27	0.54
Jul 2014	36.48	41.26	0.18	0.36
Jun 2014	38.2	41.01	0.2	0.41
May 2014	44.54	48.26	0.14	0.36
Apr 2014	45.39	47.27	0.29	0.37

Mar 2014	37.53	40.37	0.33	0.47
Feb 2014	40.39	47.27	0.29	0.57
Jan 2014	40.19	47.27	0.29	0.57
Dec 2013	32.2	37.8	0.1	0.4
Nov 2013	39.32	45.7	0.32	0.4
Oct 2013	40.8	44.32	0.3	0.42
Sep 2013	34.05	33.75	0.15	0.45
Aug 2013	32.12	40.2	0.22	0.3
Jul 2013	41.99	34.43	0.19	0.33
Jun 2013	35.87	37.02	0.17	0.32
May 2013	42.87	40.35	0.27	0.25
Apr 2013	38.8	47.58	0.2	0.38
Mar 2013	49.09	44.69	0.39	0.19
Feb 2013	46.43	44.12	0.23	0.32
Jan 2013	37.62	42.29	0.12	0.19
Dec 2012	36.8	40.67	0.1	0.17
Nov 2012	36.63	43.95	0.33	0.25
Oct 2012	35.85	36.32	0.15	0.22
Sep 2012	36.2	35.07	0.4	0.37
Aug 2012	31.6	42.92	0.2	0.42
Jul 2012	37.8	42.1	0.1	0.2
Jun 2012	37.1	39.8	0.1	0.4
May 2012	36.5	43.1	0.2	0.2
Apr 2012	35.3	35.5	0.1	0.2
Mar 2012	36.3	50.1	0.1	0.3
Feb 2012	43.7	42.6	0.3	0.1

Supplementary Information Table S2, S3, S4 and S5

Table S2 Model distributions and inputs defined for Biotransfer Factors used in the determination of arsenic transfer

Produce	Description	Distribution	Units
Poultry	BTF	Uniform (Mean 0.001, Stdev0.83)	µg g^{-1}
Eggs	BTF	Uniform (Mean 0.0008, Stdev 0.44)	µg g^{-1}
Beef	BTF	Triangular (0.00000862997, 0.0024, 0.0024)	µg g^{-1}
Milk	BTF	Lognorm (Mean 0.00031499, Stdev 0.0010885)	µg g^{-1}

Table S3 Human Intake model distribution

Produce	Description	Distribution	Units
Poultry	Hi	LogNorm (Mean 31, Stdev 25) [1, 2]	g day^{-1}
Eggs	Hi	LogNorm (Mean 25, Stdev 22) [1, 2]	g day^{-1}
Beef	Hi	LogNorm (Mean 116.89, Stdev 56) [1, 2]	g day^{-1}
Milk	Hi	LogNorm (Mean 205, Stdev 192) [1, 2]	g day^{-1}
Reference		(1) IUNA (2011) (2) IUNA (2001)	

Table S4 Simulated versus permitted arsenic concentration limits in livestock produce

Produce	Mean inorganic arsenic concentration	Maximum permitted limit (inorganic arsenic)	Units
Poultry	0.00015	1.4[1]	µg g^{-1}
Eggs	0.00029	1.4[1]	µg g^{-1}
Beef	0.00198	1.4[1]	µg g^{-1}
Milk	0.00035	0.01[2]	µg g^{-1}
Reference	(1) Choi (2011) (2) International Dairy Federation (1986)		

Table S5 Range of arsenic levels as a result of grain size

Form	LG-SAF	SG-SAF	Units
As_{Org}	30.70 - 48.70	33.30 – 55.70	µg g^{-1}
As_{Inorg}	0.10 - 1.28	0.10 - 1.40	µg g^{-1}
As_{Tot}	31.05 – 49.09	33.75 – 56.25	µg g^{-1}

Appendix B

Supplementary Information Chapter 6

Supplementary Information Figure S3

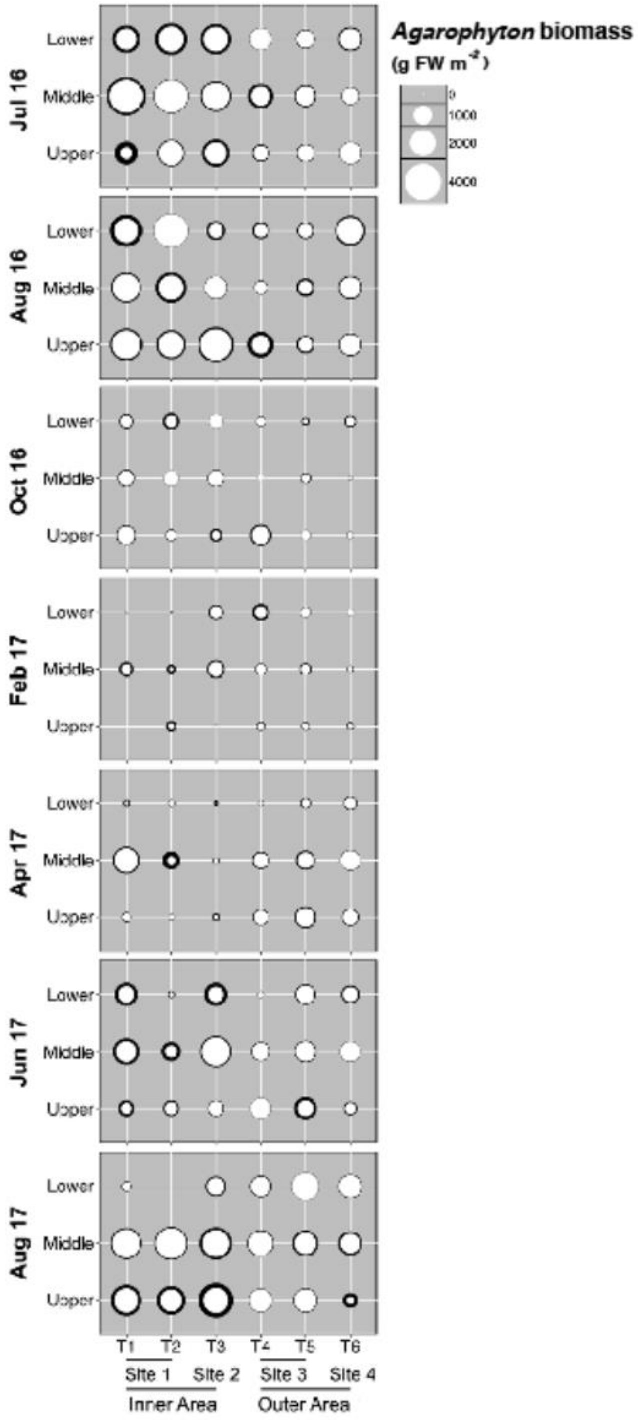

Fig. S3 Spatial distribution of Agarophyton vermiculophyllum biomass (g FW m^{-2}) over seven sampling occasions in the Clonakilty estuary. Black circles represent the 75th quartile; white circles represent the 25th quartile. n=3

Appendix C

Supplementary Information Chapter 7

Supplementary Information Table S6 – S21

Table S6 Field survey data on the location and magnitude of annual recurring *Ulva* blooms in North-Eastern Atlantic coastal and transitional waters collected as part of a European WFD intercalibration exercise

European agency	Provided data for
Irish Environmental Protection Agency (EPA)	Ireland
Centre d'Etude et de Valorisation des Algues (CEVA)	Brittany
Environment Agency	England
The Scottish Environment Protection Agency (SEPA)	Scotland
Lower Saxon State Department for Waterway, Coastal and Nature Conservation (NLWKN)	Germany*
The Department of Agriculture, Environment and Rural Affairs	Northern Ireland

*the Wadden Sea is transboundary whose extension covers both the Netherlands and Germany

