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Gilles Lepoint

Glenn A. Hyndes

Edith Cowan University, g.hyndes@ecu.edu.au

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EDITED BY

Zhijian Jiang,
South China Sea Institute of
Oceanology (CAS), China

REVIEWED BY

Kun-Seop Lee,
Pusan National University, South Korea
Delian Huang,
South China Sea Fisheries Research
Institute (CAFS), China

*CORRESPONDENCE

Gilles Lepoint
G.Lepoint@uliege.be

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Tropicalization of seagrass macrophytodetritrus accumulations and associated food webs

Gilles Lepoint^{1*} and Glenn A. Hyndes²

¹Laboratory of Trophic and Isotopes Ecology, Department of Biology, Ecology and Evolution, University of Liège, Liège, Belgium, ²Centre for Marine Ecosystems Research, School of Science, Edith Cowan University, Joondalup, WA, Australia

Seagrass, systems export significant amounts of their primary production as large detritus (i.e. macrophytodetritrus). Accumulations of exported macrophytodetritrus (AEM) are found in many areas in coastal environment. Dead seagrass leaves are often a dominant component of these accumulations, offering shelter and/or food to numerous organisms. AEM are particular habitats, different from donor habitats (i.e. seagrass meadow, kelp or macroalgae habitats) and with their own characteristics and dynamics. They have received less attention than donor habitats despite the fact they often connect different coastal habitats, are the place of intense remineralization processes and shelter associated detritus food web. As for seagrass meadows themselves, AEM are potentially affected by global change and by tropicalization processes. Here, we review briefly general characteristic of AEM with a focus on Mediterranean Sea and Western Australia and we provide some hypotheses concerning their tropicalization in a near future. We conclude that AEM functioning could change either through: (1) declines in biomass or loss of seagrass directly due to increased ocean temperatures or increased herbivory from tropicalized herbivores; (2) increased degradation and processing of seagrass detritus within seagrass meadows leading to reduced export; (3) replacement of large temperate seagrass species with smaller tropical seagrass species; and/or (4) loss or changes to macroalgae species in neighboring habitats that export detritus. These processes will alter the amount, composition, quality, timing and frequency of inputs of detritus into ecosystems that rely on AEM as trophic subsidies, which will alter the suitability of AEM as habitat and food for invertebrates.

KEYWORDS

seagrass, tropicalization, detritivore, food web, macroalgae, climate change, carbon cycle, detritus

Introduction

Seagrasses form highly productive ecosystems that provide a range of important ecosystem functions in coastal environments, including carbon sequestration, habitat provision, and a direct and indirect food source for a range of consumers (e.g. Orth et al., 2006). They are net autotrophic ecosystems (e.g. Champenois and Borges, 2012; Champenois and Borges, 2021), capable of exporting massive detrital primary production to other coastal and offshore habitats (Mann, 1988; Cebrian, 2002; Heck et al., 2008). While herbivory can remove high proportions of primary production, forming the green food web, the extent of this process depends on seagrass system type, latitude or local variability (Valentine and Heck, 2021; Heck et al., 2021). Nevertheless, whatever the importance of herbivory, a significant part of the primary production is not consumed and forms detritus, fueling the brown food web (Cebrian, 2002; Mateo et al., 2006). However, both the green and brown food webs linked to seagrass ecosystems are almost certainly being impacted by the loss of seagrass in many parts of the world (Waycott et al., 2009), while the relative importance of each will likely be affected by ocean warming, shifting distributions of seagrass species, and functional change in seagrass meadows (Hyndes et al., 2016).

Production of detritus in seagrass meadows is enhanced by the fact that seagrass leaves senesce, die and are released from the plant. This is a process controlled by the plant physiology, allowing nutrient reclamation by seagrass shoots (Stapel and Hemminga, 1997; Lepoint et al., 2002) and elimination of epiphytic biomass (Orth and Van Montfrans, 1984; Borowitzka et al., 2006). Leaf fall can be a continuous phenomenon, particularly in tropical and subtropical areas, or a more seasonal one, particularly in temperate areas. This detritus material (or necromass) can form seagrass litter that lays and decomposes among seagrass shoots (Walker et al., 2001), and in which fauna contribute to decomposition *via* mechanical fragmentation, production of feces and assimilation of seagrass carbon (Harrison, 1989). Residence time of seagrass litter in the meadow itself is highly variable (i.e. from hours to months), depending on meadow depth, microbial and mechanical degradation rates, fauna processing and local hydrodynamics (i.e. swell, current, wind gust or storm) or local seascape morphology (Hyndes et al., 2014; Ricart et al., 2015; Ricart et al., 2017; Costa et al., 2019). In many cases, a significant part of this detritus can be exported outside the meadow as large fragments (i.e. macrophytodetritus) (e.g. Boudouresque et al., 2016). It is estimated that, as a global average, between 15 and 25% of carbon fixed by seagrass is exported to adjacent system (Cebrian, 2002; Mateo et al., 2006) but this can vary between few percent and 100% depending of the seagrass system and local environmental condition (seascape, hydrodynamics for example) (reviewed in Heck et al., 2008 and Mateo et al., 2006). Long term study by

Champenois and Borges (2021) in Calvi (i.e. 12 year mooring survey) estimate to 80% the total NPP produced in *Posidonia oceanica* bed exported to adjacent systems, matching the calculation of Pergent et al., 1997 for this system (40 – 70% of leaf production). Thus, seagrass detritus can fuel the brown food web both within the seagrass meadow and in connected ecosystems, depending on seagrass and seascape characteristics and hydrodynamics (Hyndes et al., 2014). For examples, massive release of *Posidonia oceanica* (L.) Delile leaves starts in the Mediterranean Sea in late summer, but export is often delayed to mid to late autumn, depending of autumnal storms (Pergent et al., 1997; Gobert et al., 2006). This means that exported material is already modified by decomposition (i.e. impoverished in N and P) and colonized by microbial decomposers (Mateo and Romero, 1997). In temperate Western Australia, detritus production in meadows of *Posidonia* spp. occurs throughout the year, but peaks in late summer while export occurs in autumn (Cambridge and Hocking, 1997). Compared to temperate systems, decomposition rates in the tropics are generally faster than for temperate seagrass systems. For example, in Indonesia, Vonk and Stapel (2008) measured decomposition rates (k) for leaf biomass of *Thalassia hemprichii*; *Cymodocea rotundata* or *Halodule uninervis* ranging from 0.023 to 0.070 d⁻¹. In comparison, in similar litter bag experiences, measured decomposition rate of *P. oceanica* dead leaves ranged from 0.003 (Costa et al., 2019) to a maximum of 0.022 d⁻¹ (Mateo and Romero, 1997). Faster decomposition rate can lead to efficient nutrient recycling inside the meadows (Vonk and Stapel, 2008) and, therefore, to less NPP export (Hyndes et al., 2014). In their data compilation, Hyndes et al. (2014) calculate that, in tropical seagrass meadow, a greater proportion of seagrass net primary production (NPP) is being processed through decomposition and herbivory than in temperate seagrass meadow (global average 85.2 vs. 34.1% of annual NPP (calculated from Table 1 in Hyndes et al., 2014) indicating as a general observation that NPP export is proportionally lower in tropical seagrass meadow than in temperate seagrass meadows.

