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Mestrado em Biologia Marinha

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Declaração de autoria de trabalho (Statement of Authorship)

Comparison of the epifaunal assemblage of the invasive and native macroalgae.

Declaro ser o autor deste trabalho, que é original e inédito. Autores e trabalhos consultados estão devidamente citados no texto e constam da listagem de referências incluída.

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ABSTRACT

The rapid spread of introduced seaweeds is of essential concern, as they can have a deleterious impact on coastal native seaweed and seagrass communities. However, non-indigenous species can generate mixed responses when introduced to native assemblages, and increase habitat complexity, depending on the spatial and ecological context. By taking advantage of the co-occurrence of the native *Ulva* seaweeds and the non-native *Agarophyton vermiculophyllum* in the Clonakilty estuary (Cork, Ireland) we aim to assess the differences of the epifaunal community of the native and invasive macroalgal species and how epifaunal biodiversity may be affected by the invasive. In four locations over four sampling occasions, a total of 253 quadrants of algae and epifaunal biomass were sampled. The *Ulva* dominated sections mainly contained macroalgae with tubular morphotypes and some sporadic patches of laminar *Ulva rigida*. The average algal biomass of both species was similar, however, the biomass of the red seaweed was highly variable throughout the seasons. The native algal canopy hosted up to four times more epifaunal biomass compared to the invasive rhodophyte. Moreover, the epifaunal community of both canopies differed substantially, whereas deposit-feeding organisms had a higher abundance in *Ulva* spp. canopies and the carnivorous crab, *Carcinus maenas,* was much more abundant in *A. vermiculophyllum* samples. The native green macroalgae hosted more invertebrate taxa, however no difference in biodiversity was found. Increased predation on deposit-feeders and grazers, as well as, the structural and chemical resistance of *A. vermiculophyllum* against grazing and overgrowth by epiphytes may reduce the trophic transfer from primary production toward higher trophic levels.

Keywords: *Agarophyton vermiculophyllum, Ulva*, invasive macroalgae, community composition, native species

Resumo
(Summary)

Introdução. As introduções de espécies exóticas ocorrem já há vários séculos, de forma intencional para ganho comercial ou involuntariamente, maioritariamente por transporte marítimo como passageiros escondidos em águas de lastro ou agarrados ao casco do navio. A rápida dispersão de algas não-indígenas é uma preocupação básica, já que podem ter impactos nocivos nas comunidades algas e ervas marinhas costeiras indígenas e são, juntamente com as alterações climáticas, um dos fatores de *stress* mais significativos dos ecossistemas de hoje. Estes impactos incluem a modificação da estrutura da comunidade da fauna, redução de biodiversidade e alteração das dinâmicas de nutrientes estuarinas, que podem, em última instância, acelerar a mudança de macrófitas de crescimento lento para macroalgas efémeras, aumentando o risco de afloramentos de macroalgas. No entanto, as espécies não-indígenas podem gerar respostas mistas quando introduzidas em agrupamentos nativos, e aumentar a complexidade do habitat, dependendo do contexto espacial e ecológico. Os factores de *stress* antropogénicos como o aumento dos níveis de nutrientes podem intensificar a magnitude de tais eventos e aumentar a sua frequência. A referida eutrofização aparente de sistemas costeiros pode fomentar as invasões de macrófitas, assim como a sua resistência a *grazing* o que aumenta ainda mais a probabilidade de afloramentos de macroalgas. Duas espécies indígenas de forma laminar (*Ulva rigida* e *Ulva gigantea*) e duas espécies indígenas de forma tubular (*Ulva prolifera* e *Ulva compressa*) do género *Ulva* bem como a rodófita não-indígena *A.vermiculophyllum* foram identificadas no estuário de Clonakilty (Condado de Cork, Irlanda) e estão a formar canópias distintas próximas umas das outras. A identificação de efeitos positivos ou negativos de uma espécie não-indígena em ecossistemas estuarinos e a forma como é controlada teria implicações notáveis nas estratégias de gestão de espécies invasivas fundacionais. Os vários impactos ecológicos na diversidade da epifauna e a utilização de nutrientes precisam de ser avaliados, especialmente no contexto do sobre-enriquecimento de nutrientes antropogénico local e a mudança global para reconhecer e recomendar uma estratégia apropriada (activa ou passiva). Ao tirar proveito da co-ocorrência de algas indígenas e não-indígenas neste estuário, tivemos como objectivos: (i) a comparação de padrões espaciais e temporais na estrutura de comunidades de epifauna em ambas as algas; (ii) caracterizar o seu

papel na formação de habitats de ambas as espécies e as suas implicações em diferentes taxa da fauna; (iii) explorar implicações ecológicas para diferentes guildas alimentares e discutir o impacto em cascadas tróficas; e (iv) a avaliação da biodiversidade da epifauna e a riqueza das espécies de macroalgas.

Métodos. O estuário de Clonakilty (condado de Cork), localizado no sudoeste da Irlanda na costa atlântica é afectado por afloramentos de algas verdes (espécies de *Ulva* nativas) e vermelhas (espécie não-nativa *Agarophython vermiculophyllum*). O estuário experiencia elevados influxos de nutrientes, sobretudo derivados de escoamento agrícola, como consequência da intensa pecuária leiteira na área circundante e de uma estação de tratamento de águas residuais nas proximidades. O seu aspecto pouco profundo e a baixa taxa de renovação da água, em combinação com o elevado influxo de nutrientes tornam o estuário susceptível a sobre-enriquecimento de nutrientes, favorecendo o desenvolvimento de blooms de macroalgas. Tirando proveito da co-ocorrência de espécies formadoras de afloramentos nativas e não-nativas neste estuário, foram comparados os agrupamentos de epifauna em relação às espécies fundacionais. Em quatro visitas a cada local, foram recolhidos quinze a vinte quadrantes 25 x 25 cm por secção por ocasião de amostragem, o que resultou num total de 253 amostras. Subsequentemente, as espécies de epifauna foram identificadas ao nível de táxon mais elevado possível e foram exploradas as comunidades faunais utilizando análise de dados multivariada e univariada.

Resultados. Em todas as quatro localizações, A, B, C e D, foram analisadas a biomassa das algas e da fauna e os dados da comunidade. Os locais A e B eram dominados por um dossel de *A. vermiculophyllum* e os locais C e D por canópias de *Ulva* spp.. As zonas dominadas por *Ulva* spp. continham, principalmente, macroalgas de morfótipo tubular (*Ulva compressa* e *Ulva prolifera*) e algumas parcelas esporádicas de *Ulva rigida* laminar. A biomassa algácea média de ambas as espécies foi semelhante; no entanto, a biomassa de *A. vermiculophyllum* foi muito variável ao longo das estações, enquanto que a biomassa de *Ulva* spp. demonstrou-se mais constante sendo ainda provável que não tenha ocorrido limitação de azoto. As canópias de *Ulva* spp. suportaram até quatro vezes mais biomassa de fauna que *A. vermiculophyllum* e um efeito sazonal na biomassa de fauna encontrada em amostras de *Ulva*. A composição de epifauna entre ambas as algas apresentou diferenças consideráveis, sendo encontrados mais taxa em amostras de algas verdes. Além disso, organismos com dieta à base de detritos eram mais abundantes em amostras de *Ulva* spp. e o caranguejo carnívoro, *Carcinus maenas*, era

muito mais abundante em amostras de *A. vermiculophyllum*, ainda que com menor peso por indivíduo.

Discussão. Sabe-se que a espécie *A. vermiculophyllum* pode causar uma alteração radical de ecossistemas e numa larga extensão espacial, o que altera, não só os agrupamentos de epifauna, como também o metabolismo do ecossistema, incluindo os processos de decomposição da biomassa. Devido à ausência de estudos a longo prazo acerca do seu efeito em ecossistemas estuarinos, a incorporação desta espécie na gestão da restauração mantém-se disputável. Ademais, isto é algo que tem que ser avaliado caso a caso, considerando que a recuperação de algas nativas formadoras de habitats pode restaurar a diversidade da fauna por associação, ainda que seja um processo complicado e a longo prazo. Portanto, considerando: (i) a biomassa de *A. vermiculophyllum* variou notavelmente ao longo das estações, o que pode ser resultado de reduzida transferência trófica; (ii) o agrupamento de epifauna diferia das *Ulva* spp. indígenas e a abundância do caranguejo predatório *Carcinus maenas* foi muito elevada o que pode afectar herbívoros e organismos que se alimentam de detritos; (iii) a resistência estrutural de *A. vermiculophyllum* e o aumento de predação podem promover organismos secundários que se alimentam de depósitos ao suprimir as espécies predominantes e autóctones (i.e. *Hydrobia ulvae*) no agrupamento; (iv) dentro do mesmo estuário, as macroalgas não nativas tiveram menor riqueza de espécies de epifauna e um efeito inexistente ou negativo na biodiversidade, comparadas com canópias de *Ulva* spp.. É proposta uma avaliação mais profunda dos efeitos de espécies invasoras fundacionais antes de se avançar com acções de gestão passivas (e.g. a não-remoção de espécies invasoras) em costas que experienciaram uma perda de habitats fundacionais nativos (i.e. ostreiras e pradarias de ervas marinhas indígenas). O problema das macroalgas invasivas está fortemente ligado a outras situações problemática que ocorrem em zonas costeiras, como a sobrepesca e a eutrofização. Assim, as ações de gestão recomendadas não podem substituir uma estratégia de gestão abrangente e o estabelecimento de zonas pristinas protegidas que providenciam reservas de biodiversidade, que promovem ainda mais a habilidade dos ecossistemas fornecerem as suas funções e de resistirem a perturbações.

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CHAPTER 1: GENERAL INTRODUCTION

1.1 ESTUARINE ECOSYSTEMS

Estuaries are defined as the transition zone of riverine freshwater and coastal seawater and are considered the world's most productive ecosystems regarding carbon sequestration (reviewed by McGlathery *et al.*, 2012). These areas are the preferred habitat for many crustaceans, shellfish, juvenile and adult fish species, birds, and, due to this immense amount of resources, also the preferred settlement regions of humans since ancient times (Knox, 1986). The most distinctive feature of estuarine systems is that they are the place of the mixing of sea and fresh water, however, this mixing does not occur statically, but is influenced by freshwater input, tidal action and waves. The salinity of estuaries generally ranges from 0 ‰ to ~35 ‰ salt content, depending on the oceanic salt content, which is usually at 35 ‰ (Castro and Huber, 2015). The tidal activity is shifting this mixing zone back and forth in the estuary and is also changing the water level, and periodically exposing the sediment and the benthic flora and fauna to the sun. However, the impact of tidal action strongly depends on the region, whereby the tidal range can account for several centimetres (e.g. most of the Mediterranean sea) to several meters (i.e. North-East Atlantic; Trujillo and Thurman, 2016).

Living in estuarine habitats requires a certain set of adaptations. Therefore, estuarine plant and animal species are often marked by the tolerance to desiccation and a broad range of salinities (euryhaline) and temperatures. Species with either marine or freshwater origin, which only possess the ability to cope with a relatively small range of salinities (stenohaline, a small number of species) are usually not found evenly distributed within an estuary, but limited to areas showing a salt content similar to their preferred salinity (Castro and Huber, 2015).

ESTUARINE FOOD WEBS

After tropical rainforests, submerged macrophytes and saltmarshes are the most productive plant systems (in the ranges of 2.9 to 7.5 kg organic dry weight per square meter per year), excluding agricultural systems (Westlake, 1963). The average NPP (net primary production) for an entire estuary is estimated at 2 kg organic dry weight per square meter per year, which

is thirteen times higher than the average NPP of the entire ocean and almost three times higher than the total land NPP (reviewed by Knox, 2000). Schelske and Odum (1962) tried to explain the high productivity of estuarine systems by, first, the high availability of externally sourced nutrients (e.g. through rivers or upwellings); second, the effective nutrient cycling within the estuary. This is caused by the reuptake of buried nutrients by the water column, which is facilitated by bioturbation and the mixing of the water through tides. Thirdly, that there are multiple types of primary producers (phytoplankton, marsh plants, and macroalgae), which can optimise assimilation throughout the seasons. However, at higher latitudes, estuaries are primarily productive in warmer seasons (McGlathery *et al.*, 2007).