Table S7 Information on sensor and acquisition date

Satellite	Country	Estuary	Date
S2	Ireland	Tolka	14.01.2016
S2	Ireland	Tolka	13.02.2016
S2	Ireland	Tolka	15.03.2016
S2	Ireland	Tolka	14.04.2016
S2	Ireland	Tolka	26.04.2016
L8	Ireland	Tolka	03.06.2016
S2	Ireland	Tolka	06.08.2016
L8	Ireland	Tolka	29.08.2016
S2	Ireland	Tolka	22.09.2016
S2	Ireland	Tolka	09.11.2016
S2	Ireland	Tolka	19.11.2016
S2	Ireland	Tolka	29.12.2016
S2	Ireland	Tolka	14.01.2016
S2	Ireland	Tolka	09.03.2017
L8	Ireland	Tolka	22.03.2017
S2	Ireland	Tolka	08.04.2017
S2	Ireland	Tolka	01.05.2017
S2	Ireland	Tolka	20.16.2017
S2	Ireland	Tolka	17.07.2017
S2	Ireland	Tolka	15.09.2017
S2	Ireland	Tolka	25.09.2017
S2	Ireland	Tolka	30.10.2017
S2	Ireland	Tolka	29.11.2017
S2	Ireland	Tolka	27.12.2017
S2	Ireland	Tolka	26.01.2018

S2	Ireland	Tolka	25.02.2018
S2	Ireland	Tolka	24.03.2018
S2	Ireland	Tolka	21.04.2018
S2	Ireland	Tolka	07.06.2018
S2	Ireland	Tolka	22.06.2018
S2	Ireland	Tolka	02.07.2018
S2	Ireland	Tolka	16.08.2018
S2	Ireland	Tolka	18.09.2018
S2	Ireland	Tolka	20.10.2018
S2	Ireland	Tolka	29.11.2018
S2	Ireland	Tolka	22.12.2018
S2	Ireland	Tolka	28.01.2019
S2	Ireland	Tolka	25.02.2019
S2	Ireland	Tolka	29.03.2019
S2	Ireland	Tolka	13.04.2019
S2	Ireland	Tolka	13.05.2019
S2	Ireland	Tolka	10.06.2019
L8	Ireland	Tolka	06.07.2019
S2	Ireland	Tolka	05.09.2019
S2	Ireland	Tolka	18.09.2019
S2	Ireland	Tolka	20.09.2019
S2	Ireland	Tolka	11.11.2019
S2	Ireland	Tolka	14.12.2019
S2	Ireland	Tolka	03.01.2020
S2	Ireland	Tolka	02.02.2020
S2	Ireland	Tolka	03.03.2020
S2	Ireland	Tolka	15.04.2020
S2	Ireland	Tolka	27.05.20
S2	Ireland	Tolka	14.06.20
S2	Ireland	Tolka	26.06.20
S2	Ireland	Tolka	14.09.2020
S2	Ireland	Tolka	27.09.20
S2	Ireland	Tolka	06.11.20
S2	Ireland	Tolka	12.11.20
S2	Ireland	Tolka	18.12.20
S2	Ireland	Dungarvin	07.01.2016
S2	Ireland	Dungarvin	09.03.2016
S2	Ireland	Dungarvin	09.03.2016
S2	Ireland	Dungarvin	08.04.2016
S2	Ireland	Dungarvin	26.04.2016
S2	Ireland	Dungarvin	06.06.2016
S2	Ireland	Dungarvin	06.08.2016
S2	Ireland	Dungarvin	06.08.2016

S2	Ireland	Dungarvin	30.09.2016
S2	Ireland	Dungarvin	20.10.2016
S2	Ireland	Dungarvin	29.11.2016
S2	Ireland	Dungarvin	29.11.2016
S2	Ireland	Dungarvin	28.01.2017
S2	Ireland	Dungarvin	27.02.2017
S2	Ireland	Dungarvin	12.03.2017
S2	Ireland	Dungarvin	08.05.2017
S2	Ireland	Dungarvin	11.05.2017
S2	Ireland	Dungarvin	15.07.2017
S2	Ireland	Dungarvin	27.07.2017
S2	Ireland	Dungarvin	09.08.2017
S2	Ireland	Dungarvin	18.09.2017
S2	Ireland	Dungarvin	05.10.2017
S2	Ireland	Dungarvin	07.11.2017
S2	Ireland	Dungarvin	27.12.2017
S2	Ireland	Dungarvin	18.01.2018
S2	Ireland	Dungarvin	20.02.2018
L8	Ireland	Dungarvin	28.03.2018
S2	Ireland	Dungarvin	18.04.2018
S2	Ireland	Dungarvin	18.05.2018
S2	Ireland	Dungarvin	27.06.2018
S2	Ireland	Dungarvin	30.07.2018
S2	Ireland	Dungarvin	30.07.2018
S2	Ireland	Dungarvin	10.10.2018
S2	Ireland	Dungarvin	28.10.2018
L8	Ireland	Dungarvin	09.12.2018
S2	Ireland	Dungarvin	22.12.2018
S2	Ireland	Dungarvin	28.01.2018
S2	Ireland	Dungarvin	07.02.2019
S2	Ireland	Dungarvin	17.03.2019
S2	Ireland	Dungarvin	03.04.2019
S2	Ireland	Dungarvin	21.05.2019
S2	Ireland	Dungarvin	02.06.2019
S2	Ireland	Dungarvin	05.07.2019
S2	Ireland	Dungarvin	13.09.2019
S2	Ireland	Dungarvin	18.09.2019
S2	Ireland	Dungarvin	18.10.2019
S2	Ireland	Dungarvin	29.11.2019
S2	Ireland	Dungarvin	24.12.2019
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S2	Ireland	Dungarvin	27.02.2020
S2	Ireland	Dungarvin	26.03.2020

S2	Ireland	Dungarvin	22.04.2020
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S2	Ireland	Dungarvin	21.06.2020
S2	Ireland	Dungarvin	24.06.2020
S2	Ireland	Dungarvin	20.08.2020
S2	Ireland	Dungarvin	19.09.2020
S2	Ireland	Dungarvin	02.10.2020
S2	Ireland	Dungarvin	18.11.2020
S2	Ireland	Dungarvin	31.12.2020
S2	Ireland	Clonakilty	07.01.2016
S2	Ireland	Clonakilty	09.03.2016
S2	Ireland	Clonakilty	09.03.2016
S2	Ireland	Clonakilty	08.04.2016
S2	Ireland	Clonakilty	26.04.2016
S2	Ireland	Clonakilty	08.06.2016
S2	Ireland	Clonakilty	18.07.2016
S2	Ireland	Clonakilty	17.08.2016
S2	Ireland	Clonakilty	10.06.2016
S2	Ireland	Clonakilty	06.11.2016
S2	Ireland	Clonakilty	25.11.2016
S2	Ireland	Clonakilty	02.12.2016
S2	Ireland	Clonakilty	10.01.2017
S2	Ireland	Clonakilty	20.02.2017
S2	Ireland	Clonakilty	25.03.2017
S2	Ireland	Clonakilty	01.04.2017
S2	Ireland	Clonakilty	11.05.2017
S2	Ireland	Clonakilty	21.05.2017
S2	Ireland	Clonakilty	30.06.2017
S2	Ireland	Clonakilty	11.09.2017
S2	Ireland	Clonakilty	21.09.2017
S2	Ireland	Clonakilty	11.10.2017
S2	Ireland	Clonakilty	07.11.2017
S2	Ireland	Clonakilty	15.12.2017
S2	Ireland	Clonakilty	04.01.2018
S2	Ireland	Clonakilty	05.02.2018
S2	Ireland	Clonakilty	20.03.2018
S2	Ireland	Clonakilty	21.04.2018
S2	Ireland	Clonakilty	16.05.2018
S2	Ireland	Clonakilty	25.06.2018
S2	Ireland	Clonakilty	30.07.2018
S2	Ireland	Clonakilty	29.08.2018
S2	Ireland	Clonakilty	28.09.2018
S2	Ireland	Clonakilty	28.10.2018