Accumulations of exported macrophytodetritus (AEM) (also known as dead leaf mat, wrack, beach cast or exported litter in the literature) can be found in a wide range of ecosystems including the ocean floor of the deep sea and continental shelf, to coastal systems including coral reefs, saltmarshes, mangroves, beaches and dunes (Table 1). Seagrass detritus forms part of beach-cast wrack across the globe (Hyndes et al., in press), often constituting high proportions in regions where large seagrass meadows occur, particularly in the Mediterranean Sea and southern Australia, but also in tropical areas (Figure 1). Accumulations of dead seagrass leaves are also found in subtidal areas, close or distant to meadow sources (Figure 2). This is particularly the case in the initial phase of detritus export before mechanical fragmentation. Fossil evidence for extinct (Jagt et al., 2019) and extant (Moissette et al., 2007) seagrass species indicates that this process has been occurring for millions of years.

TABLE 1 Published examples of habitats and locations in which seagrass detritus has been linked to habitat or trophic associations with fauna in coastal and offshore systems.

Recipient habitat	Associated fauna	Trophic link	Seagrass genus	Location	Country	Other forms of detritus	Article
Beach		Invertebrates	<i>Phyllospadix</i>	California	USA	Kelp	Lastra et al. (2008)
Beach		Invertebrates	<i>Phyllospadix</i>	California	USA	Kelp	Michaud et al. (2019)
Beach		Invertebrates	<i>Zostera</i>	New South Wales	Australia	Brown algae	Poore and Gallagher (2013)
Beach	Invertebrates			California	USA	Kelp	Dugan et al. (2003)
Beach	Invertebrates		<i>Thalassodendron</i>	Mombasa	Kenya		Ochieng & Erfemeijer (1999)
Beach	Invertebrates		<i>Zostera marina</i>	Hel (Baltic Sea)	Poland		Jedrzejczak (2002)
Beach		Invertebrate	<i>Posidonia oceanica</i>	Tuscany	Italy		Colombini et al. (2009)
Beach	Invertebrates		<i>Cymodocea, Zostera</i>	Cadiz	Spain	Macroalgae	Ruiz-Delgado et al. (2016)
Beach			<i>Zostera</i>	Banc d'Arguin	Mauritania		Hemminga and Nieuwenhuize (1990)
Beach			<i>Phyllospadix</i>	British Columbia	Canada	Macrocystis	Orr et al. (2005)
Beach			<i>Cymodocea nodosa</i>	Tarragona	Spain		Mateo (2010)
Bay			<i>Thalassia, Thalassodendron, Cymodocea, Syringodium</i>	Gazy Bay	Kenya	Mangrove leaves	Slim et al. (1996)
Lagoon			<i>Zostera noltii</i>	Thau Lagoon	France		Costa et al. (2021)
Estuaries	Invertebrates		<i>Cymodocea, Zostera spp.</i>	Po River Delta	Italy	Reed detritus	Mancinelli and Rossi (2002)
Surf zone		Invertebrates, fish	<i>Posidonia, Amphibolis</i>	Western Australia	Australia	Kelp, Red algae	Crawley et al. (2009)
Surf zone	Fish		<i>Posidonia, Amphibolis</i>	Western Australia	Australia	Kelp, Red algae	Lenanton et al. (1982)
Bay			<i>Zostera</i>	Boha Sea	China		Min et al. (2019)
Bay			<i>Syringodium</i>	Florida Bay	USA		Perry et al. (2018)
Bay		Meiofauna, macro-invertebrate, vertebrates	<i>Posidonia oceanica</i>	Corsica	France	macroalgae	Mascart et al. (2018), Remy et al. (2018, 2021)
Bay	Invertebrates		<i>Posidonia oceanica</i>	Corsica	France	macroalgae	Gallmetzer et al. (2005); Lepoint et al. (2006), Sturaro et al., (2010)
Offshore		Fish	<i>Zostera</i>	Tasmania	Australia		Thresher et al. (1992)
Offshore			<i>Zostera spp</i>	Hokkaido Island	Japan	Sargassum, Kelp, Red algae	Kokubu et al. (2019)
Submarine canyon		Invertebrates	<i>Phyllospadix</i>	California	USA	Kelp	Vetter (1994)
Submarine canyon		Invertebrates	<i>Phyllospadix</i>	California	USA	Kelp	Vetter (1998)
Deep Sea (abyssal plain)	Invertebrates	Invertebrates	<i>Thalassia testudinum</i>	Puerto Rico	USA	wood, leaves, fruits, and Sargassum	Wolff (1979)
Deep Sea (abyssal plain)			<i>Thalassia testudinum</i>	North Carolina	USA		Menzies and Rowe (1969)

Seagrass genus and location (including country) are provided, along with other detrital macrophytes in the detrital accumulations. The published examples are not exhaustive, particularly for beach habitats where numerous studies have examined accumulations of detritus (see Hyndes et al. In press) for extensive list on beach systems.