Estuarine trophic dynamics (Figure 1.1), including food webs and energy flow, differ significantly from the ones predominant in the open ocean and are, due to the many influencing entities, that are rather complex (Hagy and Kemp, 2012). Most of the produced organic matter (~90%; reviewed by Knox, 2000) is processed over the detrital food web. Moreover, inflowing rivers are adding a considerable amount of organic matter to this system (Hagy and Kemp, 2012).
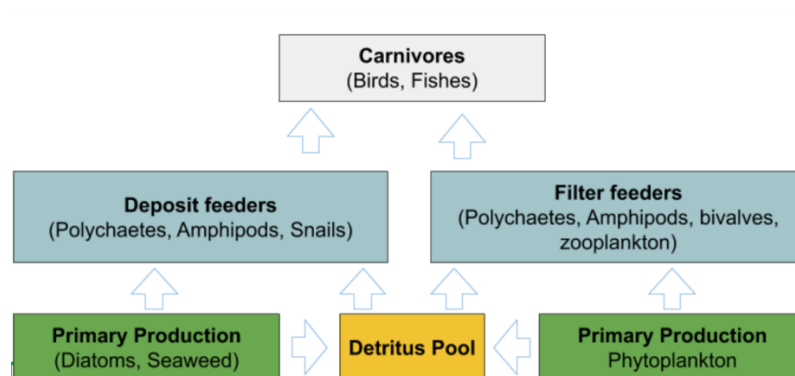
Figure 1.1: Conceptual model of the main nutrient flows in temperate estuarine systems (after Castro and Huber, 2015, fig. 12.24)

THE SHIFT FROM SEAGRASS TO SEAWEEDS IN ESTUARINE SYSTEMS

Due to eutrophication increasing in the 20th century, temperate estuaries are shifting from systems characterised by slow-growing macrophytes (e.g. seagrasses) towards rather short-lived opportunistic bloom-forming macroalgae and phytoplankton (Duarte *et al.*, 2009; Little *et al.*, 2017; Pedersen and Borum, 1996; Valiela *et al.*, 1997). Moreover, this shift on the very base of the ecosystem may have caused ecological functioning and controls of the ecosystem

to change (Cacabelos *et al.*, 2012; Tuya *et al.*, 2014). However, the effects of this shift are not simple to assess and highly context-dependent, whereas the increased primary production can have devastating effects in sandy or muddy intertidal habitats. Some taxa of macroalgae can increase habitat complexity and invertebrate abundance in other areas (Lyons *et al.*, 2014).

Primary production is majorly bottom-up controlled by nutrients sourcing naturally in upwellings, which are then carried into the estuary by tides, further river erosion and runoff, and nutrients cycled within the system, as mentioned above. Additionally, it is also enhanced by anthropogenic sourced nutrient subsidies (Fox *et al.*, 2008; Valiela *et al.*, 1997). On the other hand, top-down control by grazing may also be an essential factor for biomass removal (Geertz-Hansen *et al.*, 1993; Valentine and Duffy, 2006). However, nitrogen load and grazing are negatively correlated, and grazers may be overwhelmed by the production of new biomass, which lessens their controlling effect (Fox *et al.*, 2012; Hauxwell *et al.*, 1998) and can ultimately lead to algal blooms and hypoxic conditions in coastal zones.

THE ROLE OF EPIFAUNA

The epifauna, invertebrates living on seaweeds and seagrasses, are inhabiting estuarine systems and play a major role in energy flow by fostering decomposition of detritus, nutrient cycling and nutrient mobilisation, and increasing the oxygen content in the sediment via bioturbation (reviewed by Wilson and Fleeger, 2012). The mud snail *Hydrobia ulvae* was found to serve as substratum for *Ulva* spp. germlings, facilitating algal succession (Schorieslr *et al.*, 2000). Some species are processing organic matter directly through herbivory or are stimulating decomposition (e.g. by fungi) to then subsequently consume the decomposer (Silliman and Bertness, 2002) and are linking primary production to higher trophic levels. Those invertebrates serve as food for predatory fish and scavenging birds and are therefore directly affecting fish stocks (Rönnbäck *et al.*, 2007). On the other hand, the reasons of variability of epifauna within one and the same algal species are usually environmental factors like sedimentation and hydrodynamics, as well as random deviations (Sánchez-Moyano *et al.*, 2000).

THE ROLE OF SEAWEED IN HABITAT FORMATION

The community composition of the epifauna depends on abiotic factors such as salinity or temperature and can be altered by overfishing predatory fish (Eriksson *et al.*, 2009). The assemblages, primarily consisting of polychaetes, gastropod molluscs and crustaceans, are also associated with the identity of the macroalgal host (Gestoso *et al.*, 2012), but especially to the

structural complexity provided by the algae (Bates and DeWreede, 2007; Gartner *et al.*, 2013; Lutz *et al.*, 2019; Saarinen *et al.*, 2018; Veiga *et al.*, 2014). Macroalgae were also found to reduce water flow and alter light penetration, and thus create favourable conditions for benthic fauna. Many epifaunal species prefer algal canopies, which can protect them from predation and wave action (Wernberg *et al.*, 2013), and also those of which can serve them as a nutritious food source (Berke *et al.*, 2020). Macroalgal exudates further impact colonisation and grazing of invertebrates.

1.2 THREATS TO ESTUARINE ECOSYSTEMS

Estuaries have been a principal settlement area for humans because they are providing a high abundance of edible and non-edible resources and their connection to the sea made them a principal site for commerce. Until today, areas around estuaries have extremely high human population densities, which explains the magnitude of our interventions on those systems, as we depend on the provided goods (Day *et al.*, 2012a, 2012b). Since the end of the 19th century, it is estimated that close to 30% of submerged plant area have been lost (Waycott *et al.*, 2009). Human impacts on these systems are manifold and range from direct hydrological interventions (e.g. channelling of rivers), over-enrichment with toxins and nutrients, to indirect impacts, such as climate change and acidification due to increased CO_2 levels (Robins *et al.*, 2016; Rybczyk *et al.*, 2012).

EFFECTS OF NUTRIENT ENRICHMENT AND MACROALGAL BLOOMS

The current human population growth is supplied by intense land use and industrial agriculture, which is utilising high amounts of artificial fertilisers. Moreover, coastal urban agglomerations are generating industrial and domestic effluents which are high in phosphorus and nitrogen (Day *et al.*, 2012b). In the first half of the 20th century, the nutrient levels in adjacent estuarine and coastal waters subsequently increased, and eutrophication now represents one of the most critical stressors and threats to European estuarine ecosystems (Hering *et al.*, 2010).

Elevated nutrient levels lead to increased growth of marine macrophytes, as they are bottom-up controlled by nutrient input (Luo *et al.*, 2012; Valiela *et al.*, 1997) and since the late 1970's occurrences of green tides have been increasingly observed in the North-East Atlantic region (Charlier *et al.*, 2006). Estuarine waters, as productive and diverse ecosystems, are especially being affected by the development of macroalgal blooms and their consequences. To begin with, already the sheer amount of biomass produced during these seaweed tides in some areas

can cause severe problems for ecosystems as well as for shore-based human activities (Charlier *et al.*, 2008; Wan *et al.*, 2017; Ye *et al.*, 2011). As soon as a certain limit of biomass is reached, massive piles of beached, decaying biomass in many areas like in the Britannia are often resulting in high costs for removal and unpleasant as well as hazardous odours. The most commonly used example for outbreaks of so-called "green tides" (blooms generated by *Ulva* spp.), is the Chinese city of Qingdao at the Yellow Sea, with an extent of bloom coverage of up to 2100 km^2 (Ye *et al.*, 2011). As historical examples expose, this can quickly add up to immense economic impacts (e.g. €1.8 million in Brittany, 1992 and €200 million Qingdao, China in 2008; Charlier *et al.*, 2008). Moreover, secondary economic impacts of macroalgal blooms are costs (or losses) in human health, fisheries, tourism, and recreation (Sanseverino *et al.*, 2016), which can be significantly reduced if pursuing monitoring and controlling strategies (Smith *et al.*, 2019).

During the time of undocumented nutrient status, the communities of the coastal seas have shifted substantially towards macroalgae coverage (Hughes, 1994; Valiela *et al.*, 1997), which changed nutrient cycling. Several studies have shown that macroalgal blooms change biogeochemical cycles, alter food chains and community structures, and produce hypoxic conditions, which are caused by the decay of accumulated algal masses (Howarth *et al.*, 2011; Smetacek and Zingone, 2013). The subsequent anoxic decomposition of the algae releases sulphur compounds, which can also be a threat to humans and animals (Diaz and Rosenberg, 2008; Green-Gavrielidis *et al.*, 2018; Pedersen and Johnsen, 2017; Rossi, 2006; Valiela *et al.*, 1997).

Another factor which is affecting algal growth may be unsustainable fishing of large predatory fish, which feed on smaller fish, predating invertebrate grazers of macroalgae (Eriksson *et al.*, 2009; Hughes, 1994; Sieben *et al.*, 2011; Valiela *et al.*, 1997). An increase of coastal temperatures may also have (and probably will further) lead to macroalgal dominance at the Irish coasts (Cannaby and Hüsrevoğlu, 2009; Fan *et al.*, 2014; Floreto *et al.*, 1993; Lee and Kang, 2020). Those altered contexts may promote the susceptibility to macrophyte invasions in Ireland (Bermejo *et al.*, 2020).

INVASIVE SEAWEEDS

Introductions of non-indigenous species have been increasing significantly since the second half of the 20th century, correlating with the advances of maritime trade (reviewed by Ojaveer *et al.*, 2018). Marine invasions affect local floral and faunal communities to a great extent

(Molnar *et al.*, 2008). However, not all introduced species are able to establish themselves in new environments and even if they are, they are still not automatically harmful. In contrast, invasive species are mostly considered introduced species that have a negative impact on the ecosystem or the economy; still, this classification is far from finding a consensus (reviewed by Chapman *et al.*, 2006).

Several green (*Caulerpa taxifolia, Caulerpa racemosa, Codium fragile*), brown (*Fucus evanescens, Undaria pinnatifida, Sargassum muticum)* and red (*Agarophyton vermiculophyllum* and other Gracilariales; discussed detailed below) algae are considered highly invasive species and are expanding their range rapidly (reviewed by Chapman *et al.*, 2006). Many seaweeds are particularly well adapted to invade estuaries, as they are generally able to propagate vegetatively and can form new individuals from detached fragments. This fragmentation occurs rather often in hydrologically active coastal zones and facilitates the fast range expansion of those seaweeds, depending on drift capacity (Kolar and Lodge, 2001; Krueger-Hadfield *et al.*, 2017b).

Invasive macrophytes are capable of reshaping the composition and abundances of the native epifaunal community, as they are changing the structural architecture of habitat and food sources, which are often epiphytes, or decomposers growing on the algae themselves (Drouin *et al.*, 2011; Lutz *et al.*, 2019; Lyons *et al.*, 2014). Grazing invertebrates are rather generalist and they hardly depend on a specific alga to feed on (Saarinen *et al.*, 2018; Taylor and Brown, 2006). However, grazers' preference of native seagrasses may give non-native algae advantages and make them able to outcompete the local species (Berke *et al.*, 2020).

1.3 SEAWEEDS OF IRISH ESTUARIES

Ireland is characterised by high precipitation throughout the year. In Clonakilty, County Cork in the South-West (Figure 1.2), average precipitation was ~1150 mm per square meter per year for the last five years, whereas in the east of the island precipitation is only ~650 mm per square meter per year (MET Éireann, 2020). The tidal range of up to six meters is creating massive hydrological activity (Marine Institute, n.d.) and the high rainfall forges rivers meandering their way to the ocean, forming gigantic estuaries (e.g. Shannon river in the West and Tolka river in the East). Those estuaries are of high aesthetic and economical value, and anthropogenic effects on those systems are of upmost interest (Norton *et al.*, 2018).
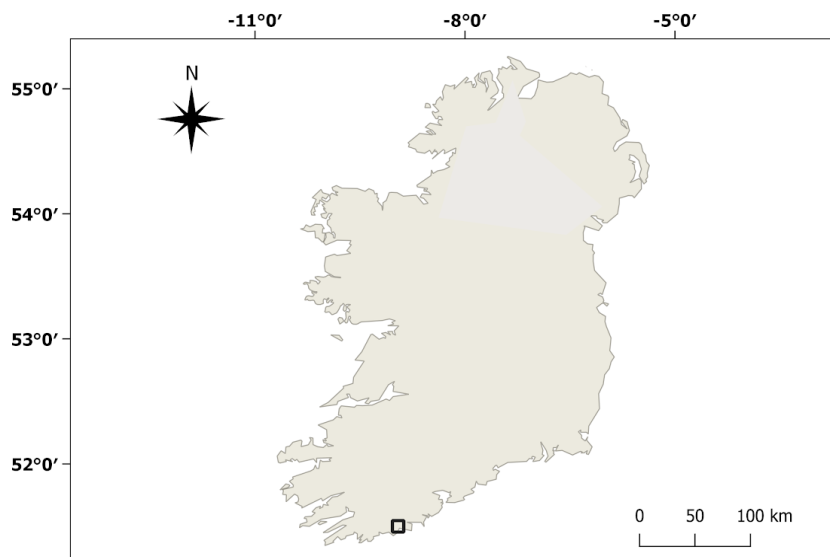
Figure 1.2: Map of Ireland with the labelled position of Clonakilty, County Cork

The industrial dairy agriculture and the high population densities at the coast are enriching those estuarine systems with nutrients, which is facilitating macroalgal blooms. According to Bermejo *et al.* (2019), the Tolka (Co. Dublin), the Argideen and the Clonakilty (both Co. Cork) estuaries were all equally unable to reach the "Good Ecological Status" specified by the EU Water Framework Directive (WFD; 2000/60/EC) due to massive seaweed tide occurrences in these estuaries. However, the nutrient contents in Irish coastal waters were only measured since the end of the millennium. After regulatory action was taken to reduce nutrient runoff, the phosphorus and ammonia levels in estuaries decreased for the last two decades, however, the total nitrogen remained on a high level (O'Boyle *et al.*, 2016). Seeing this decreasing pattern

is somewhat misleading, as nutrient levels may have peaked by the end of the 1990s where no nutrient data is available.

In Ireland, the biomass of *A. vermiculophyllum* was found to be >2 kg per square metre during the peak in the Clonakilty estuary, according to Bermejo *et al.* (Bermejo *et al.*, 2020), whereas accumulations of *Ulva* spp. led to an average of ~1.7 kg per square metre and a total of 2164 metric tonnes in the Argideen estuary (Wan *et al.*, 2017). The cost of landfill disposal is estimated at €260 per tonne and €16 per tonne for disposal on arable land (Sea Lettuce Task Force, 2010) in Ireland.