S2	Ireland	Clonakilty	27.11.2018
S2	Ireland	Clonakilty	22.12.2018
S2	Ireland	Clonakilty	19.01.2019
S2	Ireland	Clonakilty	08.02.2019
S2	Ireland	Clonakilty	07.03.2019
S2	Ireland	Clonakilty	19.04.2019
S2	Ireland	Clonakilty	21.05.2019
S2	Ireland	Clonakilty	03.07.2019
S2	Ireland	Clonakilty	05.07.2019
S2	Ireland	Clonakilty	13.09.2019
S2	Ireland	Clonakilty	18.09.2019
S2	Ireland	Clonakilty	18.10.2019
S2	Ireland	Clonakilty	15.11.2019
S2	Ireland	Clonakilty	17.12.2019
S2	Ireland	Clonakilty	05.02.2020
S2	Ireland	Clonakilty	13.02.2020
S2	Ireland	Clonakilty	26.03.2020
S2	Ireland	Clonakilty	13.04.2020
S2	Ireland	Clonakilty	28.05.2020
S2	Ireland	Clonakilty	19.06.2020
S2	Ireland	Clonakilty	27.06.2020
S2	Ireland	Clonakilty	25.09.2020
S2	Ireland	Clonakilty	20.09.2020
S2	Ireland	Clonakilty	22.10.2020
S2	Ireland	Clonakilty	14.11.2020
S2	Ireland	Clonakilty	04.12.2020
S2	Ireland	Argideen	07.01.2016
S2	Ireland	Argideen	09.03.2016
S2	Ireland	Argideen	08.04.2016
S2	Ireland	Argideen	30.04.2016
S2	Ireland	Argideen	08.06.2016
S2	Ireland	Argideen	18.07.2016
S2	Ireland	Argideen	07.08.2016
S2	Ireland	Argideen	12.11.2016
S2	Ireland	Argideen	25.11.2016
S2	Ireland	Argideen	02.12.2016
S2	Ireland	Argideen	01.01.2017
S2	Ireland	Argideen	20.02.2017
S2	Ireland	Argideen	12.03.2017
S2	Ireland	Argideen	29.04.2017
S2	Ireland	Argideen	01.05.2017
S2	Ireland	Argideen	20.06.2017
S2	Ireland	Argideen	20.07.2017

S2	Ireland	Argideen	18.09.2017
S2	Ireland	Argideen	21.09.2017
S2	Ireland	Argideen	11.10.2017
S2	Ireland	Argideen	07.11.2017
S2	Ireland	Argideen	30.11.2017
S2	Ireland	Argideen	04.01.2018
S2	Ireland	Argideen	05.02.2018
S2	Ireland	Argideen	20.03.2018
S2	Ireland	Argideen	21.04.2018
S2	Ireland	Argideen	23.05.2018
S2	Ireland	Argideen	25.06.2018
S2	Ireland	Argideen	30.07.2018
S2	Ireland	Argideen	01.09.2018
S2	Ireland	Argideen	28.09.2018
S2	Ireland	Argideen	28.10.2018
S2	Ireland	Argideen	27.11.2018
S2	Ireland	Argideen	22.12.2018
S2	Ireland	Argideen	19.01.2019
S2	Ireland	Argideen	08.02.2019
S2	Ireland	Argideen	07.03.2019
S2	Ireland	Argideen	19.04.2019
S2	Ireland	Argideen	21.05.2019
S2	Ireland	Argideen	26.05.2019
S2	Ireland	Argideen	05.07.2019
S2	Ireland	Argideen	14.09.2019
S2	Ireland	Argideen	18.09.2019
S2	Ireland	Argideen	18.10.2019
S2	Ireland	Argideen	15.11.2019
S2	Ireland	Argideen	17.12.2019
S2	Ireland	Argideen	19.01.2020
S2	Ireland	Argideen	05.02.2020
S2	Ireland	Argideen	26.03.2020
S2	Ireland	Argideen	13.04.2020
S2	Ireland	Argideen	20.05.2020
S2	Ireland	Argideen	25.05.2020
L8	Ireland	Argideen	27.09.2020
S2	Ireland	Argideen	20.09.2020
S2	Ireland	Argideen	22.10.2020
S2	Ireland	Argideen	14.11.2020
S2	Ireland	Argideen	04.12.2020
S2	France	Pouldon	29.12.2015
S2	France	Pouldon	10.02.2016
S2	France	Pouldon	31.03.2016

S2	France	Pouldon	08.04.2016
S2	France	Pouldon	27.05.2016
S2	France	Pouldon	06.06.2016
S2	France	Pouldon	15.08.2016
S2	France	Pouldon	05.08.2016
S2	France	Pouldon	16.09.2016
S2	France	Pouldon	14.10.2016
S2	France	Pouldon	06.11.2016
S2	France	Pouldon	13.12.2016
S2	France	Pouldon	25.01.2017
S2	France	Pouldon	14.02.2017
S2	France	Pouldon	16.03.2017
S2	France	Pouldon	12.04.2017
S2	France	Pouldon	25.05.2017
S2	France	Pouldon	14.06.2017
S2	France	Pouldon	24.07.2017
S2	France	Pouldon	23.08.2017
S2	France	Pouldon	22.09.2017
S2	France	Pouldon	06.11.2017
S2	France	Pouldon	18.11.2017
S2	France	Pouldon	01.12.2017
S2	France	Pouldon	17.01.2018
S2	France	Pouldon	16.02.2018
S2	France	Pouldon	18.03.2018
S2	France	Pouldon	20.04.2018
S2	France	Pouldon	20.05.2018
S2	France	Pouldon	29.06.2018
S2	France	Pouldon	14.07.2018
S2	France	Pouldon	03.08.2018
S2	France	Pouldon	27.09.2018
S2	France	Pouldon	09.10.2018
S2	France	Pouldon	26.11.2018
S2	France	Pouldon	26.12.2018
S2	France	Pouldon	19.01.2019
S2	France	Pouldon	08.02.2019
S2	France	Pouldon	17.03.2019
S2	France	Pouldon	19.04.2019
S2	France	Pouldon	21.05.2019
S2	France	Pouldon	26.05.2019
S2	France	Pouldon	05.07.2019
S2	France	Pouldon	14.09.2019
S2	France	Pouldon	18.09.2019
S2	France	Pouldon	18.10.2019

S2	France	Pouldon	15.11.2019
S2	France	Pouldon	17.12.2019
S2	France	Pouldon	02.01.2020
S2	France	Pouldon	05.02.2020
S2	France	Pouldon	26.03.2020
S2	France	Pouldon	13.04.2020
S2	France	Pouldon	25.05.2020
S2	France	Pouldon	20.05.2020
S2	France	Pouldon	20.05.2020
S2	France	Pouldon	18.07.2020
S2	France	Pouldon	02.10.2020
S2	France	Pouldon	22.10.2020
S2	France	Pouldon	14.11.2020
S2	France	Pouldon	04.12.2020
S2	France	Penze	29.12.2015
S2	France	Penze	08.04.2016
S2	France	Penze	17.04.2015
S2	France	Penze	17.04.2016
S2	France	Penze	05.06.2016
S2	France	Penze	16.07.2016
S2	France	Penze	05.08.2016
S2	France	Penze	06.09.2016
S2	France	Penze	14.10.2016
S2	France	Penze	03.12.2016
S2	France	Penze	13.12.2016
S2	France	Penze	25.01.2017
S2	France	Penze	14.02.2017
S2	France	Penze	13.03.2017
S2	France	Penze	25.04.2017
S2	France	Penze	25.05.2017
S2	France	Penze	14.06.2017
S2	France	Penze	24.07.2017
S2	France	Penze	27.08.2017
S2	France	Penze	14.09.2017
S2	France	Penze	06.11.2017
S2	France	Penze	18.11.2017
S2	France	Penze	17.01.2018
S2	France	Penze	16.02.2018
S2	France	Penze	26.02.2018
S2	France	Penze	30.04.2018
S2	France	Penze	17.05.2018
S2	France	Penze	29.06.2018
S2	France	Penze	14.07.2018