Here we discuss the potential flow-on effects of tropicalization of temperate seagrass meadows to the functioning of other inter-connected habitats in the coastal seascape, focusing on shifts in the quantity and quality of detritus exported from seagrass meadows and imported into

AEM habitats (Figure 3). We use the term tropicalization to refer both to the expansion of tropical species to temperate areas (Arntz and Tarazona, 1990) and to the functional change occurring in temperate ecosystems due to this species shift (Vergés et al., 2014a). We will focus in particular on seagrass

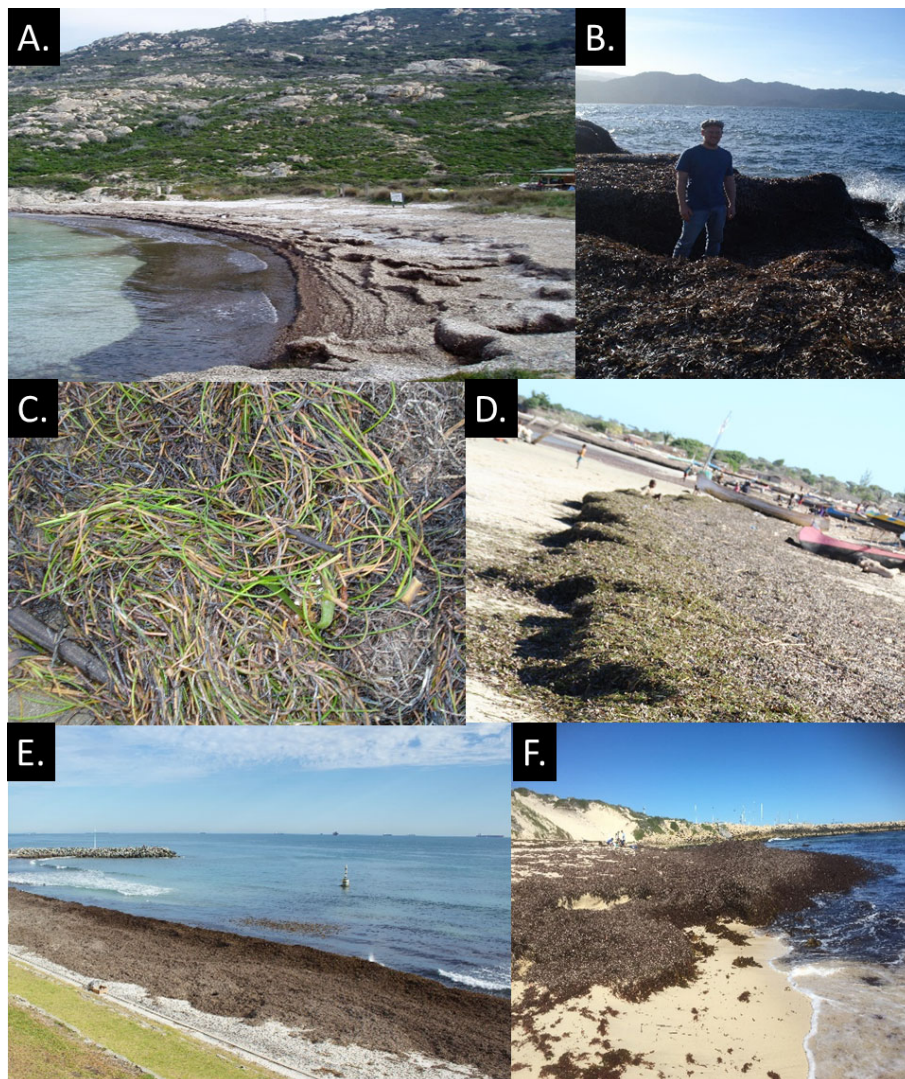


FIGURE 1

Some example of seagrass beach cast. **(A)** beach accumulation of *Posidonia oceanica* dead leaves, also known locally as “banquette”, on Alga Bay Beach, Calvi, Corsica, March 2007; **(B)** 2 m high banquette on a beach in St Florent Gulf, St Florent, Corsica; **(C)** beach cast of *Syringodium filiforme* and other tropical species on a Guadeloupe beach (Caribbean Sea); **(D)** brown and green leaves of diverse tropical species (mainly *Cymodocea serrulata*, *Syringodium isoetifolium*, *Thalassia empirchii* and *Halodule uninervis*) on Andravo beach (Toliara, Madagascar), May 2018; **(E)** and **(F)** beach cast in the Perth region of southwestern Western Australia. Typically, it comprises *Posidonia* spp., *Amphibolis* spp., the kelp *Ecklonia radiata* and other brown and red macroalgae.

ecosystems and AEM in temperate Western Australia and Mediterranean Sea, regions which are characterized by large and expansive seagrass meadows comprising the genus *Posidonia* and have been shown to be already affected by tropicalization (Vergés et al., 2014a) and where structure and function of subtidal or intertidal AEM are relatively well documented. We will also refer to tropical seagrass meadows functioning as a possible functional scenario for temperate areas under tropicalization threats. Prior to this discussion, we provide a synopsis of what is currently known about the ecosystem functioning of AEM habitats.

Macrophytodetrititus accumulation as habitats

Unlike seagrass meadows that support both green and brown food webs, habitats formed by AEM generally support brown food webs and display their own characteristics compared to seagrass meadows or the surrounding environment (Boudouresque et al., 2016). For example, AEM may experience very fast change in detrital composition and quantity (height, cover) or in oxygenation (Mascart et al., 2015; Ricart et al., 2015), and be highly variable across seasons



FIGURE 2

Subtidal accumulation of *Posidonia oceanica* macro detritus. Left: November 2010, recently exported dead leaves (80 cm thick), 10 m depth, Revellata Bay, Calvi, Mediterranean Sea. Right: June 2012, fragmented macrophytodetritrus with uprooted living *P. oceanica* shoots, 10 m depth, Revellata Bay, Calvi Corsica.

in temperate regions particularly (Romero et al., 1992). In Calvi bay, studied AEM accumulation height varies seasonally from 5cm (i.e. less than 400 gDM.m⁻²) of very compact and degraded material in spring to more than 50cm (1800 gDM.m⁻²) of less compacted material just after the dead leaf export in November (Mascart et al., 2015). Depending on hydrodynamics and seascape morphology, subtidal AEM habitats can be highly mobile, displaced or disrupted by tidal currents, waves and storms (Ricart et al., 2015; Slim et al., 1996). Oxygen is often depleted inside the AEM due to decomposition and remineralization processes and intrusion of reduced compounds from sediment (e.g. sulfides, ammonium) (Vetter and Dayton, 1998; Gallmetzer et al., 2005) and hypoxia is often experienced by fauna (Gallmetzer et al., 2005; Mascart et al., 2015). Furthermore, composition of these AEM is highly variable. In temperate regions, they are often mixed with various macroalgae detached from their substrate (e.g. Lepoint et al., 2006; Crawley et al., 2009), or with litter from terrestrial or salt marsh origin, notably in areas close to estuaries or transitional waters (Mancinelli and Rossi, 2002; Mascart et al., 2015) (Table 1). In the tropics, mangrove leaves as well as detached macroalgae from rocks and coral reefs can contribute to the AEM (Slim et al., 1996). In addition, anthropogenic material such as microfiber can be present and enter the food web (Remy et al., 2015). While AEM is generally considered heterotrophic with high respiration and remineralization rates, detached macroalgae can still be living and photosynthetically active in subtidal habitats (Frontier et al., 2021), providing an autotrophic source of production for a period prior to the algae senescing. Furthermore, leaf litter can be colonized by macro and micro epiphytes (e.g. microalgae including diatoms) (Lepoint et al., 2006), paradoxically, providing a source of primary production in a heterotrophic system. Despite this, AEM is typically driven by decomposition through the colonization and expansion of microbial decomposers

(bacteria, fungi) (Cuomo et al., 1987; Lepoint et al., 2006; Singh et al., 2021). Little is known about the microbial communities in AEM, but microbial decomposers can contribute to a large part of nitrogen and other nutrients found within the dead material of salt marshes (Newell et al., 1989) and it could also be the case in seagrass AEM.