SPECIES OF IRISH SEAWEED TIDES

Using molecular investigation tools, Bermejo *et al.* (2019) identified four species of *Ulva* and two species of *Agarophyton* (formerly *Gracilaria*) in the Clonakilty estuary (see Table 1.1).

Table 1.1: Classification of different algae species in the Clonakilty estuary by genus and morphotype (Bermejo *et al.*, 2019).

Phylum	*Chlorophyta*		*Rhodophyta*
Genus	*Ulva*		*Agarophyton*
morphotype	laminar	tubular	tubular
Species	*U. rigida*	*U. compressa*	*A. vermiculophyllum*
	*U. gigantea**	*U. prolifera*	*A. gracilis**

*A. gracilis was only identified once and *U. gigantea* only twice, both play only a minor role in bloom forming in the Clonakilty estuary (Bermejo *et al.*, 2019).

Ulva Linnaeus (formerly *Enteromorpha*) is a genus of an opportunistic and bloom-forming cosmopolitan green seaweed (Ulvophyceae, Chlorophyta), currently holding 408 species (Guiry and Guiry, 2020) with a few native to Great Britain and Ireland. It occurs worldwide in fresh, brackish, and saline habitats. *Ulva* species are isomorphic, meaning that morphologies are nearly identical in their haploid and diploid phase. They are alternating between haploid

(gametophytes) and diploid (sporophyte) live stages when reproducing sexually, and can propagate by fragmentation (Bunker *et al.*, 2017, p. 228 f.; Føyn, 1958; Wichard *et al.*, 2015).
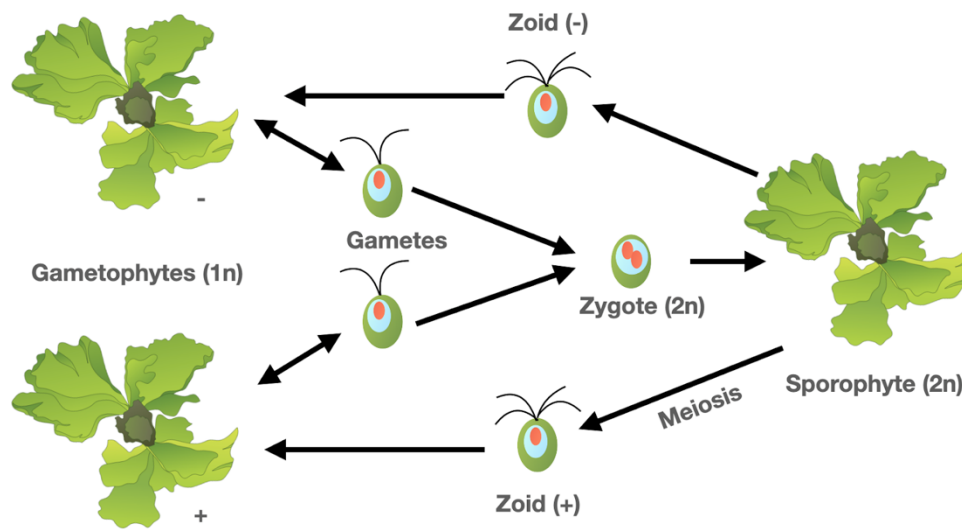
Figure 1.3 Isomorphic (haplodiplontic) life stages of Ulva spp. (IAN, 2020; adapted from Wichard, 2015, Fig. 1)

The primordial structure of those seaweeds and the variability of their morphology due to the environment (e.g. Ulva compressa can have a laminar appearance; Loughnane *et al.*, 2008), restricts classification with certain confidence and may only be achieved with molecular identification tools (Malta *et al.*, 1999).
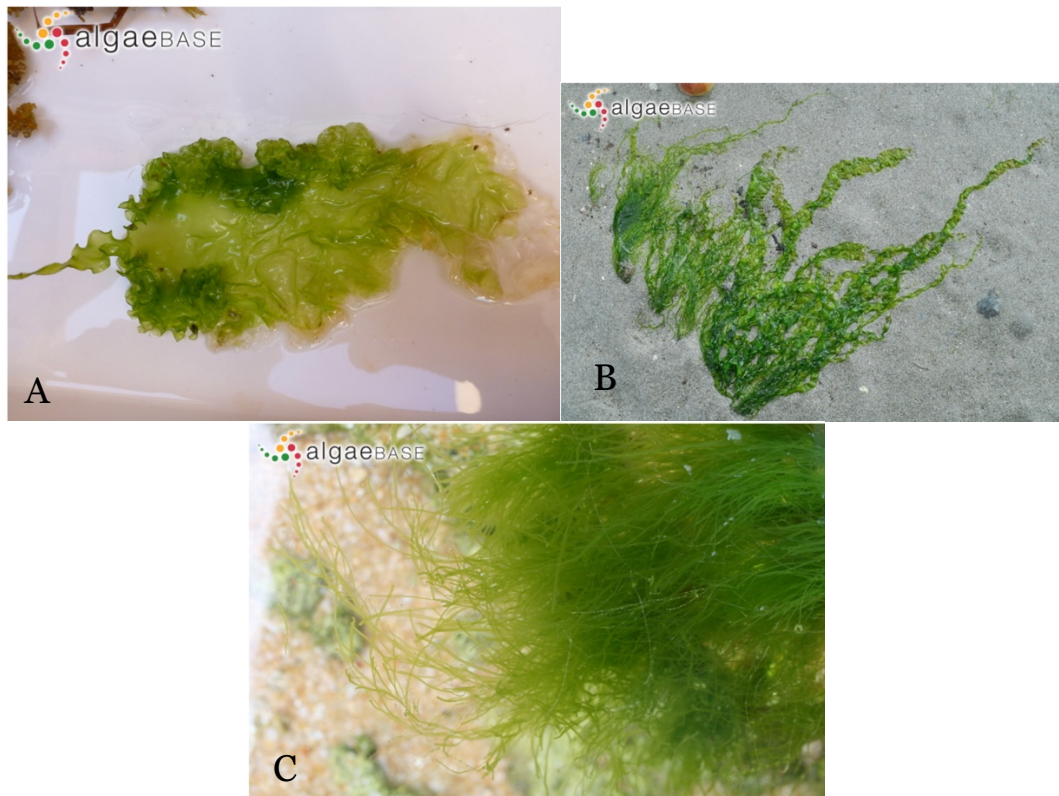
Figure 1.4: Thalli of (A) *Ulva rigida* (Guiry and Guiry, 2020, Image Ref. 25126); (B) *Ulva compressa* rigida (Guiry and Guiry, 2020, Image Ref. 11698); (C) *Ulva prolifera* (Guiry and Guiry, 2020, Image Ref. 11477)

The following three *Ulva* species are considered the major bloom formers in nutrient enriched (e.g. Clonakilty estuary, Cork) estuaries (Bermejo *et al.*, 2019). ***Ulva rigida,*** the "rigid sea lettuce" (Figure 1.4, A), does usually have a foliose thallus and is normally free-floating in the tidal areas and its thalli can be up to 30 cm long. Due to its appearance and maybe also because of its edibility, it carries the common name "sea lettuce", because the appearance of the thalli shows similarity to salad (Bunker *et al.*, 2017, p. 230; Guiry and Guiry, 2020). ***Ulva compressa***, the tape weed, (figure 1.4, B) forms branches up to 60 cm long (Bunker *et al.*, 2017, p. 230). ***Ulva prolifera,*** proliferous gut weed (figure 1.4, C), has small and highly branched tubes. It can get up to 50 cm long (Bunker *et al.*, 2017, p. 230). It can be considered one of the most hazardous bloom forming algae, causing extensive blooms in the Yellow Sea, China (Zhang *et al.*, 2019).

AGAROPHYTON SPECIES

***Agarophyton vermiculophyllum* (Ohmi)**, formerly known as *Gracilaria vermiculophylla* (Papenfuss) is a red alga originating from the North West Pacific, especially Japan and the Korean peninsula (reviewed by Krueger-Hadfield *et al.*, 2017a). The thallus (see figure 1.5) has a red-brownish colour and its shoots are 4-30 cm long with alternating branches with short (1 - 5 mm) ramuli, its diameter is from 1 to 3 mm. (Ohmi, 1956). This rhodophyte can reproduce sexually and asexually through fragmentation, and the population can both contain isomorphic diploid and haploid individuals (see *Ulva*). However, regions which were invaded tend to have higher numbers of diploid individuals than regions where this algae is native(Krueger-Hadfield *et al.*, 2016). This diploid bias is suggested to result from a shift to asexual reproduction when the species is colonising new

Figure 1.5: Thallus of *Agarophyton vermiculophyllum* (Guiry and Guiry, 2020, Image Ref. 14860)

habitats (Krueger-Hadfield *et al.*, 2016). Berke *et al.* (2020) found that this alga is less likely to be chosen by grazers, as it is less palatable for native invertebrates, furthermore Nylund *et al.* (2011) found that *A. vermiculophyllum* has sophisticated chemical defence mechanisms induced by tissue damage.

A. vermiculophyllum is considered a highly invasive species and has been recorded in the Eastern Pacific, Western and Eastern Atlantic Oceans in the northern hemisphere as well as the Mediterranean Sea and has been spreading for over a century (Kim *et al.*, 2010; Krueger-Hadfield *et al.*, 2018). Utilising Microsatellite analysis, Krueger-Hadfield *et al.* (2017a) suggested that this global surge was probably facilitated by oyster export by ship from Japan in the 20th century. *A. vermiculophyllum* was first reported in the British Isles in 2014 by Krueger-Hadfield *et al.* (2017b). Due to its limited occurrence in soft-sediment habitats, the introduced rhodophyte was not documented in the algal surveys conducted at the rocky shores of Great Britain and Ireland at that time. Soft-sediment habitats exhibit a relatively low diversity of macroalgae as a consequence of a restricted amount of hard substratum areas

needed for algal spore recruitment. For this reason, these estuarine zones, where *A. vermiculophyllum* is now thriving, were not studied as intensively as rocky shores.

Assessing positive or negative effects on benthic and epifaunal communities, resulting from the introduction of introduced macroalgae like *A. vermiculophyllum*, is of utmost importance in order to decide if invasive management needs to be applied or if monitoring is sufficient. The problem of invasive macroalgae is strongly connected to other issues in coastal zones, such as overfishing, and eutrophication (Anderson, 2007; Williams and Smith, 2007). Therefore, symptomatic management actions (eradication) cannot replace an overarching management strategy (Williams and Grosholz, 2008).

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CHAPTER 2:

COMPARISON OF THE EPIFAUNAL ASSEMBLAGE OF THE INVASIVE MACROALGAE

AGAROPHYTON VERMICULOPHYLLUM (FORMERLY *GRACILARIA VERMICULOPHYLLA*)

AND NATIVE *ULVA* SPP. IN A NORTH-EAST-ATLANTIC ESTUARY.

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2.1 ABSTRACT

The rapid spread of introduced seaweeds is of essential concern, as they can have a deleterious impact on coastal native seaweed and seagrass communities. However, non-indigenous species can generate mixed responses when introduced to native assemblages, and increase habitat complexity, depending on the spatial and ecological context. The identification of positive or negative effects of a non-indigenous species in estuarine ecosystems and its controls has notable implications on management strategies. By taking advantage of the co-occurrence of the native *Ulva* seaweeds and the non-native *Agarophyton vermiculophyllum* in the Clonakilty estuary (Cork, Ireland) we aim to assess the contribution to habitat complexity, by evaluating the biodiversity and species richness of the native and invasive macroalgal species. At four locations over four sampling occasions, a total of 253 algal samples were collected, including inhabiting epifaunal species. The *Ulva* dominated locations mainly contained macroalgae with tubular morphotypes (i.e. *Ulva prolifera* and *Ulva compressa*) and some sporadic patches of

laminar *Ulva rigida*. The average algal biomass per area of the two canopy formers was similar, however the biomass of *A. vermiculophyllum* was highly variable throughout the seasons. Epifaunal biomass was highly dependent on underlying algal biomass, moreover, *Ulva* spp. canopies supported up to four times more epifaunal biomass per algal biomass than *A. vermiculophyllum*. The epifaunal community of both macrophytes differed majorly, whereas deposit-feeding organisms had a higher abundance in *Ulva* spp. samples and the carnivorous crab, *Carcinus maenas,* was much more abundant in *A. vermiculophyllum* samples. The invasive species had either no or a negative effect on biodiversity.

2.2 INTRODUCTION

Introductions of foreign species have been taking place for several centuries, either intentionally for commercial gain or unintentionally, mostly by seafaring as hidden passengers in ballast water or attached to the ship's shell (reviewed by Ojaveer *et al.*, 2018). The rapid spread of introduced seaweeds is of essential concern, as they can have a deleterious impact on coastal native seaweed and seagrass communities and are together with climate change one of the most significant stressors of today's ecosystems (Molnar *et al.*, 2008; Stachowicz *et al.*, 2002). Those impacts include the modification of faunal community structure, reduction of biodiversity, and alteration of estuarine nutrient dynamics, which may ultimately accelerate the shift from slow-growing macrophytes to ephemeral macroalgae, increasing the risk of macroalgal blooms (Bittick *et al.*, 2018; Chapman *et al.*, 2006; Green-Gavrielidis *et al.*, 2018; Krueger-Hadfield *et al.*, 2018; Schaffelke and Hewitt, 2007; Williams and Smith, 2007). However, non-indigenous species can generate mixed responses when introduced to native assemblages, and are even able to increase habitat complexity, depending on spatial and ecological context (Buschbaum *et al.*, 2006; Jones and Thornber, 2010; Keller *et al.*, 2019; Lyons *et al.*, 2014; Sotka and Byers, 2019).