S2	France	Penze	30.07.2018
S2	France	Penze	27.09.2018
S2	France	Penze	09.10.2018
S2	France	Penze	26.11.2018
S2	France	Penze	26.12.2018
S2	France	Penze	27.01.2019
L8	France	Penze	22.02.2019
S2	France	Penze	23.03.2019
S2	France	Penze	20.04.2019
S2	France	Penze	22.05.2019
S2	France	Penze	01.06.2019
S2	France	Penze	04.07.2019
S2	France	Penze	20.08.2019
S2	France	Penze	19.09.2019
S2	France	Penze	22.10.2019
S2	France	Penze	11.11.2019
S2	France	Penze	26.12.2019
S2	France	Penze	06.02.2020
S2	France	Penze	26.02.2020
S2	France	Penze	11.04.2020
S2	France	Penze	09.04.2020
S2	France	Penze	09.05.2020
S2	France	Penze	23.06.2020
S2	France	Penze	18.07.2020
L8	France	Penze	03.08.2020
S2	France	Penze	08.09.2020
S2	France	Penze	02.11.2020
S2	France	Penze	15.11.2020
S2	France	Penze	17.12.2020
S2	France	TyNod	29.12.2015
S2	France	TyNod	07.04.2016
S2	France	TyNod	08.04.2016
S2	France	TyNod	17.04.2016
S2	France	TyNod	05.06.2016
S2	France	TyNod	16.07.2016
S2	France	TyNod	15.08.2016
S2	France	TyNod	16.09.2016
S2	France	TyNod	14.10.2016
S2	France	TyNod	03.12.2016
S2	France	TyNod	23.12.2016
S2	France	TyNod	25.01.2017
S2	France	TyNod	14.02.2017
S2	France	TyNod	13.03.2017

S2	France	TyNod	07.05.2017
L8	France	TyNod	15.05.2017
S2	France	TyNod	21.06.2017
S2	France	TyNod	04.07.2017
S2	France	TyNod	09.09.2017
S2	France	TyNod	22.09.2017
S2	France	TyNod	06.11.2017
S2	France	TyNod	18.11.2017
S2	France	TyNod	17.01.2018
S2	France	TyNod	16.02.2018
S2	France	TyNod	18.03.2018
S2	France	TyNod	30.04.2018
S2	France	TyNod	17.05.2018
S2	France	TyNod	29.06.2018
S2	France	TyNod	14.07.2018
S2	France	TyNod	25.08.2018
S2	France	TyNod	27.09.2018
S2	France	TyNod	09.10.2018
S2	France	TyNod	26.11.2018
S2	France	TyNod	26.12.2018
S2	France	TyNod	06.02.2019
L8	France	TyNod	22.02.2019
S2	France	TyNod	23.03.2019
S2	France	TyNod	20.04.2019
S2	France	TyNod	22.05.2019
S2	France	TyNod	01.06.2019
S2	France	TyNod	04.07.2019
S2	France	TyNod	20.08.2019
S2	France	TyNod	19.09.2019
S2	France	TyNod	27.09.2019
S2	France	TyNod	11.11.2019
S2	France	TyNod	26.12.2019
S2	France	TyNod	06.02.2020
S2	France	TyNod	26.02.2020
S2	France	TyNod	11.04.2020
S2	France	TyNod	09.04.2020
S2	France	TyNod	09.05.2020
S2	France	TyNod	23.06.2020
S2	France	TyNod	18.07.2020
S2	France	TyNod	07.08.2020
S2	France	TyNod	08.09.2020
S2	France	TyNod	02.11.2020
S2	France	TyNod	05.11.2020

S2	France	TyNod	17.12.2020
S2	Scotland	Tyne	11.01.2016
S2	Scotland	Tyne	10.02.2016
S2	Scotland	Tyne	15.03.2016
S2	Scotland	Tyne	01.05.2016
S2	Scotland	Tyne	20.04.2016
L8	Scotland	Tyne	03.06.2016
S2	Scotland	Tyne	19.07.2016
S2	Scotland	Tyne	01.08.2016
S2	Scotland	Tyne	21.08.2016
S2	Scotland	Tyne	11.10.2016
S2	Scotland	Tyne	16.11.2016
S2	Scotland	Tyne	29.11.2016
S2	Scotland	Tyne	11.01.2017
S2	Scotland	Tyne	24.02.2017
S2	Scotland	Tyne	26.03.2017
L8	Scotland	Tyne	12.04.2017
S2	Scotland	Tyne	25.05.2017
S2	Scotland	Tyne	17.06.2017
S2	Scotland	Tyne	17.07.2017
S2	Scotland	Tyne	13.08.2017
S2	Scotland	Tyne	05.10.2017
S2	Scotland	Tyne	20.10.2017
S2	Scotland	Tyne	11.11.2017
S2	Scotland	Tyne	26.12.2017
S2	Scotland	Tyne	09.02.2018
S2	Scotland	Tyne	24.02.2018
S2	Scotland	Tyne	24.03.2018
S2	Scotland	Tyne	30.04.2018
S2	Scotland	Tyne	02.06.2018
S2	Scotland	Tyne	07.06.2018
S2	Scotland	Tyne	07.07.2018
S2	Scotland	Tyne	16.08.2018
S2	Scotland	Tyne	10.10.2018
S2	Scotland	Tyne	15.10.2018
S2	Scotland	Tyne	01.11.2018
S2	Scotland	Tyne	24.12.2018
S2	Scotland	Tyne	23.01.2019
S2	Scotland	Tyne	27.02.2019
S2	Scotland	Tyne	14.03.2019
S2	Scotland	Tyne	05.04.2019
S2	Scotland	Tyne	10.05.2019
S2	Scotland	Tyne	27.06.2019

S2	Scotland	Tyne	24.07.2019
S2	Scotland	Tyne	03.08.2019
S2	Scotland	Tyne	07.09.2019
S2	Scotland	Tyne	02.10.2019
S2	Scotland	Tyne	29.11.2019
S2	Scotland	Tyne	01.12.2019
S2	Scotland	Tyne	28.01.2020
S2	Scotland	Tyne	29.02.2020
S2	Scotland	Tyne	03.03.2020
S2	Scotland	Tyne	22.04.2020
S2	Scotland	Tyne	29.05.2020
S2	Scotland	Tyne	08.06.2020
L8	Scotland	Tyne	09.07.2020
S2	Scotland	Tyne	04.09.2020
S2	Scotland	Tyne	29.09.2020
S2	Scotland	Tyne	09.10.2020
S2	Scotland	Tyne	28.11.2020
S2	Scotland	Tyne	12.01.2021

Table S8 Penze recorded *Ulva* extension Jan 2016 - Dec 2020 (in Hectares)

	2020	**2019**	**2018**	**2017**	**2016**
Jan	0.0	0.0	0.0	0.0	0.0
Feb	0.0	0.0	6.2	0.0	0.0
Mar	10.3	20.4	20.5	45.1	3.8
Apr	61.7	109.6	58.5	77.5	47.6
May	121.2	115.2	147.8	119.0	104.2
Jun	143.0	175.2	174.2	150.5	188.5
Jul	179.1	181.9	158.4	193.9	196.0
Aug	205.5	132.2	180.3	176.1	150.8
Sep	93.0	114.6	168.3	101.8	96.1
Oct	71.0	91.6	128.5	76.3	58.0
Nov	54.7	51.2	5.5	10.2	0.0
Dec	0.0	0.0	0.0	0.0	0.0