AEM can be viewed as a pulsed system (Yang et al., 2008), where litter pulses provide both habitat and food for resident fauna (Mancinelli and Rossi, 2002; Remy et al., 2017; Costa et al., 2021). Beach AEM is generally colonized by specialized semi-aquatic fauna. Crustaceans, particularly talitrid amphipods and isopods, are by far the dominant taxa in beach-cast systems (see Hyndes et al., In press). In subtidal AEM, species are more related to adjacent donor ecosystems (i.e. macroalgae or seagrass habitats), but are often inhabited by fewer species than vegetated habitats (Borg et al., 2006; Como et al., 2008; Calizza et al., 2013). It is likely that some of the small vagile species found in AEM are exported from donor habitats *via* their substrate (dead leaf or ripped macroalgae). Fauna transport *via* rafting (floating or not) is known to be an important colonizing process in coastal areas (Thiel and Gutow, 2005). Regardless of the composition of the AEM (seagrass, reed, macroalgae or kelp), these less diverse macrofauna communities are dominated by crustaceans (particularly amphipods and isopods), and to a lesser extent, annelids, mollusks and echinoderms (Vetter, 1995; Vetter, 1998; Gallmetzer et al., 2005; Mancinelli et al., 2007; Duggins et al., 2016; Costa et al., 2019; de Bettignies et al., 2020). Copepods generally dominate the meiofauna of subtidal AEM (Mascart et al., 2015), but the hypoxic sediment under AEM or beach cast are often dominated by nematodes (Vetter and Dayton, 1998). Meiofauna and macrofaunal densities in AEM, whatever their composition, are generally huge (densities from 1×10⁵ to 1×10⁷ individuals m⁻¹ are often observed), often far above densities measured in seagrass meadows (Vetter, 1998; Norkko et al., 2000; Gallmetzer et al., 2005; Como et al., 2008; Mascart et al.,

2015). These high invertebrate densities are likely to provide an accessible foraging resource for the many fishes that are observed around intertidal and subtidal AEM (Crawley et al., 2006; Boudouresque et al., 2016; Baring et al., 2019). In Mediterranean surf zones, these fishes, mostly represented by invertivorous (e.g., labrids) and omnivorous species, are observed feeding in *P. oceanica* AEM and using the resuspended dark-brown vegetal fragments to hide; higher species richness and fish density are observed on AEM than on sand. (Bussotti et al., 2022).

The food web in subtidal *P. oceanica* AEM in the Mediterranean Sea is simplified when compared to *P. oceanica* meadows due to a lower species diversity and the absence of trophic guilds such as suspension feeders (Remy et al., 2018). Herbivorous fishes such as *Sarpa salpa* that are dominant in *P. oceanica* meadows (Havelange et al., 1997) can be observed around AEM but not feeding in them (Jadot et al., 2006). Consumers of AEM are dominated by detritivores (i.e. consumers of dead material), but herbivores (consumers of living macrophytes or microepiphytes) or consumers switching between the two modes are also present and sometimes dominant (Remy et al., 2018). While there is no evidence of direct consumption of *P. oceanica* detritus by talitrid amphipods in beach cast (Colombini et al., 2009), gut contents provide evidence of the ingestion of dead seagrass material by dominant taxa, in particular by amphipods in subtidal AEM (Lepoint et al., 2006). Furthermore, stable isotopes show that these dominant species also assimilate carbon from ingested seagrass (Vizzini and Mazzola, 2008; Remy et al., 2018). This assimilation occurs directly (i.e. digestive ability of the species itself) or indirectly (i.e. assimilation of microbial biomass degrading seagrass detritus). The first enhances mechanical degradation of macro-detritus (Costa et al., 2019), while the second way is potentially important for most species of meiofauna (Mascart et al., 2018). Additionally, it is demonstrated that the food web responds to seasonal pulses of litter, with an increase of litter contribution to the diets of dominant invertebrates, including meiofauna, in autumn (Mascart et al., 2018; Remy et al., 2021). Compared to the Mediterranean, there is limited evidence of direct consumption of seagrass detritus in Western Australia. Similar to seagrass meadows (Smit et al., 2005; Smit et al., 2006), macroalgae typically fuel the food web (Hyndes and Lavery, 2005), although seagrass detritus may contribute as a food source for a limited number of species on beaches (Ince et al., 2007). Indeed, the dominant detritivore in surf-zone AEM in the region, the amphipod *Allorchestes compressa*, feeds preferentially and almost exclusively on macroalgae, particularly kelp and other brown algae (Crawley and Hyndes, 2007; Crawley et al., 2009), and these detritivores form the bulk of the diet of fish in the AEM (71–99%; Crawley et al., 2006). Thus, this semi-aquatic amphipod, like many other species in beach ecosystems elsewhere in the world (Hyndes et al., In press), displays high feeding rates and preferences for kelp.

Tropicalization

The poleward expansion of tropical species resulting from ocean warming has occurred throughout the world, including seagrasses (Kim et al., 2009; Virnstein and Hall, 2009; Gorman et al., 2016). The pole-ward range extensions of tropical herbivorous fishes have had profound effects on ecosystem structure and functioning of kelp forests in Japan, Australia and the Mediterranean Sea (Vergés et al., 2014a). Spread of tropical species into the Mediterranean Sea has occurred since the opening of the Suez Canal in 1869, resulting in the introduction of Red Sea species in east Mediterranean Sea (known as Lessepsian species) (Bianchi and Morri, 2000). Additionally, tropical species of macroalgae, seagrasses, invertebrates and fishes have been introduced *via* tropical aquarium release and maritime transport (Katsanevakis et al., 2014; Galil et al., 2018; Zenetos and Galanidi, 2020). Until recently, many introduced species were only settled in the southern basin of the Mediterranean Sea and often considered as native by present day fishermen, but recent sea temperature increases have now allowed Lessepsian species to expand their range northward (all Aegean Sea, and Adriatic and northern Mediterranean basin) (Katsanevakis et al., 2014; Zenetos and Galanidi, 2020; Thibaut et al., 2022). This has also allowed species that have recently been introduced *via* ballast water, yachting or aquarium trading to acclimate themselves in Adriatic and north-western Mediterranean waters (Katsanevakis et al., 2014).