Marine macroalgae play a significant role in facilitating ecosystem functions such as nutrient cycling, primary production, and habitat formation in eutrophic zones of estuarine systems (Jorgensen *et al.*, 2010). They are considered ecosystem engineers, as they are adding structural complexity to the substratum, affecting epiphytic and epifaunal communities (Chemello and

Milazzo, 2002). However, the functions provided by those macrophytes are density-dependent (Green and Fong, 2016) and, after a certain threshold of algal biomass is exceeded, the subsequent decomposition of the algal biomass can cause hypoxia events, releasing hydrogen sulfide and limiting estuarine services and the goods that they provide (Lyons *et al.*, 2014). A macroalgal bloom can cause enormous direct economic cost for management effort, as historical examples. For instance, the green seaweed bloom in Qingdao, China, in 2008 (remediation costs of €200 million) and in Brittany 1992 (remediation costs of €1.8 million) show (Charlier *et al.*, 2008). Furthermore, macroalgal blooms are indirectly impacting human health, fisheries, tourism, and leisure activities (Sanseverino *et al.*, 2016).

Abiotic factors, such as temperature, salinity, hydrodynamics, light, and, foremost, nutrient availability, drive macroalgal growth (Valiela *et al.*, 1997). Anthropogenic stressors such as elevated nutrient levels may enhance the magnitude of such events and increase their frequency (Jones and Pinn, 2006). Due to the advances in synthetic fertiliser production to facilitate the industrial agriculture of the twentieth century, estuaries around the world shifted from seagrass meadows to eutrophied states, where opportunistic bloom-forming algae now occupy a primary role in habitat formation (Bittick *et al.*, 2018; Duarte *et al.*, 2009; Little *et al.*, 2017; Pedersen and Borum, 1996; Santos *et al.*, 2020; Valiela *et al.*, 1997). The apparent eutrophication of coastal systems might foster macrophyte invasions (Chapman *et al.*, 2006; Kolar and Lodge, 2001), and their resistance to grazing (Nejrup *et al.*, 2012; Nejrup and Pedersen, 2010) increases the likelihood of macroalgal blooms even more.

Non-indigenous macrophytes were found to be capable of altering the composition of the native epifaunal community, since many epifaunal invertebrates feed on epiphytes and decomposers growing on the predominant macrophyte, which also comprise different architectural and structural characteristics (Drouin *et al.*, 2011; Lutz *et al.*, 2019; Lyons *et al.*, 2014). Nonetheless, the dimension of those effects is determined by the invader's ecology, the native community itself and geological as well as hydrological properties (Chapman, 1998). Epifaunal species are mainly considered to be generalists and are often able to adapt to new habitat formers using them as a host or food (Saarinen *et al.*, 2018; Taylor and Brown, 2006), although grazers often prefer the native over the alien macroalgae (Berke *et al.*, 2020; Nejrup *et al.*, 2012; Tomas *et al.*, 2011; Williams and Smith, 2007). The invertebrates living on algae form an essential link from the primary producers to higher trophic levels as birds (Macneil *et al.*, 1999) and fish (Eriksson *et al.*, 2009), also affecting fish stocks (Rönnbäck *et al.*, 2007). Moreover, the epifauna plays an essential role in facilitating the decomposition of detritus, by

breaking it up into smaller pieces and stimulating decay (reviewed by Wilson and Fleeger, 2012), releasing nutrients back into the estuary. Finally, bioturbation oxygenates the sediment and mobilises nutrients. Evaluating epifaunal assemblages has been used to examine the effects of invasive macroalgae and assessing the biotic resistance against algal invasions and alternations of ecosystem functioning (Veiga *et al.*, 2016).

The rhodophyte *Agarophyton vermiculophyllum* (formerly *Gracilaria vermiculophylla*) is invading estuaries in the northern hemisphere (Hu and Juan, 2014; Krueger-Hadfield *et al.*, 2018) and blooms have been recorded in Ireland since 2014 (Bermejo *et al.*, 2020; Krueger-Hadfield *et al.*, 2017). Classical remediation and eradication of invasive algae does come with immense costs and is challenging to manage (Anderson, 2007; Jorgensen *et al.*, 2010). This invasive alga is comparably resistant to various other environmental stressors, for instance, reduced light, shifting salinities, elevated temperatures, desiccation (Abreu *et al.*, 2011; Nejrup and Pedersen, 2010; Pedersen and Johnsen, 2017), and thriving in areas where native seagrasses (Cacabelos *et al.*, 2012) and macroalgae have thrived formerly (Bermejo *et al.*, 2020).

In recent years, several studies assessed density-dependent positive effects of invasive *A. vermiculophyllum* on several ecosystem services, including nursery habitat production, sediment stabilisation, wave attenuation, nutrient cycling, and biodiversity (Lyons *et al.*, 2014; Sfriso *et al.*, 2020; Thomsen, 2010). Furthermore, invasions by *A. vermiculophyllum* may compensate for the vanishing of native habitat formers, for instance by positively impacting ecosystem complexity such as increasing nursery taxa abundance and species richness (Ramus *et al.*, 2017; Thomsen *et al.*, 2019). Incorporating *A. vermiculophyllum* into managing strategies was controversially discussed as an alternative approach (Sotka and Byers, 2019), as it may facilitate similar ecosystem functions also provided by *Ulva* sp. (Ramus *et al.*, 2017; Rodriguez, 2006).

Two native laminar formed (*Ulva rigida* and *Ulva gigantea*), two native tubular formed (*Ulva prolifera* and *Ulva compressa*) species of the genus *Ulva,* and the non-indigenous rhodophyte *A. vermiculophyllum* were identified in the Clonakilty estuary (County Cork, Ireland), forming distinct canopies located next to each other (Bermejo *et al.*, 2019a; Wan *et al.*, 2017). In general, *Ulva* spp., and especially foliose forms, are more prone to grazing by benthic invertebrates than *Agarophyton vermicullophyllum* (Jorgensen *et al.*, 2010). Free-floating laminar forms are more susceptible to tidal currents or wind, while tubular forms anchor

themselves in the sediment, therefore reaching higher stability and usually more biomass in transitional waterbodies (Bermejo *et al.*, 2019a). Compared to tubular *Ulva* species, *Agarophyton vermiculophyllum* has an even more rigid structure and thick thalli, and sophisticated chemical defence mechanisms against grazing (Berke *et al.*, 2020; Nylund *et al.*, 2011).

The identification of positive or negative effects of a non-indigenous species on estuarine ecosystems and how it is controlled would have notable implications on management strategies of invasive foundation species. The various ecological impacts on epifaunal diversity and nutrient utilisation need to be assessed, especially in the context of local anthropogenic nutrient over-enrichment and global change to recognise and recommend an appropriate management strategy (active or passive). By taking advantage of the co-occurrence of native and non-native seaweeds in this estuary, we aimed to (i) compare spatial and temporal patterns in epifaunal community structure in both algae; (ii) characterise the role in habitat formation of both species and their implications on different faunal taxa; (iii) explore ecological implications for different feeding guilds and discuss the impact on trophic cascades; and (iv) evaluating the epifaunal biodiversity and species richness of the macroalgal species.

2.3 MATERIALS AND METHODS

SAMPLING SITE AND SAMPLE COLLECTION

The Clonakilty estuary (Co. Cork), located in the South-West of Ireland (51°36'45"N 8°52'13"W) at the Atlantic coast is affected by green (native *Ulva* spp.) and red seaweed blooms (non-native species *Agarophyton vermiculophyllum*; Bermejo *et al.*, 2020). The estuary experiences elevated nutrient influxes, mainly derived from agricultural runoff, as the consequence of intense dairy farming in the surrounding area, and a close-by wastewater treatment plant (Bermejo *et al.*, 2019b). Its shallow appearance and low water renewal rate in combination with high nutrient inflow cause the estuary to be susceptible to nutrient over-enrichment (Bermejo *et al.*, 2019b), favouring the development of macroalgal blooms. By taking advantage of the co-occurrence of native and non-native bloom-forming species in this estuary, the epifaunal assemblages in relation to the foundational species were compared. On four sampling occasions during 2016 and 2017 (i.e. August 2016, October 2016, February 2017 and June 2017), four locations within the Clonakilty estuary covered by large patches of *A. vermiculophyllum* (A [51°37'08"N 8°52'44"W] and B [51°36'42"N 8°51'01"W]) and *Ulva* spp. blooms (C [51°36'37"N 8°52'28"W] and D [51°36'20"N 8°52'24"W]) were sampled at low tide

(see Figure 1). At each location, fifteen to twenty 25 x 25 cm quadrants were collected per location per sampling occasion, which led to a total of 253 samples. Invertebrates and macroalgae present in each quadrant was collected and transported separately in labelled plastic bags (Table 2.1).

Table 2.1: Description of the macroalgal species of the collected in the Clonakilty Estuary, County Cork, Ireland.

Species	Phylum	No. of samples				Sample weight	Description
		Aug 16	Oct 16	Feb 17	Jun 17	kg cleaned algae	
Agarophyton vermiculophyllum	Rhodophyta	34	35	29	36	7.644	Dark red elastic 1 to 4 mm thick branches growing up to 2 m in length
Ulva spp. (mostly tubular morphology)	Chlorophyta	38	29	20	32	2.594 (laminar) 4.162 (tubular) 6.756 (total)	**tubular:** proliferous; forming small branches up to 50 cm long (most likely *Ulva prolifera*) or forming flattened branched tubes (most likely *Ulva compressa*); **laminar:** firm foliose thalli with blades up to 20 cm (most likely *Ulva rigida*)
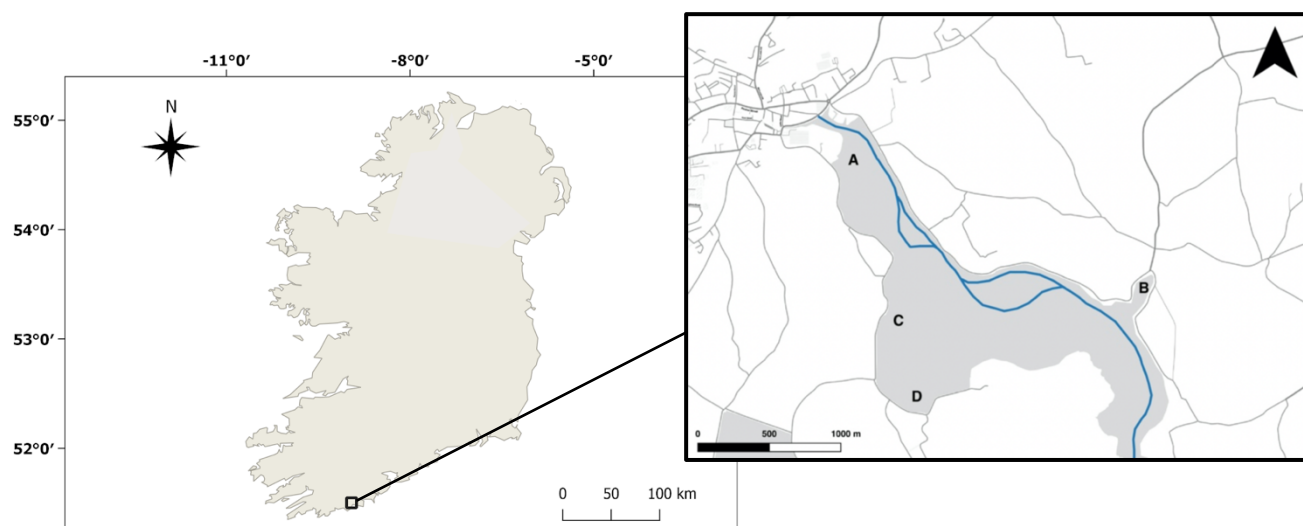
Figure 2.1 Sampling locations of sampling in the Clonakilty estuary of areas of *A. vermiculophyllum* blooms (A and B) and *Ulva* spp. (C and D).

SAMPLE PROCESSING

All seaweeds were rinsed with freshwater to remove adherent sediments, particles and organisms. Once washed, seaweed specimens were separated in different species, or tubular

and laminar morphologies in the case of *Ulva* spp., respectively. Excess water was removed using a hand centrifuge, and the fresh weight (g) was obtained for each taxon using a balance (PBW-3200 Lab Balance, IntelWeigh). The water used for rinsing seaweeds was passed through a 1 mm sieve, and the retained fauna was separated from sediments, pebbles, seaweed fragments, shells and other materials. Benthic fauna biomass for each sample was individually preserved in 4% Formalin until taxonomical identification. Three sub-samples of seaweed biomass per sampling occasion and location were rinsed with distilled water, freeze-dried and stored in silica gel until further elemental analyses. To examine the tissue nitrogen content, the thalli of the freeze-dried at -52°C seaweeds were homogenised to powder with a tissue lyser (TissueLyser II, QIAGEN) and tungsten balls. The nitrogen content was measured with an elemental analyser (Vario ISOTOPE Cube Elementar Analysensysteme GmbH, Hanau).