Table S9 Ty Nod recorded *Ulva* extension Jan 2016 - Dec 2020 (in Hectares)

	2020	**2019**	**2018**	**2017**	**2016**
Jan	0.0	0.0	0.0	0.0	0.0
Feb	0.0	0.0	0.0	0.0	0.0
Mar	13.9	20.1	0.0	39.9	0.0
Apr	66.8	104.4	76.0	74.8	50.5
May	110.2	121.5	133.9	90.5	101.1
Jun	141.1	136.0	229.8	150.6	151.1
Jul	218.8	211.8	235.2	195.4	221.3
Aug	299.4	251.6	238.4	213.8	257.4
Sep	109.6	129.6	158.0	139.3	141.8
Oct	98.3	83.8	157.5	119.3	107.9
Nov	21.1	25.1	8.4	0.0	10.2
Dec	0.0	0.0	0.0	0.0	0.0

Table S10 Pouldon recorded *Ulva* extension Jan 2016 - Dec 2020 (in Hectares)

	2020	**2019**	**2018**	**2017**	**2016**
Jan	0.0	0.0	0.0	0.0	0.0
Feb	0.0	0.0	0.0	0.0	0.0
Mar	4.0	10.4	6.5	15.8	0.9
Apr	2.3	23.6	24.9	42.7	28.2
May	38.0	24.3	35.5	53.1	58.1
Jun	126.5	71.7	149.9	102.3	145.8
Jul	139.6	119.3	155.0	128.4	154.3
Aug	158.9	105.2	155.3	156.8	142.1
Sep	69.5	76.5	124.8	76.2	76.5
Oct	41.6	9.2	111.3	80.7	81.6
Nov	0.0	0.0	6.3	13.3	0.0
Dec	0.0	0.0	0.0	0.0	0.0

Table S11 Tolka recorded *Ulva* extension Jan. 2016 - Dec. 2020 (in Hectares)

	2020	**2019**	**2018**	**2017**	**2016**
Jan	0.0	0.0	0.0	0.0	0.0
Feb	0.0	0.0	0.0	0.0	0.0
Mar	4.8	4.5	0.0	4.7	9.7
Apr	8.8	6.2	13.3	3.1	11.7
May	30.3	21.5	15.7	16.0	13.1
Jun	38.2	35.4	39.4	35.2	33.0
Jul	28.5	25.6	31.4	33.9	31.3
Aug	26.4	20.3	29.0	28.1	24.0
Sep	24.5	20.1	20.8	18.7	12.9
Oct	11.9	14.7	9.7	9.9	9.6
Nov	0.4	0.0	5.1	4.3	0.0
Dec	0.0	0.0	0.0	0.0	0.0

Table S12 Clonakilty recorded *Ulva* extension Jan 2016 - Dec 2020 (in Hectares)

	2020	**2019**	**2018**	**2017**	**2016**
Jan	0.0	9.9	10.6	10.0	6.3
Feb	1.0	10.8	5.2	12.6	10.7
Mar	7.0	2.9	14.7	12.8	10.3
Apr	11.6	6.1	6.4	20.6	15.2
May	18.4	15.7	22.9	24.7	24.7
Jun	32.0	29.1	34.0	29.4	26.5
Jul	33.4	32.5	36.5	27.0	31.8
Aug	36.8	28.8	35.1	24.8	32.9
Sep	30.7	28.9	33.3	20.8	28.1
Oct	23.1	23.6	22.1	18.1	26.2
Nov	10.9	18.9	4.3	3.9	17.5
Dec	7.8	8.0	0.0	14.3	18.7

Table S13 Dungarvin recorded *Ulva* extension Jan 2016 - Dec 2020 (in Hectares)

	2020	**2019**	**2018**	**2017**	**2016**
Jan	0.0	0.0	0.0	17.1	0.0
Feb	0.0	0.0	0.0	0.0	0.0
Mar	0.0	1.4	0.0	0.0	0.0
Apr	0.0	0.0	5.0	27.4	0.0
May	26.8	27.9	32.3	30.7	24.8
Jun	70.3	68.3	79.3	31.2	86.3
Jul	78.3	100.5	137.5	59.5	104.2
Aug	113.2	127.7	109.3	94.5	128.2
Sep	91.3	123.6	106.1	92.2	128.2
Oct	75.0	92.3	84.2	84.9	104.1
Nov	42.0	3.0	0.0	0.0	79.2
Dec	0.0	0.0	0.0	0.0	62.3

Table S14 Argideen recorded *Ulva* extension Jan 2016 - Dec 2020 (in Hectares)

	2020	**2019**	**2018**	**2017**	**2016**
Jan	0.0	0.0	0.0	0.0	0.0
Feb	0.0	0.0	0.0	0.0	0.0
Mar	0.0	0.0	0.0	0.0	0.0
Apr	7.6	0.0	5.9	10.5	10.4
May	17.7	19.7	21.2	17.6	13.5
Jun	21.3	24.6	25.1	25.8	36.5
Jul	-	43.9	28.3	46.2	49.8
Aug	46.5	50.8	28.7	55.7	59.4
Sep	40.8	41.1	23.8	54.1	-
Oct	20.9	30.3	18.2	35.4	20.1
Nov	10.0	21.9	8.2	6.5	15.4
Dec	0.0	0.0	0.0	0.0	13.4

Table S15 Tyne recorded *Ulva* extension Jan 2016 - Dec 2020 (in Hectares)

	2020	**2019**	**2018**	**2017**	**2016**
Jan	0.0	0.0	-	0.0	0.0
Feb	0.0	0.0	0.0	0.0	0.0
Mar	0.0	0.0	0.0	0.0	0.0
Apr	1.3	1.3	0.6	6.7	17.5
May	6.0	8.8	13.6	8.9	20.5
Jun	11.0	18.4	18.7	12.3	20.5
Jul	26.6	11.7	11.8	13.3	26.8
Aug	19.0	25.5	28.3	27.1	30.8
Sep	12.9	20.2	13.7	11.8	27.1
Oct	9.5	9.7	13.6	11.5	11.4
Nov	0.0	0.0	8.5	2.1	1.1
Dec	0.0	0.0	0.0	0.0	0.0

Table S16 Land use change between 2012 and 2018, Argideen-Clonakilty catchment

2012	**Land use**	**2018**	**Land use**	**Hectares converted**
	Non-irrigated arable land		Pastures	1278
	Pastures		Non-irrigated arable land	619
	Pastures		Transitional woodland-shrub	52
	Land principally occupied by agriculture, with significant areas of natural vegetation		Transitional woodland-shrub	4
	Coniferous forest		Transitional woodland-shrub	98
	Transitional woodland-shrub		Broad-leaved forest	102

Table S17 Land use change between 2012 and 2018, Dungarvin catchment

2012	Land use	2018	Land use	Hectares converted
	Construction sites		Industrial or commercial units	13
	Non-irrigated arable land		Pastures	1010
	Pastures		Construction sites	8
	Pastures		Non-irrigated arable land	543
	Pastures		Transitional woodland-shrub	64
	Pastures		Industrial or commercial units	3
	Land principally occupied by agriculture, with significant areas of natural vegetation		Transitional woodland-shrub	7
	Coniferous forest		Transitional woodland-shrub	317
	Transitional woodland-shrub		Broad-leaved forest	37
	Transitional woodland-shrub		Coniferous forest	407
	Transitional woodland-shrub		Mixed forest	67
	Transitional woodland-shrub		Transitional woodland-shrub	18