In Western Australia, a warm pole-ward flowing current, the Leeuwin Current, strongly influences the coastal waters along the entire west coast. While this current has been a feature of the coast for millennia, ocean temperatures have been increasing ~0.1°C per decade for the last 100 years, increasing to ~0.3°C per decade since the mid-1980s (Pearce and Feng, 2007; Lough, 2008). On top of this, a marine heatwave event in the summer of 2010/11 increased sea surface temperatures by up to 5°C above average, leading to the transport and maintenance of tropical species in temperate waters, and major seagrass loss in the subtropics (Strydom et al., 2020) and functional changes to temperate reefs due to declining kelp biomass and increasing abundances of herbivorous fishes (Wernberg et al., 2013). Since the 2010/11 marine heatwave, several tropical fish species have been observed in temperate coastal waters (Lenanton et al., 2017; Zarco-Perello et al., 2020). The impact on temperate seagrasses by these tropical invaders is currently unknown, but it is predicted that they will substantially increase grazing rates on seagrass leaves over the next century (Hyndes et al., 2016). This will be enhanced by the pole-ward shift in the distribution of the seagrass-grazing megafauna dugongs and green turtles, and ultimately, there will be a shift in seagrass species to those from the tropics (Hyndes et al., 2016). Combined, this tropicalization will lead to fundamental changes in the ecosystem functioning of seagrasses in the region.

Shifts in animal community living in AEM

Most AEM macrofauna are dominated in diversity and abundance by small crustacea (mainly amphipods and copepods, sometimes isopods, decapods and leptostracans), small mollusks and errant annelids. Most of them are also found in the litter layer of the meadow itself (Como et al., 2008). Moreover, they are generally not specific to one type of detritus accumulation: species colonizing seagrass AEM are also found in macroalgae or reed detritus (Péres and Picard, 1964, Mancinelli and Rossi, 2002). Physico-chemical and biological conditions act as a strong environmental filter: most AEM macrofauna are opportunist species tolerant to short-term environmental change (oxygen, salinity, temperature) and able to cope with habitat and food source variability and quality. Beside diversity or abundance changes linked to change of their composition (Haram et al., 2020) (see below), AEM are likely to be also colonized by non-native species and therefore to be subject to biodiversity tropicalization. AEM have presently received little attention from an invading species point of view and, globally, small invertebrate changes are clearly less known than changes in macrophytes, large invertebrates or fishes. Nevertheless, in Mediterranean Sea, Lessepsian amphipod invaders are recorded in Levantine waters, Aegean Sea and South Western Mediterranean and are likely to spread north like other taxa (Sezgin et al., 2007; Christodoulou et al., 2013; Khammassi et al., 2019). We can predict that tropical species invading AEM will possess opportunistic behavior, plastic trophic ecology and high tolerance to short-term environment parameter changes (e.g. oxygen), like native AEM macrofauna. It is difficult to predict if their tropical origin will give them competitive advantage over native fauna (such as higher metabolism, higher growth and reproductive rate) and it is possible that current AEM communities resist these new invaders. Nevertheless, if current AEM macrofauna is outcompeted and replaced by other species, it is likely to have consequences on coastal fish that use AEM as nursery or as foraging habitats.

Shifts in the export of seagrass detritus

Tropicalization of seagrass ecosystems is predicted to influence the supply of seagrass detritus to other ecosystems through a number of processes: (1) increases in tropical grazers will lead to greater consumption of seagrass biomass and reduced release of leaves for internal processing or export; (2) increases in microbial and invertebrate processing with increasing temperatures and invasive invertebrates will lead to less export due to increased internal cycling and a change in the quality of litter being exported; (3) shifts in seagrass species to tropical species will lead to less export of detritus; and/or (4) seagrass meadows exhibiting a shift from seagrass

to macroalgae will shift the quality of the material in AEM. Most of these potential changes will affect AEM as habitat for associated fauna and AEM trophic functioning. It must be noted that these processes are not mutually exclusive, and are likely to have a compounding influence on the amount of seagrass detritus being exported from seagrass systems.

Seagrass beds in tropical areas show higher herbivore diversity than temperate areas and, potentially, higher herbivory rate in relation with absence of biomass seasonality (i.e. continuous grazing) (Heck and Valentine, 2021). Tropical herbivore fishes, mainly rabbitfishes and parrotfishes, are successfully expanding from tropical to more temperate waters where they have been shown to increase grazing on macroalgae (Vergés et al., 2014a; Vergés et al. 2014b). Far less is known about the effects of these and other grazers on seagrass meadows, but we do know that seagrass grazing fishes are far more abundant and diverse in the tropics compared temperate seagrass beds (Valentine and Duffy 2006; Heck et al., 2021). In Western Australia, Hyndes et al. (2016) predicted that these tropical fishes will be the first to increase their ranges to temperate regions, with a *Siganus* species already establishing a viable population in southwest Western Australia (Lenanton et al., 2017) and occurring in seagrass meadows (Zarco-Perello et al., 2020). Little is known of their impact on the temperate seagrasses, but very little herbivory occurs in these temperate systems normally. In the Mediterranean Sea, the endemic sparid *S. salpa* can graze on significant amounts of the dominant seagrass, *P. oceanica*, in the region (Havelange et al., 1997, Tomas et al., 2005). However, tropical species have moved into the Mediterranean. In eastern Mediterranean Sea, occurrences of rabbitfish have been reported since the beginning of 20th century (Shakman and Kinzelbach, 2007). Furthermore, *Siganus* spp. and parrotfishes have invaded *P. oceanica* meadows, sometimes replacing *S. salpa* in the region. This invasion has significantly increased the diversity and abundance of herbivore fishes in Mediterranean (Stergiou and Karpouzi, 2002), where they have been shown to consume *P. oceanica* (Stergiou, 1988). Both in Western Australia and in Mediterranean Sea, this has increased the functional diversity as the co-existing species have different trophic niches (Azzurro et al., 2007; Zarco-Perello et al., 2020). High herbivory rates are often recorded in tropical seagrass meadows (Heck et al., 2021), and with tropicalization of herbivores, it is the likely fate of temperate seagrass meadows. Increases in abundance, species diversity and functional diversity of herbivores will likely lead to an increase of the proportion of primary production removed by herbivores (Ozvarol et al., 2011; Hyndes et al., 2016; Zarco-Perello et al., 2020) and, therefore, reduce macrophytodeposit production, disrupt the detritus cycle and reduce its export (Hyndes et al., 2016). This would likely result in a decrease of AEM occurrence and abundance in recipient ecosystems and, therefore, reduce the subsidies this material provides in those ecosystems.