IDENTIFICATION AND COUNTING OF BENTHIC FAUNA

Before sorting and processing, samples were thoroughly rinsed with water to remove the formalin. Specimens were sorted until the lowest taxonomic level possible. Identification and sorting were carried out under a dissecting microscope following the World Register of Marine Species (2020), and Hayward and Ryland (2017). Once specimens were taxonomically sorted, they were weighed and counted. The overall number of specimens per taxon was estimated by taking pictures of them in a water-filled plastic tray using a scanner (Canon 8800F Flatbed™). ImageJ software (version IJ 1.46r) was used for both the pre-treatment of the collected images, before counting the individuals, and the subsequent count per species for every sample. Afterwards, total species fresh weight (in g) was obtained by weighing all individuals per species, and the samples were stored separately (by species) in 96% Ethanol for preservation.

DATA ANALYSIS

Prior to the statistical analyses, the algal and faunal biomass of the 25 cm x 25 cm quadrants was multiplied by 16 to transform into g_{taxon} per m^2. Subsequently, the dry weight of the seaweeds was calculated using a factor of 0.20 and 0.17 for *Ulva* and *Agarophyton*, respectively. This factor was derived from the freeze-dried samples mentioned above. As the size of the different faunal taxa varied substantially, community data was based on their biomass per m^2, and not the abundance per m^2, to obtain a less biased estimate. Hence, the faunal biomass was also divided by the algal biomass, which resulted in the measure g_{taxon} / g_{algae} (after Anderson *et al.*, 2005), as the algal biomass determines the number of grazers

inhabiting the area, this transformation makes the patches inter-comparable (Anderson *et al.*, 2005).

Statistical analyses were performed using the software R, version 4.0.2 (R Core Team, 2020), and PERMANOVA+add-on PRIMER 6 (Clarke *et al.*, 2014) for multivariate analysis. The R package "vegan" (Oksanen *et al.*, 2019) was used to calculate the Shannon-Wiener diversity index (H') based on $\log_e$ to estimate the diversity of the faunal assemblage. Linear mixed effect models were created using the R-Package "lmerTest" (Kuznetsova *et al.*, 2017) using the location as a random factor, nested in algae. Subsequently, linear models for each alga were created to assess effect sizes within the factor algae. Analysis of variance (ANOVA) and analysis of covariance (ANCOVA) were performed with the R-Package "car" (Fox and Weisberg, 2019) to test for differences in means between algae and/or season, using algae biomass as covariate. Normality assumptions of the statistical methods were graphically assessed with a QQ-Norm-Plot (Quantile-Quantile-Plot), and homogeneity variances were tested with the Levene's test (Field *et al.*, 2012). To comply with analysis assumptions, the response variable was, if necessary, square-root-transformed. Eta^2 (η^2) was used as effect size in for ANOVA models to quantify the percentage of the explained variance to the total variance. (Levine, 2002). Partial eta^2 was used as effect size in linear-mixed-effect models. Pseudo-R^2 was used as a measure of total explained variation, whereas the marginal Pseudo-R^2 represents the explained variance of the fixed effects and the conditional Pseudo-R^2 represents the explained variance of the fixed and random effects (Lüdecke, 2020a). Graphs were created using the R package "ggpubr" (Kassambara, 2020) and "sjPlot" (Lüdecke, 2020b). Means were reported as mean ±standard deviation.

The mean biomass and mean nutrient content for each location and season were calculated, as only three measurements of the nitrogen were taken per season and location. Subsequently, the spearman correlation was calculated using the calculated means.

The epifaunal assemblages were analysed using multivariate statistical methods to compare the role of *Agarophyton* and *Ulva* as habitat-forming species (Anderson *et al.*, 2008; Bermejo *et al.*, 2016, 2015). First, the biomass of each faunal taxon per g of seaweed was fourth-root-transformed, and the Bray-Curtis-distance of all samples was calculated. Using this resemblance, a Principal Coordinate Analysis (PCoA) was conducted to display and assess the distances graphically (Anderson *et al.*, 2008). Afterwards, a three-way permutational analysis of variance (PERMANOVA) considering sampling occasion (fixed factor, four levels), seaweed (fixed factor, two levels) and location (random factor nested within species, two

levels) was carried out using Type-III sum of squares, to account for the unbalanced design (Anderson *et al.*, 2008). PERMANOVA tests for differences of centroids, but not their dispersion, therefore, a distance-based test for homogeneity of multivariate dispersion (PERMDISP) was conducted (Anderson *et al.*, 2008). Additionally, pairwise testing of the differences of the locations within "algae" and sampling occasions was conducted using PERMANOVA and PERMDISP (see supplementary tables). Contribution to the differentiation of each faunal taxon was calculated using SIMPER (Similarity Percentage) analysis. The number of permutations was set to a minimum of 9999. The exact number of permutations is annotated beneath the results tables.

For each sample, the fresh weight of each faunal taxon was divided by the number of individuals, to obtain an estimation mean species weight. Subsequently, the estimation of the species weight was compared between algae with the non-parametric Wilcox-Test for unpaired samples, as homogeneity of variance assumptions were not met. This analysis was performed for all taxa which were within the first 9 deciles of % contribution (SIMPER analysis) and occurred several times in both algal canopies (i.e. *Hydrobia ulvae, Littorina littorea, Littorina sp., Rissoa parva, Carcinus maenas, Mytilus edulis,* and *Cerastoderma edule*).

2.4 RESULTS

SEAWEED BIOMASS

On average, we observed 913 g (±934 g, standard deviation) of *A. vermiculophyllum* and 908 g (±760 g, standard deviation) of *Ulva* spp. per m^2. Even though a significant main effect of the algal species was found (p=0.004, Table 2.2), the effect size indicates that this factor is neglectable (partial η^2 = 0.06). The biomass of *A. vermiculophyllum* differed substantially between both locations (mean ±SD in location A = 1177 g ±1133 g; location B = 649 g ±578 g; p = 0.000, η^2 = 0.06). In contrast, both locations of *Ulva* spp. seemed to be quite uniformous (mean ±SD in location C = 1013 g ±867 g; location D = 805 g ±628 g; p=0.16). When comparing both algal species, a distinct seasonal pattern was observed in *A. vermiculophyllum* (p=0.000, η^2= 0.40; Table 2.2)**,** but not in *Ulva* spp. (p>0.05; see Table 2.2; see Figure 2.2).
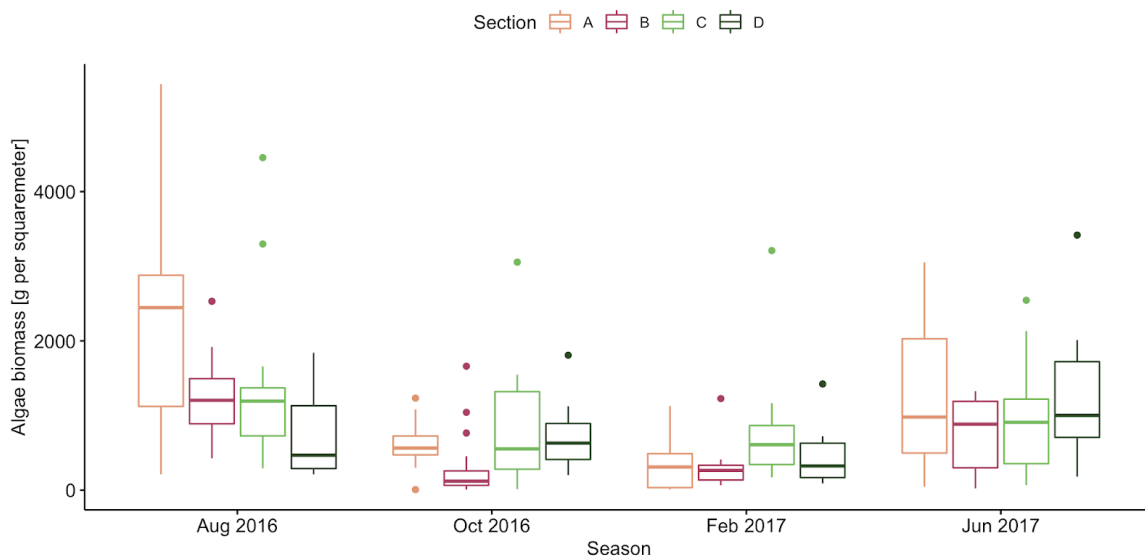
Figure 2.2: Algal biomass in g per m^2 by season and location. A and B represent locations with *A. vermiculophyllum,* and C and D represent locations with *Ulva spp.* as the main habitat former. Outliers (more than 1.5 x the interquartile range distance from the first or third quartile) are represented as dots. Whiskers represent the outer quartiles and box represents the inner quartiles. The median is represented by the horizontal line.

Table 2.2: Two-Way-ANOVA of the square-root the algal biomass by season and location.*

Source of variation	DF	Chi²	p	p. η^2	ICC
Combined model (linear mixed effects model using locations as random effects)					
(Intercept)	1	253.64	0.000		
Algae	1	8.19	0.004	0.05	
Season	3	93.11	0.000	0.23	
Algae x Season	3	24.97	0.000	0.09	
Random effect: Location (Algae)					0.04
Pseudo-R² (Fixed effects) = 0.28; Pseudo R² (Total) = 0.31					

Source of variation	SS	DF	F	p	p. η^2	η^2
A. vermiculophyllum (ordinary least squares regression)						
Season	11260	3	31.23	0.000	0.43	0.40
Location (A, B)	1638	1	13.63	0.000	0.10	0.06
Season x Location	516	3	1.43	0.237	0.03	0.02
Residuals	15142	126				
***Ulva* spp.** (ordinary least squares regression)						
Season	981	3	2.64	0.0525	0.07	0.06
Location (C, D)	241	1	1.95	0.1653	0.02	0.02
Season x Location	977	3	2.63	0.0532	0.07	0.06
Residuals	3706	111				

*DF: Degrees of freedom. p. η^2: partial eta². η^2: eta². Chi²: Type-3-Wald-Chi. ICC: intraclass correlation coefficient showing the variability of the random effect. The combined model includes the locations as a random effect (linear effects model). The OLS (ordinary least squares) regressions were used as a post-hoc procedure to estimate the local (Location) and temporal (Season) effect within each alga.

TISSUE NITROGEN CONTENT

The mean tissue nitrogen content of *A. vermiculophyllum* was 3.54 % ±0.91 with a minimum of 2.57 %, and 3.40 % ±1.16 for *Ulva* spp. with a minimum of 1.99 %. Biomass and tissue nitrogen were generally negatively correlated (p=0.031, r_s= -0.55, calculated by mapping the

mean nitrogen and mean biomass per location and season). Correlations were not significant for each alga, partly due to the small sample size of nitrogen measurements (n=16). The nitrogen content did not differ between algal species (Wilcox-test, p = 0.89), but was strongly connected to season (Kruskal-Wallis-Test, $Chi^2(3) = 12$, p-value = 0.007, $\eta^2_H = 0.75$).

FAUNAL BIOMASS

For *Ulva*, the mean rate of faunal biomass per algal biomass was 0.21 ±0.20 g_{fauna} / g_{algae}, whereas for *A. vermiculophyllum* it was about four times lower at 0.056 ±0.07 g_{fauna} / g_{algae} (p=0.000, Wilcox' r = 0.493; Table 2.3). *Ulva* spp. supports more faunal biomass than *A. vermiculophyllum* (ANCOVA, $Chi^2(1) = 4.8$, p = 0.028, partial $\eta^2 = 0.56$, Table 2.4; Figure 2.3). Generally, the faunal biomass was dependent on the algal biomass (ANCOVA, $Chi^2(1) = 44.49$, p = 0.000, partial $\eta^2 = 0.15$, Table 2.4) and this dependence showed to be stronger in *A. vermiculophyllum* ($\eta^2 = 0.31$, Table 2.4) compared to *Ulva* locations ($\eta^2 = 0.20$, Table 2.4).

Table 2.3: Mean ± standard deviation (SD) and median of the ratio of faunal biomass to algal biomass [g / g]

	Location				Habitat forming species	
	A	**B**	**C**	**D**	***A. vermiculophyllum***	***Ulva* spp.**
Mean (±SD)	0.094 (±0.067)	0.019 (±0.038)	0.260 (±0.199)	0.163 (±0.186)	0.056 (±0.066)	0.211 (±0.198)
Median	0.085	0.005	0.236	0.118	0.032	0.150

Table 2.4: ANCOVA of faunal biomass by season and location or algae species with log of algal biomass as covariate.