Table S18 Land use change between 2012 and 2018, Tolka catchment

2012	Land use	2018	Land use	Hectares converted
	Industrial or commercial units		Industrial or commercial units	7
	Mineral extraction sites		Pastures	27
	Construction sites		Discontinuous urban fabric	46
	Construction sites		Industrial or commercial units	38
	Construction sites		Construction sites	27
	Green urban areas		Construction sites	30
	Non-irrigated arable land		Industrial or commercial units	14
	Non-irrigated arable land		Construction sites	135

	Non-irrigated arable land		Sport and leisure facilities	40
	Non-irrigated arable land		Non-irrigated arable land	54
	Non-irrigated arable land		Pastures	849
	Pastures		Discontinuous urban fabric	28
	Pastures		Industrial or commercial units	84
	Pastures		Mineral extraction sites	9
	Pastures		Construction sites	386
	Pastures		Non-irrigated arable land	2009
	Pastures		Pastures	8
	Pastures		Transitional woodland-shrub	122
	Land principally occupied by agriculture, with significant areas of natural vegetation		Non-irrigated arable land	2
	Land principally occupied by agriculture, with significant areas of natural vegetation		Transitional woodland-shrub	17
	Coniferous forest		Coniferous forest	67
	Coniferous forest		Transitional woodland-shrub	639
	Natural grasslands		Burnt areas	11
	Moors and heathland		Transitional woodland-shrub	34
	Moors and heathland		Burnt areas	183
	Transitional woodland-shrub		Broad-leaved forest	61
	Transitional woodland-shrub		Coniferous forest	619
	Transitional woodland-shrub		Mixed forest	51
	Transitional woodland-shrub		Transitional woodland-shrub	22
	Peat bogs		Transitional woodland-shrub	11
	Peat bogs		Burnt areas	128

Table S19 Land use change between 2012 and 2018, Penze-Ty Nod catchment

2012	Land use	2018	Land use	Hectares converted
	Construction Sites		Discontinuous urban fabric	129
	Construction Sites		Industrial or commercial units	34
	Construction Sites		Port areas	33
	Non-irrigated arable land		Discontinuous urban fabric	12
	Non-irrigated arable land		Industrial or commercial units	27
	Non-irrigated arable land		Construction Sites	18
	Non-irrigated arable land		Pastures	35
	Pastures		Industrial or commercial units	11
	Pastures		Construction Sites	13
	Complex cultivation patterns		Discontinuous urban fabric	41
	Complex cultivation patterns		Industrial or commercial units	47
	Complex cultivation patterns		Mineral extraction sites	5
	Complex cultivation patterns		Construction Sites	21
	Land principally occupied by agriculture, with significant areas of natural vegetation		Mineral extraction sites	5
	Broad-leaved forest		Transitional woodland-shrub	103
	Coniferous forest		Transitional woodland-shrub	278
	Mixed forest		Transitional woodland-shrub	44
	Transitional woodland-shrub		Coniferous forest	25
	Transitional woodland-shrub		Mixed forest	908

Table S20 Land use change between 2012 and 2018, Tyne estuary catchment

2012	Land use	2018	Land use	Hectares converted
	Industrial or commercial units		Construction Sites	8
	Industrial or commercial units		Pastures	39
	Road and rail networks and associated land		Construction Sites	17
	Mineral extraction sites		Discontinuous urban fabric	9
	Mineral extraction sites		Construction Sites	40
	Mineral extraction sites		Non-irrigated arable land	118

	Mineral extraction sites		Pastures	264
	Mineral extraction sites		Natural grasslands	201
	Mineral extraction sites		Moors and heathland	51
	Mineral extraction sites		Waterbodies	42
	Dump Sites		Pastures	40
	Construction Sites		Discontinuous urban fabric	514
	Construction Sites		Industrial or commercial units	189
	Construction Sites		Road and rail networks and associated land	14
	Construction Sites		Green urban areas	25
	Construction Sites		Sport and leisure facilities	7
	Construction Sites		Pastures	22
	Green urban areas		Discontinuous urban fabric	21
	Green urban areas		Construction Sites	40
	Sport and leisure facilities		Construction Sites	24
	Non-irrigated arable land		Discontinuous urban fabric	125
	Non-irrigated arable land		Industrial or commercial units	10
	Non-irrigated arable land		Mineral extraction sites	48
	Non-irrigated arable land		Construction Sites	604
	Non-irrigated arable land		Sport and leisure facilities	118
	Non-irrigated arable land		Coniferous forest	8
	Pastures		Discontinuous urban fabric	49
	Pastures		Industrial or commercial units	79
	Pastures		Mineral extraction sites	46
	Pastures		Construction Sites	202
	Pastures		Non-irrigated arable land	76
	Pastures		Inland marshes	94
	Broad-leaved forest		Construction Sites	29
	Broad-leaved forest		Transitional woodland-shrub	35
	Coniferous forest		Industrial or commercial units	170

	Coniferous forest		Mineral extraction sites	13
	Coniferous forest		Construction Sites	87
	Coniferous forest		Transitional woodland-shrub	4577
	Mixed forest		Transitional woodland-shrub	99
	Natural grasslands		Industrial or commercial units	55
	Natural grasslands		Mineral extraction sites	29
	Moors and heathland		Industrial or commercial units	49
	Moors and heathland		Construction Sites	14
	Moors and heathland		Non-irrigated arable land	18
	Moors and heathland		Pastures	77
	Transitional woodland-shrub		Industrial or commercial units	88
	Transitional woodland-shrub		Mineral extraction sites	5
	Transitional woodland-shrub		Construction Sites	8
	Transitional woodland-shrub		Coniferous forest	1632
	Transitional woodland-shrub		Mixed forest	97
	Peat bogs		Industrial or commercial units	74
	Peat bogs		Mineral extraction sites	13
	Peat bogs		Construction Sites	6

Table S21 Land use characterisation 2012 – 2018 within selected riverine catchments. Data on land change taken from the CORINE land change dataset available at https://www.epa.ie/pubs/data/corinedata/

	Catchment	Tolka	Clonakilty-Argideen	Dungarvin	Tyne	Pouldon	Penze-Ty Nod
2012	**Agricultural land**	57.89%	93.57%	80.34%	52.54%	74.00%	78.62%
2018		57.47%	93.54%	80.31%	52.39%	74.00%	79.98%
2012	**Natural vegetation and forest**	23.92%	0.95%	3.01%	11.41%	9.25%	11.28%
2018		24.29%	0.95%	3.00%	11.61%	9.25%	9.87%
2012	**Residential, commercial, and industrial properties**	16.87%	4.58%	16.46%	33.33%	15.37%	9.57%
2018		16.92%	4.61%	16.45%	33.25%	15.37%	9.64%
2012	**Aquatic bodies**	1.32%	0.90%	0.19%	2.73%	1.39%	0.66%
2018		1.32%	0.89%	0.19%	2.75%	1.39%	0.66%
% of land change		0.08%	0.00%	0.11%	0.05%	0.00%	1.41%
Total Catchment Surface Area (ha)		161,485	55,289	63,571	553,661	103,866	222,941