Increases in herbivory will also shift the production of macrophytodeposit to feces (Zarco-Perello et al., 2019),

drastically changing the nature and the size of exported detritus to dissolved and fine particulate matter. This would lead to a decrease in the value of AEM as both habitat and food for fauna since seagrass-based feces do not have the same nutritive characteristics or composition than senesced detritus (Velimirov, 1984; Velimirov, 1987), and would not provide the habitat structure that senescing leaves provide. Furthermore, while larger sections of seagrass leaves are likely to be released from the foraging activities of herbivores, the release and export of these green leaves are likely to occur at different rates, times and amounts compared to the seasonal release of senescing leaves under normal temperate conditions. Furthermore, these exported green leaves would be at a lower level of decomposition compared to senesced leaves and potentially less palatable. In *P. oceanica* AEM, green leaves are generally not found in gut content of AEM macrofauna, except the crab *Lissocarcinus navigator* (Remy et al., 2018). Thus, the functional tropicalization of seagrass meadows would likely result in modified amounts and quality of macrophytodebris exported to other systems, deeply affecting AEM occurrence, location, abundance, quality as habitat, and food webs in recipient systems.

Seagrass leaf litter is initially processed in the seagrass meadow itself, when released leaves fall and lay between standing shoots. Decomposition by microbes, and consumption by animals, start in the meadow during the senescing process (Harrison, 1989). Increasing temperature is likely to increase microbial metabolism leading to a greater generation and export of dissolved versus particulate organic material in macrophyte habitats (Sävström et al., 2016). For example, a 5°C temperature increase has been shown to boost the short term decomposition rates of *Zostera muelleri* from 0.04 to 0.06 d⁻¹ and this effect increases with decomposition progress (Trevathan-Tackett et al., 2020).

Detritivores are also present in the litter laying in donor meadow (e.g. Gambi et al., 1992; Como et al., 2008 for *P. oceanica* system). Like microbes, increasing temperatures are likely to increase the metabolism of temperate detritivores in seagrass meadows, thereby increasing the consumption rate of litter, and facilitating its decomposition. Presence of detritivore is shown to boost seagrass detritus mechanical degradation (e.g. Costa et al., 2019). A shift to more tropical conditions will also likely affect the processing of detritus by macrofauna. It appears that many invertebrate species in tropical seagrass meadows depend on seagrass detritus (Vonk et al., 2008a). Additionally, tropical seagrass meadows are massively colonized by different burrowing crustaceans (e.g. Thalassanidae shrimp) (Vonk et al., 2008b; Kneer et al., 2008). Many of those crustaceans either use detritus as a food source which is found in the sediment or they actively collect plant material from the area surrounding their burrow openings (Kneer et al., 2008). The burrowing shrimps *Neaxius acanthus* and *Alpheus macellarius* have been shown to collect in their burrows an amount of seagrass leaf material

corresponding to more than 50% of the leaf production in a tropical meadow (Vonk et al., 2008b). Native burrowing shrimp are also present in the Mediterranean Sea where they also exhibit such behavior regarding macrophyte detritus (Papaspyrou et al., 2004), but their impact on litter processing is probably lower than in tropical regions considering their lower abundance and size. Presently, to our best knowledge, tropical burrowing shrimp have not been recorded in the Mediterranean Sea, but they could occur in the near future through either their range extensions *via* tropicalization or aquarium introductions. This could lead to an increase of litter processing in the meadow itself, mimicking the functioning of tropical seagrass meadow and therefore reduce the amount of exported detritus.

Increased *in situ* degradation rates and detritus fragmentation by fauna will decrease the amount of macrophytodebris exported from seagrass meadows and, therefore, alter the occurrence and abundance of AEM in other systems. It will also affect the quality of the exported material as the seagrass material will be more degraded and fragmented and will contain less epiphytes, leading to material more impoverished in nutrients. More degraded and fragmented material devoid of epiphytes are potentially less valuable as habitat or food sources for associated fauna in those recipient systems.

Ultimately, tropicalization could lead to a shift in meadow composition from temperate to tropical seagrass species (Hyndes et al., 2016). The tropical seagrass *Halophila stipulacea*, a Lessepsian species, has been observed in the southern part of Mediterranean Sea since the opening of the Suez Canal. It has progressively settled northward and has been frequently observed in Ionian Sea since the 1990s, detected in Tyrrhenian Sea in 2006 (Di Genio et al., 2021), and is presently reaching northwestern Mediterranean (Winters et al., 2020; Di Genio et al., 2021; Thibaut et al., 2022). In Cannes harbor (NW Mediterranean Sea), *H. stipulacea* was probably introduced *via* big yachting coming by Suez Canal and are establishing stable population which could indicate that conditions are now more favorable for long-term population establishment (Thibaut et al., 2022). *H. stipulacea* is presently the only non-native seagrass in the Mediterranean Sea (García-Escudero et al., 2022). It generally colonizes habitats devoid of native seagrass, forms mixed meadows with *C. nodosa* (Winters et al., 2020), or colonizes dead mat of *P. oceanica* (Thibaut et al., 2022). Presently, *H. stipulacea* is not replacing any native seagrass species, but this may occur when temperatures rise beyond the thermal tolerances of the native species (Wesselmann et al., 2021). In comparison, this invasive seagrass has already spread rapidly and displaced several native macrophytes in eastern Caribbean islands (Winters et al., 2020). *H. stipulacea* is a small seagrass species, compared to *P. oceanica* and *C. nodosa*, the two main native Mediterranean species. The lower biomass and a higher leaf renewal rate (Duarte 1991), which reduce epiphytic load (Borowitzka et al., 2006) will alter the amount and timing of detritus export, and the morphological difference in the leaves of

H. stipulacea will reduce the 3D-structure of the AEM habitat. Also, the higher levels of decomposition in tropical seagrasses (Hyndes et al., 2014), at least partly reflecting the more efficient recycling of detritus in the meadow itself (Vonk and Stapel, 2008; Hyndes et al., 2014), will reduce the export of seagrass detritus. While there is no evidence of this shift to tropical species in southern Western Australia yet, Hyndes et al. (2016) predicted that several tropical species, including *Cymodocea rotundata*, *Enhalus acoroides*, and *Thalassodendron ciliatum*, will extend their southern limit by over 500 km, and temperate species such as *Amphibolis antarctica* or *Posidonia* spp. will reduce their distribution ranges by 200 km by 2100. This is predicted to result in the tropical system replacing the current temperate seagrass ecosystem, and altering the processing and export of detritus as stated above.