Source of variation	DF	Chi²	p	p. η^2	ICC
Combined model (linear mixed effects model with location as random effect)					
log(Algae biomass per m²)	1	44.49	0.000	0.15	
Algae	1	4.84	0.028	0.56	
Season	3	4.16	0.245	0.02	
Algae x Season	3	6.81	0.078	0.03	
Random effect: Location (Algae)					0.11
Pseudo-R² (fixed effects) = 0.32; Pseudo R² (total) = 0.40					

Source of variation	SS	DF	F	p	p. η^2	η^2
A. vermiculophyllum						
log (Algae biomass per m²)	88665	1	24.44	0.000	0.41	0.31
Location	170592	1	46.97	0.000	0.26	0.16
Season	23747	3	2.18	0.094	0.05	0.02
Location x Season	70938	3	6.52	0.000	0.13	0.07
Residuals	446206	123				
Ulva spp.						
log(Algae biomass per m²)	248378	1	21.89	0.000	0.27	0.20
Location	154958	1	35.94	0.000	0.12	0.08
Season	97435	3	4.33	0.040	0.07	0.04
Location x Season	294676	3	8.66	0.000	0.19	0.13
Residuals	1225357	108				

SS: Type-2-Sum-of-Squares. DF: Degrees of freedom. p. η^2: partial eta^2. η^2: eta.
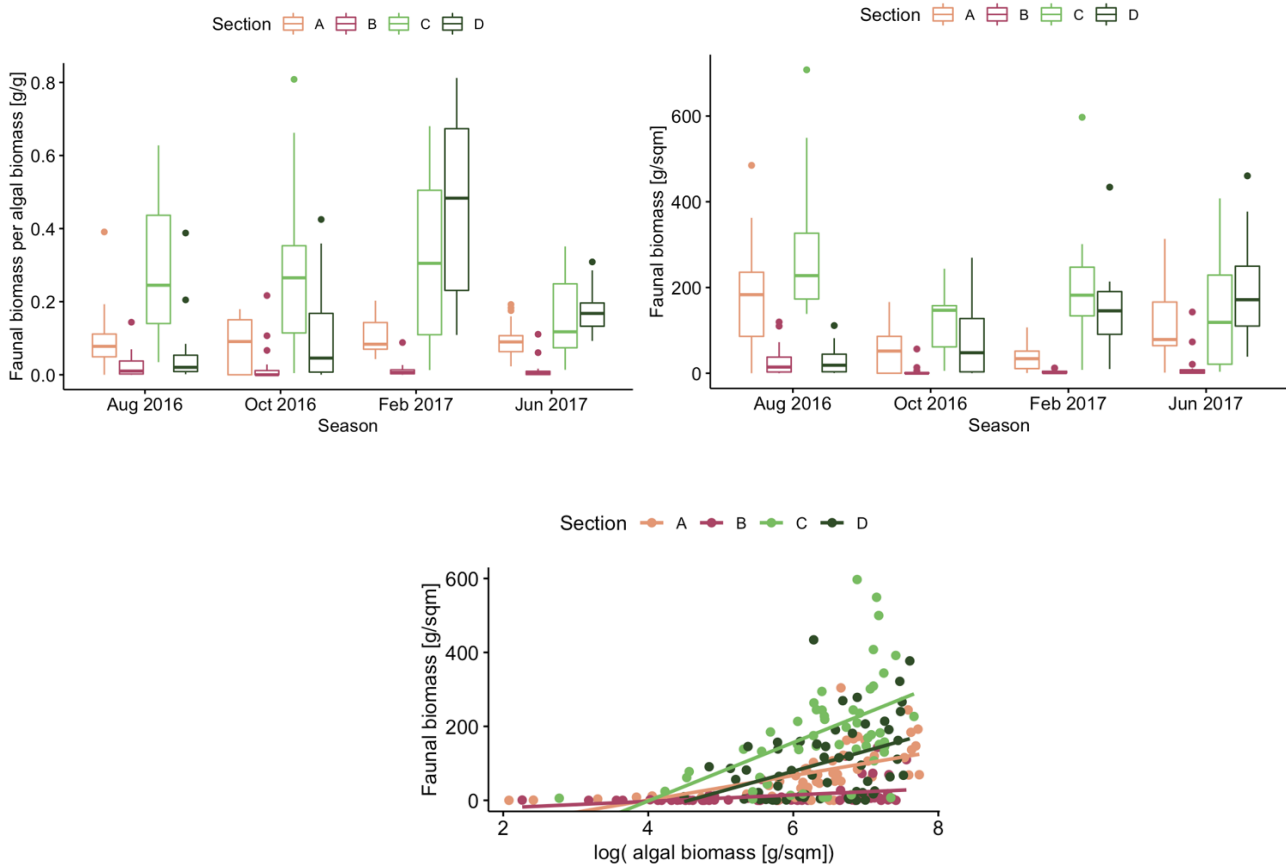
Figure 2.3: Faunal biomass per algal biomass (top, left); faunal biomass per area [g per m^2] (top, right) by season and location; Faunal biomass [g per m^2] per algal biomass [g per m^2] (bottom). A and B represent locations with *A. vermiculophyllum* canopy, and C and D represent locations with *Ulva* spp. canopy. Boxplots: Outliers (more than 1.5 x the interquartile range distance from the first or third quartile) are represented as dots. Whiskers represent the outer quartiles and box represents the inner quartiles. The median is represented by the horizontal line. Scatterplot: lines represent a linear regression line for measurements in each location, dots are measurement points.

TAXON RICHNESS AND DIVERSITY

For both algae, the number of taxa correlated positively with the algal biomass (Spearman correlation, r_s = 0.38, p = 0.000), yet *Ulva* spp. had a higher average richness (mean ±SD number of taxa: 4.10 ±1.83; p=0.000; Table 2.5; Figure 2.4) than *A. vermiculophyllum* (mean ±SD number of taxa: 2.58 ±1.26; Table 2.4; p=0.000). The number of taxa increased with algal biomass (standardised beta = 0.84, p= 0.000; Table 2.5) in both algal canopies, however, it is a logarithmic relation and therefore saturating at higher algal biomass concentrations (Figure

2.4). No seasonal effect was found to affect the taxon richness and therefore excluded (pairwise model comparison; Chi^2 (6) = 12.437; p = 0.05291).

Table 2.5: Generalised linear mixed effects model (GLMER; after Poisson) of taxon richness by algae biomass and algal species.*

	Estimate	SE	Std. Beta	z-value	P	ICC
(Intercept)	-0.053	0.237	–	-0.226	0.82	
log(Algae biomass per m²)	0.1578	0.034	0.84	4.60	0.000	
Ulva	0.4348	0.1255	0.43	3.464	0.000	
Random effect: Location (Algae)						0.01
Pseudo-R² (fixed effects) = 0.25; Pseudo R² (total) = 0.28						

*Model: number of taxa ~ log(algal biomass) + algae + (1 | location); The effect of *Agarophyton* is the outcome without the effect of *Ulva*; Seasonal effect was removed because it was not significant (p>0.05; pairwise model comparison).
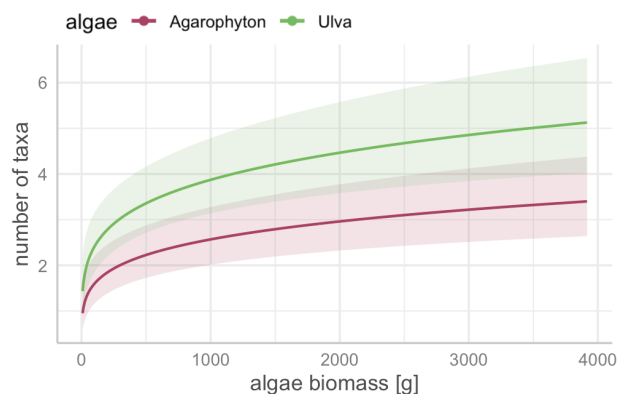
Figure 2.4: Logarithmic regression of taxon richness (count) per sample on algal biomass (g). Shading represents the standard error.

The Shannon-Diversity index H' was higher in *A. vermiculophyllum* canopies (mean ±SD, 0.418 ±0.352) compared to *Ulva* canopies (0.278 ±0.213; Figure 2.5 A). However, the first showed high local dependence and differed highly between locations (mean ±SD; location A: 018 ± 0.15; location B: 0.76 ± 0.26). Alternatively, the H' was calculated based on the faunal biomass, to get a less deviating result between locations (mean ±SD; location A 0.32 ± 0.27, location B 0.52 ± 0.28, location C 0.48 ± 0.32, D location D 0.53 ± 0.39; Figure 2.5 B). Considering the locations as a random factor, there was no main effect of algae, but of season and the interaction with algae (p=0.356, Table 2.6). Moreover, the diversity did not show to be

associated with the algal biomass (p=0.178; Table 2.6). The same results were retrieved when calculating the diversity on the base of biomass, although with a stronger interaction effect (p. $\eta^2 = 0.071$, p=0.001; Table 2.6).

Table 2.6: ANCOVA of linear mixed effects model (LMER) of Shannon-diversity-index based on abundance by algal species, season, and algae biomass as covariate.*

Source of variation	Chi²	DF	p	p. η^2	ICC
log(Algae biomass per m²)	1.81	1	0.178	0.008	
Algae	0.84	1	0.356	0.165	
Season	20.66	3	0.000	0.091	
Algae x Season	8.21	3	0.042	0.037	
Random effect: Location (Algae)					0.52
Pseudo-R² (fixed effects) = 0.16; Pseudo R² (total) = 0.60					

*DF: Degrees of freedom. p. η^2: partial eta^2. Chi^2: Type-2 Wald Chi^2. Location was defined as a random effect. ICC: Intraclass correlation
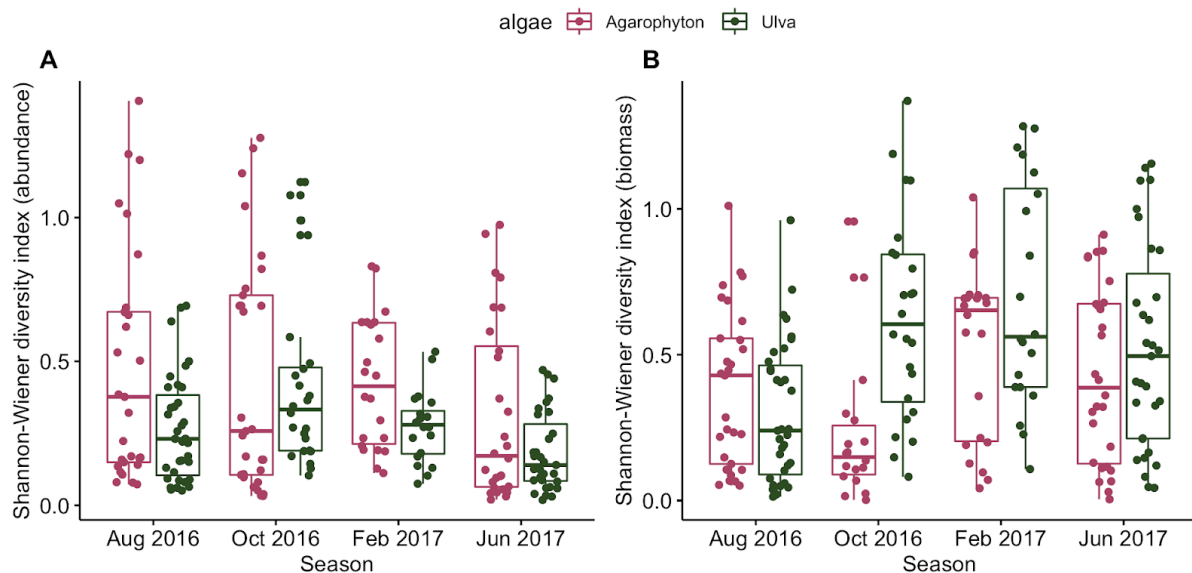
Figure 2.5: Shannon-Wiener diversity index per sample by location and algae canopy. In A: Diversity index calculated based on abundance; B: Diversity index calculated based on taxon biomass per sample. Jitter-points are representing data points. Whiskers represent the outer quartiles and box represents the inner quartiles. The median is represented by the horizontal line.

MULTIVARIATE ANALYSIS OF THE EPIFAUNAL ASSEMBLAGE

Prior to the significance testing, a Principal Coordinate Analysis (PCoA) was created to investigate the similarities graphically (see Figure 2.6). As shown in Figure 2.6, the mass of deposit-feeding organisms (i.e. *Hydrobia ulvae* and *Littorina* sp.), as well as the predators (*Carcinus maenas*), impacted the similarity of the measurements (Spearman correlation).
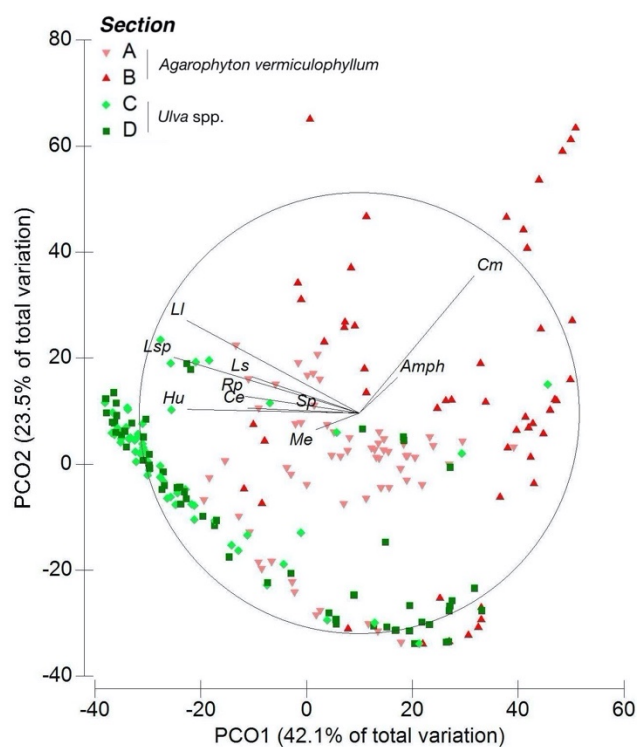
Figure 2.6: PCoA (Principal Coordinate Analysis) based on Bray-Curtis similarity of fourth root transformed fauna species biomass per g of algal biomass for *Agarophyton vermiculophylla* (Location A and B) and *Ulva* spp. (C and D). Spearman Correlation above .15 shown as vectors: **Amph** (Amphipods), **Ce** (*Cerastoderma edule*), **Cm** (*Carcinus maenas*), **Hu** (*Hydrobia ulvae*), **Ll** (*Littorina littorea*), **Ls** (*Littorina saxatilis*), **Lsp** (*Littorina* sp.), **Me** (*Mytilus edulis*), **Rp** (*Rissoa parva*), and **Sp** (*Scrobicularia plana*)

Fauna composition differed between macroalgae (PERMANOVA, algae, Ps-F(1, 214) = 7.9, p = 0.007, Table 2.7, Figure 2.6) but did not in multivariate dispersion (PERMDISP, Ps-F(1, 228) = 2.20, p= 0.179, Table 2.8). The fauna community structure did not change throughout the seasons (p=0.90, Table 2.7) and there was no interaction between algae and season (p=0.76, Table 2.7).