Supplementary Information Figure S4 - S7

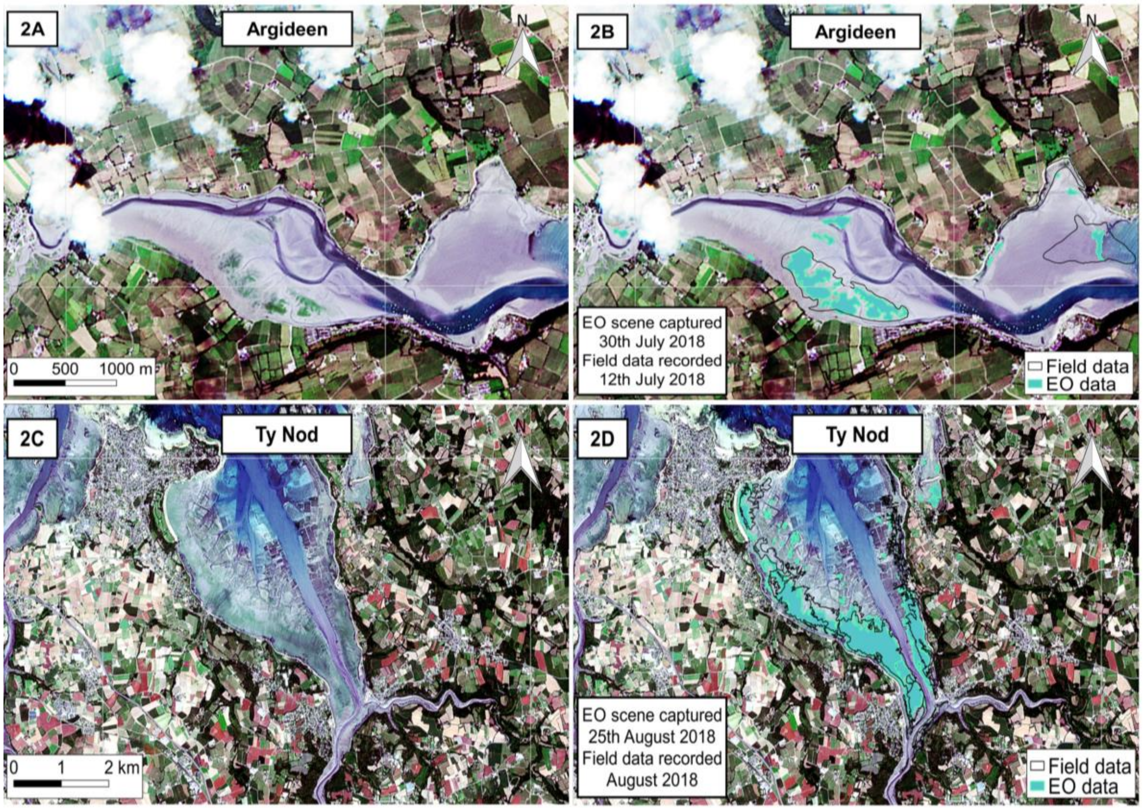

Fig. S4 Examples of Sentinel-2 scenes in different geographies highlighting *Ulva* bloom events. 2A) Sentinel-2 (True Colour Composite) scene showing macroalgal bloom occurring in Argideen, Ireland. 2B) Algae mask using maximum likelihood comparison with field sampling data. 2C) Sentinel-2 (True Colour Composite) scene showing macroalgal bloom occurring in Ty-Nod, Brittany. 2D) Algae mask using maximum likelihood comparison with field sampling data

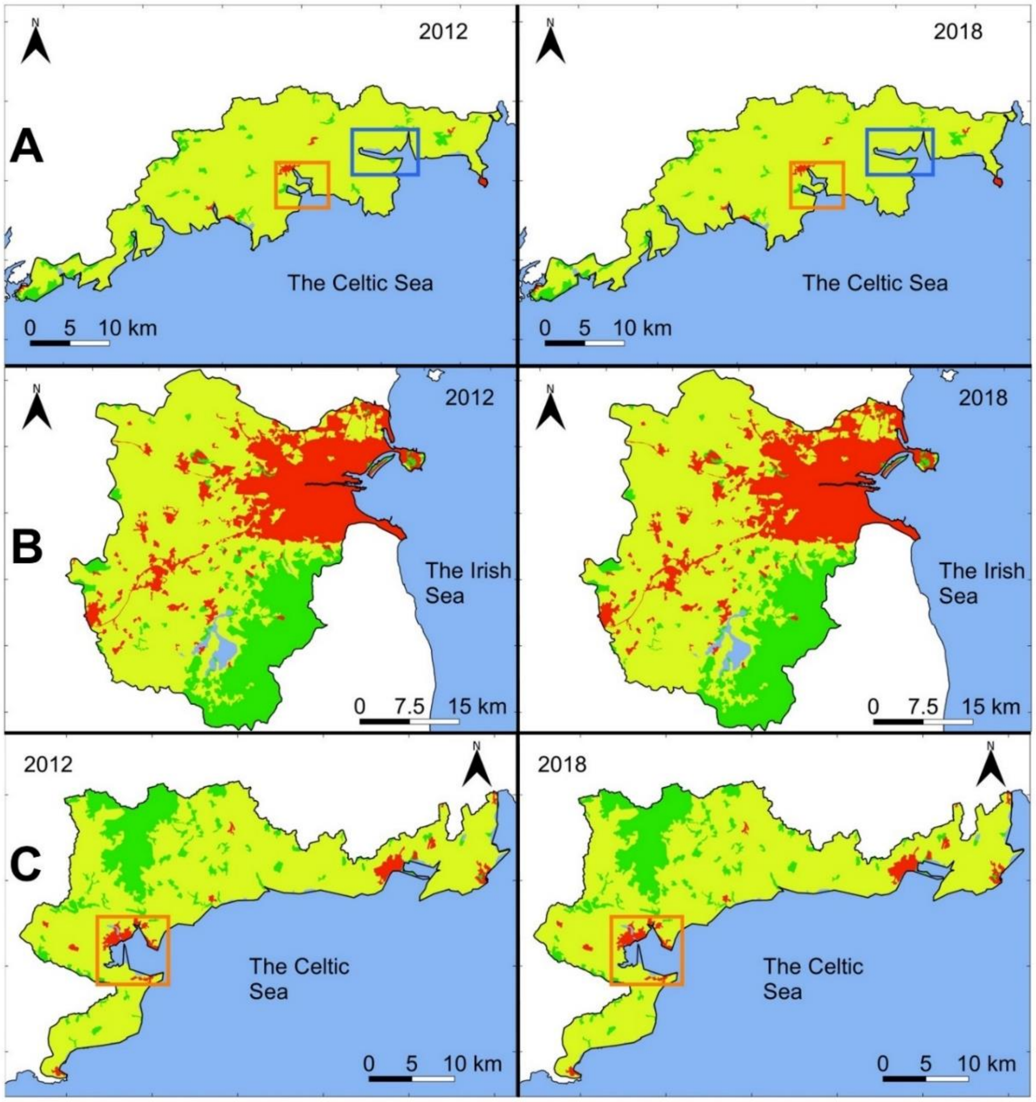

Fig. S5 Showing the change in land use between 2012 and 2018 in selected river catchments in Ireland. Highlighting A) Clonakilty-Argideen, B) Tolka, and C) Dungarvin. Areas in Red indicates Urban and industrial areas; Green indicates woodlands and area of natural forestry, Yellow indicates agricultural land, and light Blue indicates aquatic bodies. An orange box surrounds the estuaries under investigation