From the above, shifts to tropical species, along with increased processing of litter within the meadow via microbial degradation, burrowing organisms or other detritivores is likely to decrease macrophytodebris export, and, therefore occurrence and quantity of AEM. Nevertheless, global change has very complex consequences – not only tropicalization – and for example, the predicted increase of storm and wind gusts frequency could increase this export and counteract the accelerated *in situ* processing (i.e. decomposition or consumption) of litter. The influence of these two opposite trends should be determined by the match (or the mismatch) between leaf fall period (or cycle) and occurrence of export.

Shifts in other forms of detritus across the seascape

The composition of AEM is often very heterogeneous and, depending on the proximity of the recipient system to different forms of donor material (i.e. macroalgae, salt marshes or mangroves) or local conditions that contribute to its composition and retention (Mancinelli and Rossi, 2002; Wernberg et al., 2006; Mascart et al., 2015). The AEM composition and diversity influences the diversity of the communities inhabiting them (Mancinelli and Rossi, 2002; Bishop and Kelaher, 2013; Haram et al., 2020) and the food web functioning (Vonk et al., 2016). For example, the addition of detritus from the invasive *Caulerpa taxifolia* drastically changed the macroinvertebrates in soft sediments of estuaries of eastern Australia (Taylor et al., 2010). Furthermore, considering the role of drift macroalgae as raft for benthic invertebrates (Thiel and Gutow, 2005), the nature of drift macroalgae can influence the composition of AEM macrofauna (Baring et al., 2014). Absence of drift macroalgae in AEM could lead to fauna impoverishment by the absence of new colonizers. This could happen where overgrazing by new tropical grazers leads to declines of loss of macroalgae standing stock in donor systems (Vergés et al.,

2004b). Knowledge of vegetated benthic communities beyond seagrass meadows at the seascape level (e.g. macroalgae habitats, saltmarsh or mangroves) is therefore essential to understand the values and functioning of AEM (Ricart et al., 2015).

In the Mediterranean Sea, macroalgae assemblages on rocks are deeply affected by invasive species, which are often of tropical origin (Piazzi and Balata, 2009). Changes of macroalgae in hard substrate habitats have a direct effect on the material found in AEM. Multi causal and long-term trends in the loss of native forests of the macroalgae *Cystoseira* spp. in the Mediterranean Sea (Piazzi and Ceccherelli, 2017) have resulted in these algae no longer being present in the AEM (G. Lepoint, personal observation in Revellata Bay, Corsica), and being replaced as drift algae in AEM by other native brown algae or invasive species. Similar to seagrasses, another threat on macroalgae biota is the increase in herbivory due to invading herbivorous fishes. Both in Western Australia and Mediterranean Sea, they have already had drastic impacts on macroalgae habitats leading to an increase of standing stock consumption and sometimes creating barrens dominated by encrusting corallinaceae (Vergés et al., 2014b; Zarco-Perello et al., 2017). Replacement of macroalgae habitats by barrens will affect AEM composition by decreasing the contribution of drift macroalgae to detritus accumulations. Absence of macroalgae in AEM may affect the quality of habitat and food for AEM macrofauna. For example, in Western Australia, the kelp *Ecklonia radiata* provides a critical food source for the food web in AEM of surf zones comprising both seagrass and kelp (Crawley et al., 2009), yet this kelp is being lost from reefs in the region due to marine heat waves (Wernberg et al., 2016). While *Sargassum* spp. may replace kelp on reefs and can contribute to the surf-zone food web (Crawley and Hyndes, 2007), it is unclear how much of this material will contribute to the AEM in the surf zone.

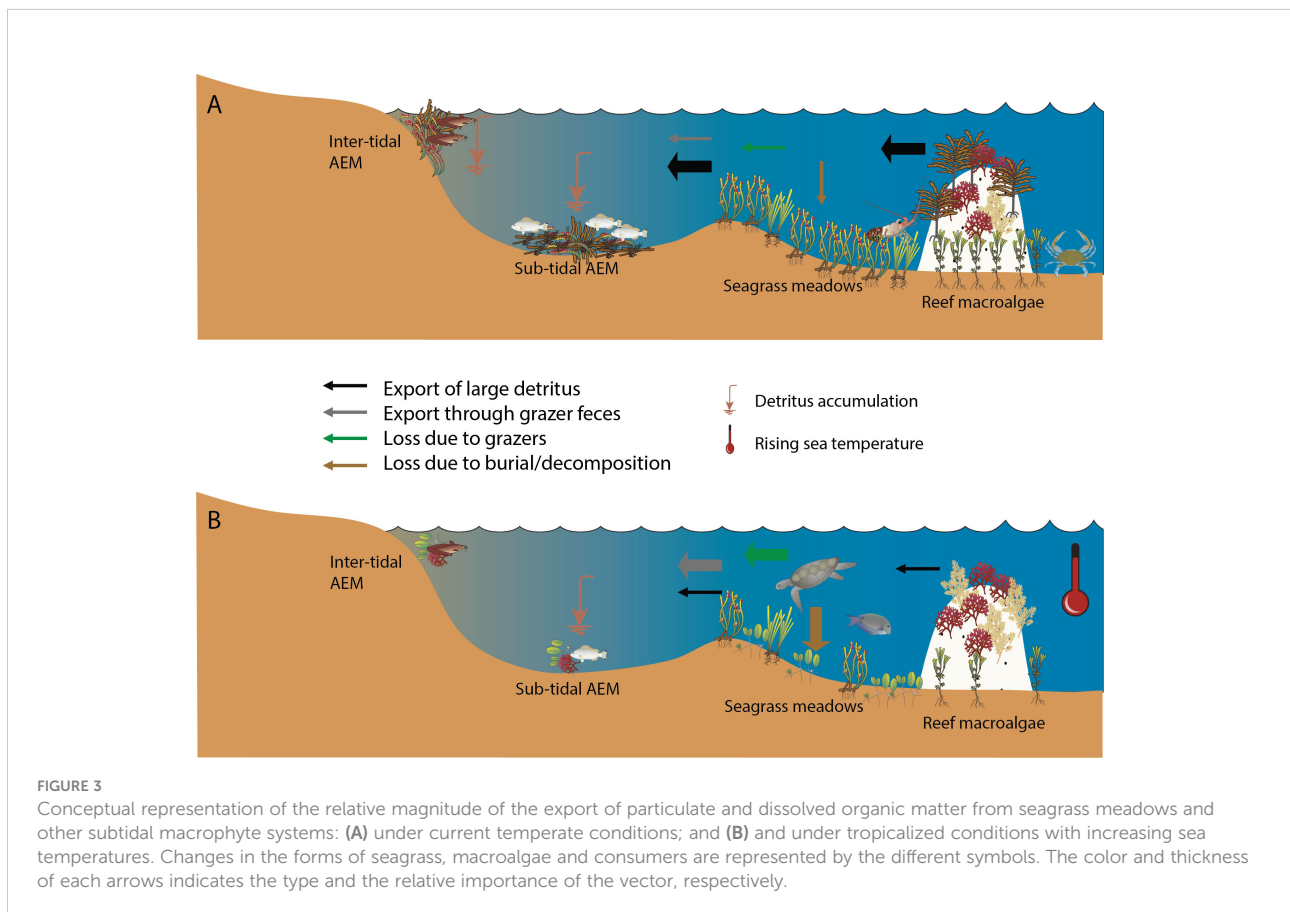
Mediterranean seagrass meadows (i.e. *P. oceanica* and *Cymodocea nodosa*) are also invaded by the green macroalga *Caulerpa cylindracea*, which was introduced via ballast water or aquarium trading (Piazzi et al., 2016 for a review). This is an endemic species from southwestern Australia that showed high development capacity throughout the central and western Mediterranean Sea at the end of the past century (Piazzi et al., 2016). Presently, *C. cylindracea* is often restricted to the meadow periphery in healthy meadows, but dead matte of *P. oceanica* meadow and anthropized areas are often heavily colonized (Piazzi et al., 2016). Where *C. cylindracea* occurs, *Caulerpa* fragments are found in *Posidonia* AEM (G. Lepoint, Pers. Obs. in Calvi Bay).