Table 2.7: Results of PERMANOVA based on community data (g taxa / g algae)*.

Source of variation	df	SS	MS	Pseudo-F	P(perm)	Permutations
Season	3	12356	4118.7	0.49342	0.886	94404
Algae	1	64513	64513	7.9043	0.0065	95419
Season x Algae	3	16821	5607.1	0.67174	0.728	94600
Location (Season x Algae)	8	68811	8601.3	9.1041	0.0000	89949
Residuals	214	202180	944.77			
Total	229	36150				

*Type-III-Sum of squares based on S17 Bray-Curtis similarity of community data of biomass taxon per biomass algae with a fourth root transformation and 99999 permutations. *Algae* and *Season* were fixed factors; however the *Location* was set as a random factor nested in *Season* and *Algae.*

Table 2.8: Results of PERMDISP based on community data (g taxa / g algae)*.

	Group 1	n_1	Group 2	n_2	t	P (perm)
Algae	*Agarophyton*	111	*Ulva*	119	1.4837	0.1803

F(1, 228): 2.2014, P(perm): 0.1793

*Based on S17 Bray-Curtis similarity of community data of biomass taxon per biomass algae with a fourth root transformation and 9999 permutations.

The average similarity of *Agarophyton* samples was 50.6% and *Ulva* samples showed 55.5% similarity. *Hydrobia ulvae* showed to be the highest contributor to differentiate between communities, moreover, *H. ulvae* had the highest abundance in both algal canopies. Moreover, all deposit and suspension feeders showed to be more abundant in *Ulva* canopies than in *A. vermiculophyllum* canopies (Table 2.9). In contrast, the predating green crab, *Carcinus maenas,* had a much higher abundance in *A. vermiculophyllum* and contributed 14.6% to the

distinction (SIMPER, Table 2.9). Notwithstanding, the bivalves *Parvicardium exiguum* and *Abra tenuis* were exclusively found in *A. vermiculophyllum* samples, and the gastropods *Hydrobia acuta*, *Littorina saxatilis*, *Melarhaphe neritoides,* and *Rissoa lilacina* were solely detected in *Ulva* samples (see Table S2).

Table 2.9: Results of similarity percentages breakdown (SIMPER) analysis based on community data (g taxa / g algae)*

Species	Feeding type		Average abundance Agarophyton	Average abundance Ulva	Contribution
Hydrobia ulvae	Gastropod	Deposit feeder	0.19%	0.29%	24.59%
Littorina littorea	Gastropod	Deposit feeder	0.06%	0.12%	18.47%
Littorina sp.	Gastropod	Deposit feeder	0.02%	0.12%	16.38%
Carcinus maenas	Crustacean	Carnivore	0.08%	0.02%	14.62%
Cerastoderma edule	Bivalve	Suspension feeder	0.01%	0.04%	7.13%
Mytilus edulis	Bivalve	Suspension feeder	0.01%	0.03%	6.23%
Rissoa parva	Gastropod	Deposit feeder	0.00%	0.03%	4.70%
Rest					7.89%

*Based on S17 Bray-Curtis similarity of community data of biomass taxon per biomass algae with a fourth-root transformation

SPECIES WEIGHT PER INDIVIDUAL

Even though *Hydrobia ulvae* differed in the abundance between canopies (Table 2.9), average species weight did not differ (Wilcox-test, p = 0.25, Figure 2.7). However, secondary grazers such as *Littorina* spp. and *Rissoa parva* differed significantly in weight between canopies (Wilcox-test, p≤0.004, Figure 2.7). In contrast, *Littorina littorea* was on average ten times bigger in *Agarophyton* canopies (Wilcox-test, p = 0.000), and other *Littorina* species were four

times smaller (Wilcox-test, p = 0.000). *Carcinus maenas* weighed on average three times more in *Ulva* canopies (Wilcox-test, p = 0.000) but had a much higher abundance in *A. vermiculophyllum* canopies (Wilcox-test, p=0.000, Wilcox' r = 0.60). No major weight differences were found between locations within algal canopies (p≥ 0.05).
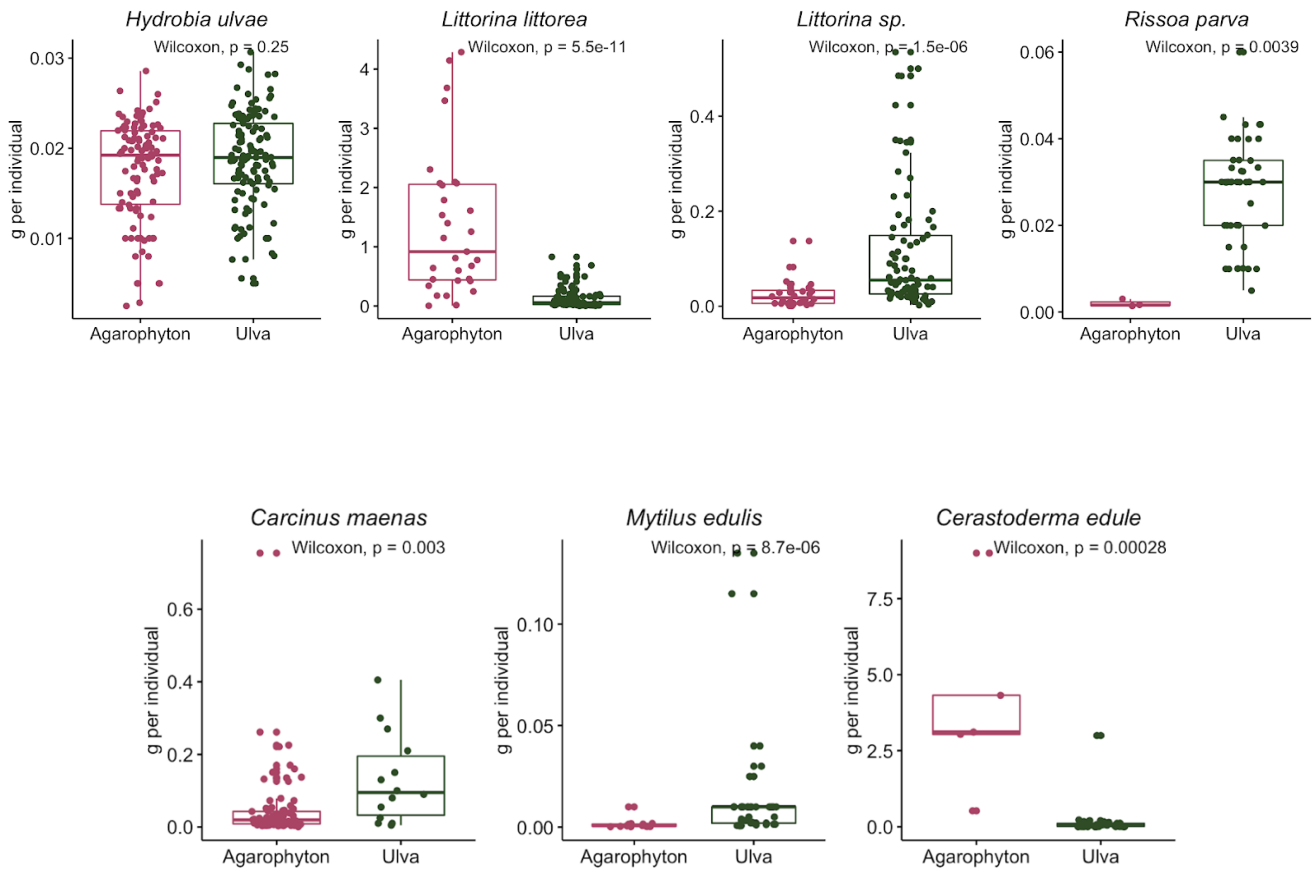

Figure 2.7: Average weight of epifaunal species per sample by algae with Wilcox-test p-value. Jitter-points are representing data points. Whiskers represent the outer quartiles and box represents the inner quartiles. The median is represented by the horizontal line.

2.5 DISCUSSION

SUMMARY OF THE RESULTS

The average algal biomass of both species was similar; however, the biomass of *A. vermiculophyllum* was highly variable throughout the seasons, whereas *Ulva* spp. biomass showed to be more constant. The tissue nitrogen content for both algae was either within or above the critical quota to sustain maximum growth, therefore nitrogen limitation was unlikely. The *Ulva* spp. canopies supported up to four times more faunal biomass than *A. vermiculophyllum* and a seasonal effect on the faunal biomass was only found in *Ulva* samples. The epifaunal composition between both algae differed substantially, with more invertebrate taxa found in *Ulva* spp.. Furthermore, deposit-feeding organisms had a higher abundance in *Ulva* spp. samples but the carnivorous crab, *Carcinus maenas*, was much more abundant in *A. vermiculophyllum* samples, although with a smaller weight per individual.

ALGAL BIOMASS AND NUTRIENT CONTENT

The algal biomass of *A. vermiculophyllum* showed a strong seasonal pattern (p=0.000, η^2= 0.40, Table 2.2), while *Ulva* spp. did not show any dependencies on season and was rather constant (p=0.052, η^2= 0.06, Table 2.2). The lowest observed tissue nitrogen content per dry weight of *A. vermiculophyllum* was 2.57% per g and 1.99% for *Ulva* spp.. This percentage may not represent limited conditions for the growth of the algae, as it is above or within the confidence interval of the critical quota (representing the minimum amount of N necessary to sustain maximum growth; Villares and Carballeira, 2004) of 2.14% for *A. vermiculophyllum* (Pedersen and Johnsen, 2017) and of 2.17% for *Ulva sp.* (95% confidence interval: 1.33 to 2.93; Ulva lactuca; Pedersen and Borum, 1996).

The reduction of tissue nitrogen (%) in higher algal biomass (p=0.31, r_s= -0.55) can be related to biomass dilution, which occurs when algal growth is not limited by the nutrient and the algal biomass increases, while the total amount of nutrients in the system stays the same (Pedersen *et al.*, 2010). However, this relationship could also result from the mediation of seasonal effects, since the tissue nitrogen content was highly associated with seasonal effects ($\eta_H^2 =$ 0.75) and not measured for every biomass sample.

DIFFERENCES IN FAUNAL BIOMASS

The underlying algal biomass represents determining factor for the supported faunal biomass (p=0.004, partial η^2 = 0.15, Table 2.4). Furthermore, it was strongly connected to the

macroalgal identity (p=0.028, partial η^2) and *A. vermiculophyllum* canopies supported on average four times less faunal biomass per algal biomass than *Ulva* spp. dominated canopies (p=0.000, Wilcox' r = 0.49; Table 2.3).

The algal biomass of *A. vermiculophyllum* showed a distinct seasonal pattern ($\eta^2 = 0.40$; Table 2.2), whereas the faunal biomass was relatively constant, however, it was the opposite in the case of *Ulva* spp. canopies. The seasonal variation of the faunal biomass (partial $\eta^2 = 0.13$; Table 2.3) in the green seaweed canopies, while the algal biomass stayed the same, may indicate trophic transfer from the algae towards the epifauna. For *A. vermiculophyllum,* no indication for this trophic transfer was evident, hence there was hardly any grazing control for this alga. Neijrup and Pedersen (2010) found that this rhodophyte may neither be limited by grazing nor by nutrients but suggested that it may be limited by physical exposure. The low grazing pressure on *A. vermiculophyllum* may be a consequence of the generally low grazer diversity of the native seagrass meadows (Gollan and Wright, 2006). Although grazing is an essential factor, export, decomposition, and other nutrient limitations than N need to be assessed to fully comprehend the differences between the native and invasive macroalgae and their implications on the ecosystem metabolism.

Epifaunal species are often able to adapt to new host algae (Taylor and Brown, 2006), and their preference may also be determined by structural characteristics of their host algae (Lutz *et al.*, 2019; Saarinen *et al.*, 2018)*,* rather than their species identity (Gestoso *et al.*, 2012)*.* However, *A. vermiculophyllum* might have a clear advantage of withstanding native grazers and deposit feeders compared to *Ulva* spp. due to highly developed chemical protection mechanisms, which species of *Ulva* spp. usually lack (Nylund *et al.*, 2011). Berke *et al.* (2020) found that grazers preferred *Ulva sp.* over Gracilariaceae, both the invasive *A. vermiculophyllum* and the native *Gracilaria tikivahiae*, yet, such preferences may be grazer-species-specific (Cacabelos *et al.*, 2010). Moreover, the alga seems also to have defence mechanisms against epiphytes, which is the main food source of many deposit feeders (Wang *et al.*, 2017). The competitive non-indigenous seaweed combines this structural resilience (Nejrup *et al.*, 2013) and fast growth rates, as well as fast asexual proliferation, which is facilitating its invasion success (Kolar and Lodge, 2001; Krueger-Hadfield *et al.*, 2016).