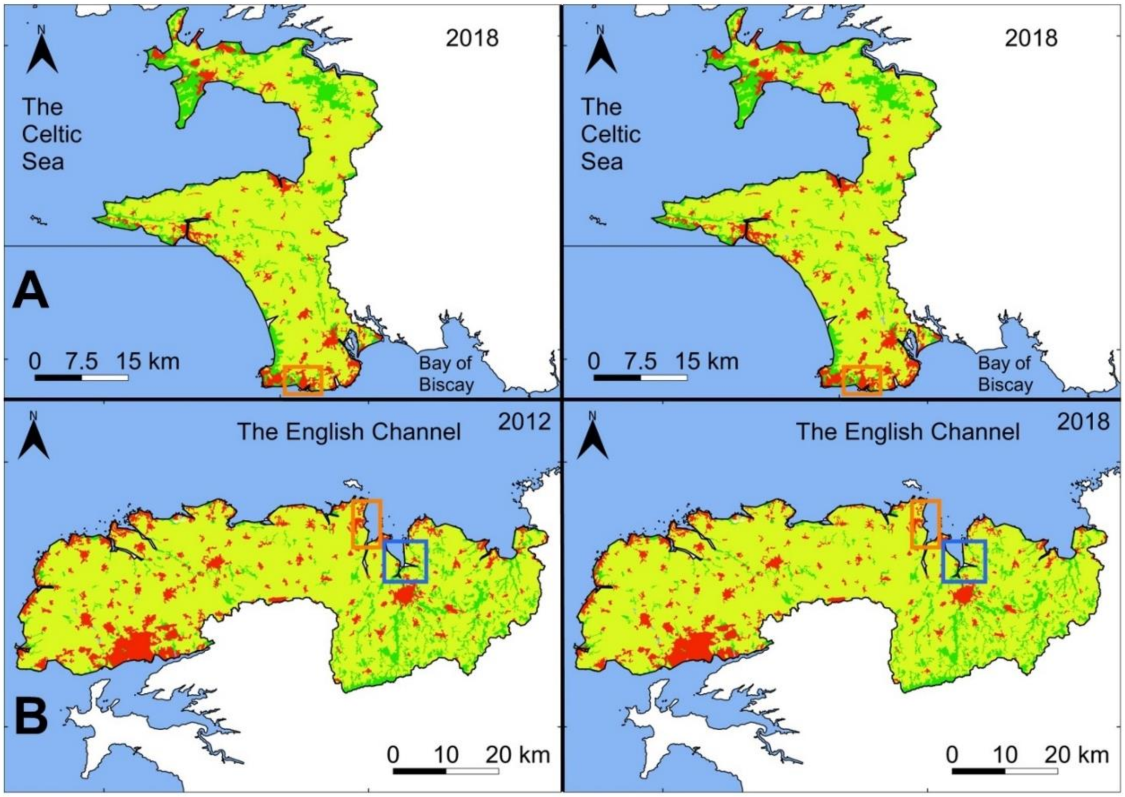

Fig. S6 Showing the change in land use between 2012 and 2018 in selected river catchments in France, highlighting A) Pouldon and B) Penze-Ty Nod. Areas in Red indicates Urban and industrial areas, Green indicates woodlands and area of natural forestry, Yellow indicates agricultural land, and light Blue indicates aquatic bodies. An orange box surrounds the estuaries under investigation

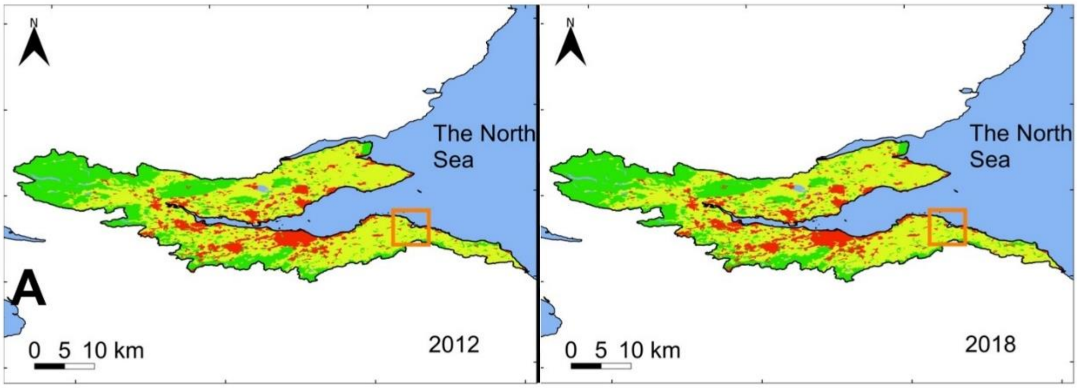

Fig. S7 Showing the change in land use between 2012 and 2018 in selected river catchments in France, highlighting A) Tyne estuary. Areas in Red indicates Urban and industrial areas; Green indicates woodlands and area of natural forestry, Yellow indicates agricultural land, and light Blue indicates aquatic bodies. An orange box surrounds the estuaries under investigation

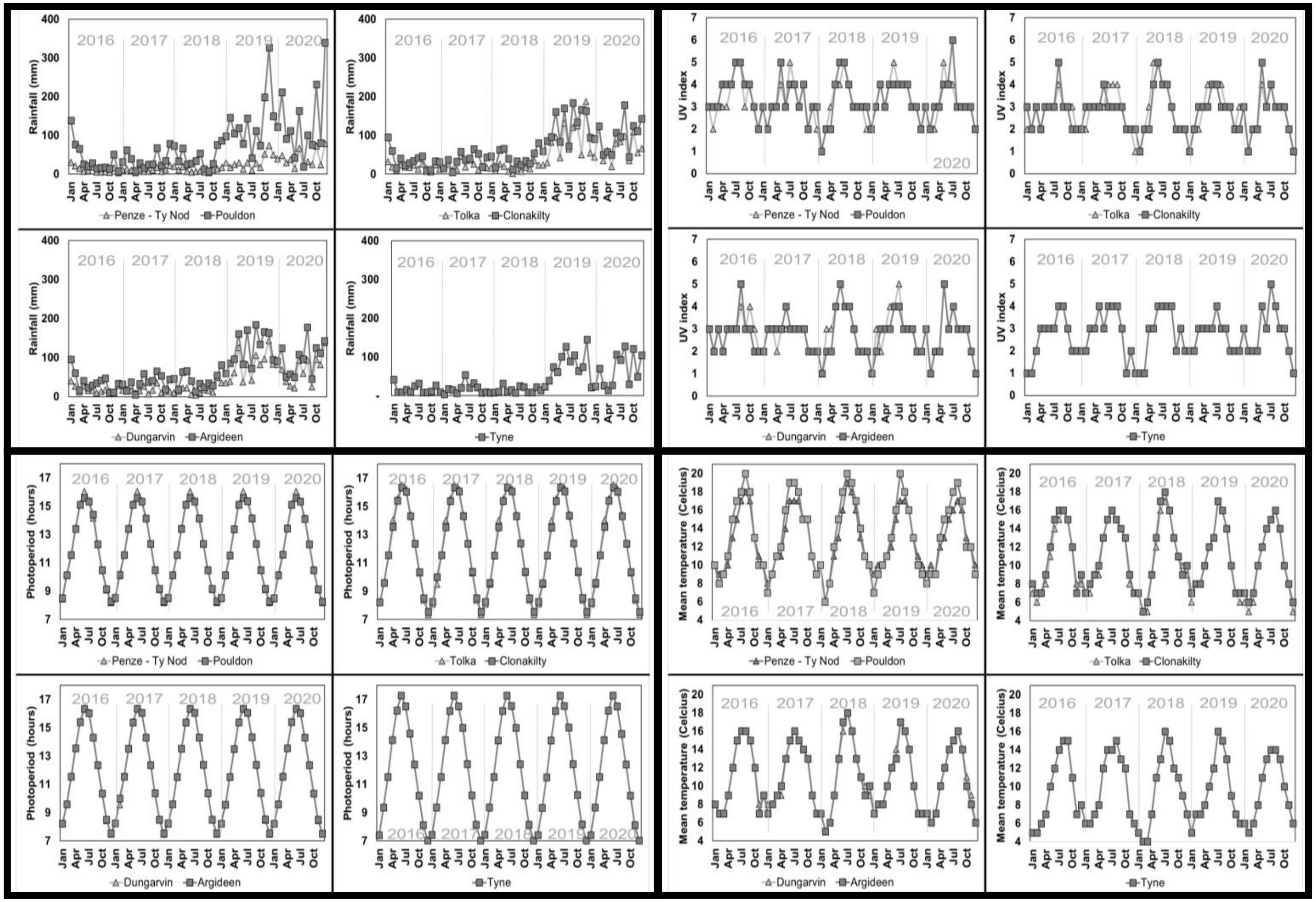

Fig. S8 Meteorological variation showing mean monthly temperature, photoperiod, rainfall and UV index for 2016-2020