Changes in contributions, but also specific diversity and quantity of dead seagrass leaves vs drifted macroalgae will probably change AEM food web topology and energy fluxes. Influence of AEM composition on food web structure is not well known but, as stated before, living algae material (i.e. micro and macro epiphytes, decaying drifted macroalgae) is often preferred

over dead seagrass material (Hyndes and Lavery, 2005), even if dominant fauna component are able to use dead seagrass and respond positively to dead material pulse (Remy et al., 2017; 2021). A relative increase of macroalgae contribution (or a relative decrease of dead seagrass contribution) would lead to green AEM food web and to select more herbivorous species. Nevertheless, many species found in subtidal AEM, particularly gammarid amphipods, are relatively plastic regarding their diet and are found in AEM whatever their composition. These more plastic and opportunist species may adapt their diet to new AEM composition. Nevertheless, changes in the source habitat may also affect AEM food web in two other ways. Firstly, many tropical algae are often better defended against herbivory (e.g. Demko et al., 2017) and, therefore, could be less integrated in the AEM food web. Change in macroalgae sourcing *via* the replacement of native species by tropical invaders is therefore likely to affect potential food sources available for AEM inhabitants, food web structure and detritus processing. Secondly, herbivory increase in tropicalized seagrass meadows would lead to an increase of feces export relative to macrophytodebris export. This could have consequence for AEM as habitat but also on AEM food web as fecal material do not have the same dietary quality than macrophytodebris (see above).

Conclusions and perspectives

There is considerable evidence that seagrass meadows are already shifting to another state under the pressure of global change (Strydom et al., 2020), and this rate of change is likely to increase in the future (Hyndes et al., 2016). In temperate areas, tropicalization of seagrass communities and/or functioning is one potential scenario of these changes. Temperate seagrass beds are recognized as a net autotrophic ecosystem, exporting variable parts of its primary production to other marine and coastal terrestrial systems. Here, we show that shifts in the quantity and quality of exported detritus is likely to impact the functioning of AEM in recipient ecosystems across the coastal seascape. AEM could change either through: (1) declines in biomass or loss of seagrass directly due to increased ocean temperatures (e.g. *via* marine heat waves) or increased herbivory from tropicalized herbivores shifting seagrass export to dissolved or finer particulate material; (2) increased degradation and processing of seagrass detritus within seagrass meadows leading to reduced export; (3) replacement of large temperate seagrass species with smaller tropical seagrass species with different leaf cycling, or macroalgae species; and/or (4) loss or changes to macroalgae species in neighboring habitats that export detritus (Figure 3B). These processes will alter the amount, composition, quality,



timing and frequency of inputs of detritus into ecosystems that rely on AEM as trophic subsidies, which will alter the suitability of AEM as habitat and food for invertebrates. In addition, changes in exported material associated with those processes could decrease “rafting” of invertebrates into recipient habitats, thereby altering recruitment of invertebrates, while the invasion of tropical opportunistic invertebrates could alter the invertebrate community structure of AEM. It is possible that present dominant species resist these invasions considering these dominant species are able to cope with a very large range of environmental conditions and are able to adapt to diverse AEM type and composition.

Ultimately, tropicalization of temperate seagrasses will alter the export of seagrass detritus, and as a result, the AEM food web will change too as food web topology and energy flow are largely linked to AEM composition. Notably, this will be largely influenced by the relative proportion of macroalgae vs seagrass detritus (Crawley et al., 2009; Haram et al., 2020; Remy et al., 2021). Increases of macroalgae contributions could shift this brown food web greener than presently when AEM has been dominated by dead seagrass leaves. However, beyond beaches and to a lesser extent surf zones, we know very little about the biodiversity and functioning of AEM in marine systems. Yet, AEM is known to accumulate in a range of habitats across the coastal seascapes and offshore systems (Table 1). Furthermore, there has been very limited advances in our knowledge on export rates of seagrass detritus since the review of Heck et al. (2008). Accumulations of kelp detritus in sub-tidal areas have recently received much more attention, showing their importance as habitats, delineating complex associated food webs and underlining their role as trophic subsidies for coastal areas (Duggins et al., 2016; Feehan et al., 2018; Filbee-Dexter et al., 2018; De Bettignies et al., 2020; Frontier et al., 2021). We therefore recommend far greater research effort into determining export rates of seagrass detritus from temperate seagrass meadows, and the role of AEM in a range of sub-tidal coastal and offshore

systems. This will allow for a greater understanding of the flow-on effects of tropicalized seagrass ecosystems beyond the systems themselves.

Author contributions

All authors listed have equally contributed to the work and approved it for publication.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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