DIFFERENCES IN TAXON RICHNESS AND DIVERSITY

Ulva spp. had a higher taxa richness than *A. vermiculophyllum* (standardised beta = 0.43; Table 2.5)*,* and richness increased with biomass for both algae (standardised beta = 0.84, Table 2.5).

The macroalgal identity had no main effect on Shannon-diversity (H'), however, a small seasonal effect and interaction of the seasonal effects with seaweed species were detected (partial $\eta^2 = 0.09$; Table 2.6). Moreover, the epifaunal diversity was not dependent on the algal biomass (p = 0.356, Table 2.6).

Shannon-diversity (H') based on abundance differed strongly between the two *Agarophyton* locations, whereas one location (B) supported a much higher diversity than *Ulva* spp. and one (A) had a similar diversity as the *Ulva* canopies. This possibly resulted from increased substratum availability and habitat heterogeneity (Buschbaum *et al.*, 2006). Thomsen *et al.* (2013) found that *A. vermiculophyllum* can increase epifaunal diversity; although, only in low density and if it is occurring in quite localised patches, as in our case. The generally low diversity (Location A, C, and D) can be explained by the over-dominance of the gastropod *Hydrobia ulvae* (see Table S2) and therefore the low evenness in those locations. Alternatively, the diversity index based on taxon biomass per sample may give a less biased estimation (Figure 2.5, B). Nonetheless, calculation on the less biased H' did also not reveal differences in diversity of the seaweed canopies.

EFFECTS OF SEAWEED SPECIES IDENTITY ON THE EPIFAUNAL ASSEMBLAGE

The epifaunal communities *A. vermiculophyllum* and *Ulva* spp. differed substantially (Figure 2.6, Table 2.7), primarily due to the differences in abundances of deposit-feeding organisms (i.e. *H. ulvae, Littorina* spp.) and the abundance of the carnivorous decapod *Carcinus maenas* (Table 2.9). Furthermore, some invertebrate species were only detected in *A. vermiculophyllum* samples (*Parvicardium exiguum* and *Abra tenuis*) and some only in *Ulva* spp. samples (*Hydrobia acuta*, *Littorina saxatilis*, *Melarhaphe neritoides,* and *Rissoa lilacina;* Table S2). Deposit and suspension feeders were generally more abundant in *Ulva* spp. samples and *C. maenas* had four times higher average abundance in *A. vermiculophyllum* samples (SIMPER, Table 2.9).

Hydrobia ulvae may still be the main deposit feeder in *A. vermiculophyllum* canopies, and no difference in taxon weight was found between algal canopies (Figure 2.7). Nevertheless, secondary deposit-feeders (e.g. *Littorina littorea*) may have increased importance within the canopies. The strong association of the seaweed *A. vermiculophyllum* and the two epifaunal species *C. maenas* and *L. littorea* were also previously observed by Nyberg *et al.* (2009), as the seaweed may provide essential nursery habitat for crabs (Johnston and Lipcius, 2012), due to its more complex architecture (Munari *et al.*, 2015). The high abundance of carnivorous

crabs (i.e. *Carcinus maenas*) may induce top-down effects, since they are predating deposit-feeders and grazers, reducing grazing control (Guidone *et al.*, 2014; Warwick *et al.*, 1981; Wootton, 1995), however, grazing control in nutrient-enriched estuaries may be a secondary factor (Fox *et al.*, 2012)

LIMITATIONS

Our observations showed that the two locations with *Uvla* spp. canopies were more homogenous than the two *A. vermiculophyllum* canopies. This may also result from differences in temperature, hydrodynamics, and salinity, which can all affect the species community, as well as random deviations (Sánchez-Moyano *et al.*, 2000). It is still not clear how those different canopies are interacting with each other, since they are within the same estuary. Predators such as *Carcinus maenas* are mobile in the system and increased recruitment of the main predator of grazers of both algae in one part of the estuary could affect other parts of the estuary, yet, this needs to be further examined (Grosholz and Ruiz, 1996; Jamieson *et al.*, 1998).

MIXED-EFFECTS AND CONTEXT-DEPENDENCY OF INVASIVE SPECIES

The role of invasive species and whether they are 'drivers' or 'passengers' (MacDougall and Turkington, 2005) of changing ecosystems has been in debate ever since the issue reached a certain magnitude. Evaluating the effect of invasives (Rodriguez, 2006; Schlaepfer, 2018) and differentiating which introduced species are harmful and which are able to contribute positively to the ecosystem, is a relatively modern phenomenon. Moreover, it may be linked to the immense cost and complexity connected to remediation and restoration, as well as the poor prognosis for native species in our changing oceans (Bertolini, 2019; Schlaepfer *et al.*, 2011).

Introduced marine organisms can modify the habitat in negative (Bermejo *et al.*, 2020; Byers *et al.*, 2012; Krueger-Hadfield *et al.*, 2018), but also in positive ways (Sfriso *et al.*, 2020; reviewed by Wallentinus and Nyberg, 2007). Many of those studies compared the services facilitated by *A. vermiculophyllum* with the ones provided by bare mudflats. They reported multiple density-dependent positive effects based on this comparison (Ramus *et al.*, 2017; Thomsen *et al.*, 2019), or zones which were troubled by habitat loss of native foundation species (Johnston and Lipcius, 2012), or a structurally less complex and therefore for epifauna less appealing macroalgae (Munari *et al.*, 2015). In this "uneven" comparison, the architectural advantages of this seaweed may facilitate this improved epifaunal diversity (Cacabelos *et al.*, 2010) rather than the macroalgal identity, which was also pointed out by mentioned authors.

Nevertheless, there is no automatism that the effect of this increased epifaunal diversity can be conveyed to higher trophic levels. Moreover, macrophyte invasions cause loss of biodiversity and habitat homogenisations (Besterman *et al.*, 2020; Rahel, 2002), since areas as bare mudflats are essential foraging grounds for some of those species (Haram *et al.*, 2018). This context-dependency and the mixed ecosystem responses to this invasive species may complicate the evaluation even further.

CONCLUSION AND FURTHER OUTLOOK

In our study, we found most epifaunal species occurring in both algal canopies, however the abundance and/or average weight were associated with the macroalgal identity. Furthermore, some invertebrates of lower abundance (i.e. *Hydrobia acuta*, *Littorina saxatilis*, *Melarhaphe neritoides,* and *Rissoa lilacina*) were solely occurring in native canopies. Epifaunal species are an essential link between the primary production of the macroalgae themselves including the associated epiphytes and higher trophic levels. Shifts in abundances of those invertebrates can have major implication on the functioning of the ecosystem (e.g. nutrient cycling, biomass removal) and may affect the risk of macroalgal blooms.

Thus, considering: (i) algal biomass of *A. vermiculophyllum* did fluctuate notably over the seasons, which may result from reduced trophic transfer; (ii) the epifaunal assemblage was different to the native *Ulva* spp. and the abundance of the predatory crab *Carcinus maenas* was elevated greatly why may affects grazers and deposit feeders; (iii) the structural resistance of *A. vermiculophyllum* and increased predation may promote secondary deposit feeders by suppressing autochthonous and predominant species (i.e. *Hydrobia ulvae*) in the assemblage; (iv) within the same estuary, the non-indigenous macroalga had a lower epifaunal species richness and had either none or a negative effect on biodiversity compared to *Ulva* spp. canopies.

Several studies have shown that *A. vermiculophyllum* can shift ecosystems radically and within vast spatial extent (e.g. Byers *et al.*, 2012), it alters not only epifaunal assemblages but also the ecosystem metabolism, including biomass decomposition processes (Haram *et al.*, 2020). Due to the absence of long-term studies on the effect on estuarine ecosystems, the incorporation of this species into restoration management remains disputable.

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2.7 SUPPLEMENTARY TABLES

Table S1: Mean and standard deviation (SD) of the algal biomass in g per m^2*

Species	*Agarophyton vermiculophyllum*		*Ulva* spp.	
Location	A	B	C	D
Season	MEAN (SD)	MEAN (SD)	MEAN (SD)	MEAN (SD)
August 2016	2254 (±1338)	1242 (±522)	1329 (±988)	720 (±547)
October 2016	617 (±297)	306 (±436)	839 (±841)	701 (±421)
February 2017	349 (±344)	300 (±282)	806 (±856)	471 (±424)
June 2017	1272 (±952)	755 (±475)	921 (±697)	1200 (±817)
Total	1177 (±1133)	649 (±578)	1013 (±867)	805 (±628)
Coefficient of variation	0.96	0.89	0.86	0.78

Table S2: Mean ±SD of weight and individuals per m^2 by Location

Species	Agarophyton vermiculophyllum				Ulva spp.			
Location	A		B		C		D	
	g / m^2	n / m^2	g / m^2	n / m^2	g / m^2	n / m^2	g / m^2	n / m^2
Hydrobia ulvae	76.36 (±72.26)	4081.9 (±3718.9)	1.98 (±3.30)	138.3 (±192.9)	156.76 (±119.42)	7878.0 (±6114.3)	79.66 (±78.66)	3890.7 (±3790.6)
Littorina littorea	5.09 (±11.96)	5.5 (±10.6)	8.73 (±25.49)	5.5 (±12.3)	13.88 (±27.67)	134.5 (±127.4)	11.32 (±23.97)	62.7 (±103.2)
Littorina sp.	0.59 (±1.19)	33.2 (±104.2)	0.04 (±0.13)	5.3 (±12.6)	14.97 (±27.93)	149.7 (±142.3)	11.49 (±24.19)	65.6 (±108.5)
Rissoa parva	0.0 (±0.03)	0.5 (±2.7)	0.01 (±0.05)	2.1 (±15.7)	0.36 (±0.61)	11.9 (±17.0)	0.28 (±0.52)	11.2 (±19.2)
Carcinus maenas	2.34 (±4.68)	59.9 (±97.1)	2.62 (±13.26)	70.9 (±104.0)	0.47 (±1.86)	3.5 (±10.3)	0.84 (±4.80)	3.7 (±12.6)
Mytilus edulis	0.16 (±1.27)	3.1 (±7.5)	0.01 (±0.03)	14.1 (±72.0)	1.90 (±8.13)	11.4 (±22.2)	1.58 (±7.96)	29.6 (±55.6)
Cerastoderma edule	17.47 (±71.16)	4.8 (±18.1)	–	–	0.94 (±2.10)	16.0 (±24.1)	2.11 (±7.02)	13.1 (±25.3)
Parvicardium exiguum	0.01 (±0.04)	1.4 (±4.6)	0.0 (±0.01)	0.2 (±2.0)	–	–	–	–
Scrobicularia plana	0.34 (±2.80)	0.2 (±2.0)	–	–	0.11 (±0.49)	0.8 (±3.5)	0.98 (±4.16)	7.2 (±39.8)
Abra tenuis	0.02 (±0.06)	12.7 (±46.4)	0.00 (±0.01)	1.0 (±4.7)	–	–	–	–
Amphipods	0.00 (±0.02)	0.2 (±2.0)	0.03 (±0.16)	13.9 (±81.3)	–	–	0.09 (±0.53)	0.8 (±4.6)
Littorina saxatilis	–	–	–	–	1.09 (±2.10)	15.2 (±23.1)	0.17 (±0.69)	2.9 (±10.4)
Melarhaphe neritoides	–	–	–	–	0.02 (±0.12)	0.3 (±2.1)	0.07 (±0.52)	0.3 (±2.1)
Rissoa lilacina	–	–	–	–	–	–	0.00 (±0.02)	0.3 (±2.1)
Hydrobia acuta	–	–	–	–	0.00 (±0.02)	0.3 (±2.1)	–	–

Table S3: Pairwise PERMANOVA results for Locations based on community data (g taxa / g algae).*

within Season	within Algae	Group 1	Group 2	t	P(perm)
August 2016	*Agarophyton*	A	B	3.326	**0.0000**
August 2016	*Ulva*	C	D	4.9027	**0.0000**
October 2016	*Agarophyton*	A	B	2.6755	**0.0017**
October 2016	*Ulva*	C	D	2.2562	**0.0064**
February 2017	*Agarophyton*	A	B	3.1183	**0.0000**
February 2017	*Ulva*	C	D	1.0437	0.3184
June 2017	*Agarophyton*	A	B	3.9637	**0.0000**
June 2017	*Ulva*	C	D	1.2431	0.2019

*Based on ~95000 permutations for each comparison.

Table S4: Results of PERMDISP based on community data (g taxa / g algae)*.

	Group 1	n_1	Group 2	n_2	t	P (perm)
Location	A	61	B	50	4.1428	**0.0000**
F(3, 226): 15.724, P(perm): 0.0001	A	61	C	59	0.0554	0.9580
	A	61	D	60	6.2239	**0.0000**
	B	50	C	59	3.9488	**0.0000**
	B	50	D	60	0.0984	0.9260
	C	59	D	60	5.8393	**0.0000**

*Based on S17 Bray-Curtis similarity of community data of biomass taxon per biomass algae with a fourth root transformation and 9999 permutations.