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Seagrass-macroalgal interactions in a changing ocean

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The number of reports highlighting the services provided by seagrass beds continues to be matched by those reporting on local seagrass declines across the world coastlines. Among the many factors driving the fate of seagrass beds, this Mini Review focuses on the interactions between seagrasses and algae, more specifically, macroalgae. Seagrasses are known to respond to sudden increases in co-occurring macroalgae, and the ongoing warming of ocean waters suggests that these interactions are most likely to grow in frequency and possibly in intensity in the decades ahead. What remains unclear is the nature (positive, neutral, negative) and the local outcome of those interactions. We examined the published evidence on explicit seagrass-algal interactions and found that in most cases these interactions have been negative, with seagrass species most often found at a competitive disadvantage with regards to macroalgae. Rising ocean temperatures are likely to add to this imbalance as at least some studies already suggest that the negative effects of macroalgae and warming are either additive or synergistic. The further examination of these effects will help predict likely future scenarios and aid in the prioritization of conservations efforts.

KEYWORDS

seagrass beds, macroalgae, interactions, resources, global warming

1 Introduction

Seagrass beds are among the most efficient carbon sinks (Duarte et al., 2010; Gattuso et al., 2018), are highly productive (Koopmans et al., 2020) and, as foundation species, influence the structure, and function of coastal communities and ecosystems. Seagrass beds also provide a variety of services including stabilization of the seabed, nutrient transfer, buffering of the negative effects of eutrophication, water oxygenation through photosynthetic activity, and habitat for the settlement and nursery of multiple invertebrates and fish (Costanza et al., 1997; Spalding et al., 2007; Heck et al., 2008; Chung et al., 2011; Smale et al., 2013; Thomson et al., 2015; Teagle et al., 2017; Surugiu et al., 2021). Unfortunately, most of these critical ecosystem services are threatened by the worldwide decline in seagrass meadows resulting from the warming of the oceans, among a series of other climate events (e.g., Orth et al., 2006; Waycott et al., 2009; Valdez et al., 2020). Ocean warming is known to cause species' ranges and distribution patterns to shift (Breeman, 1988; Parmesan and Yohe, 2003), with plant and seaweed local communities becoming reorganized due to the addition and loss of species (Wootton et al., 2008; Harley, 2011). When not in excess, macroalgae coexist with seagrass meadows and provide support to community and ecosystem secondary productivity. For instance, drift algae in the Northern Gulf of Mexico have been found to positively influence seagrass-related nekton recruitment and biomass (Correia and Smee, 2022; Correia et al., 2022b). However, the recent IPCC Special Report on the Ocean and Cryosphere in Changing Climate (Bindoff et al., 2019) reported a widespread increase in coastal stress levels, noting that since 1980, shifts in seaweeds and harmful algal blooms, that often interact negatively with seagrass meadows, have also increased in range and frequency. Rather than subside and normalize, this temporal pattern is more likely to intensify in the future.

Competitive success among primary producers is heavily dependent on stress sources and availability of resources (Harley et al., 2012), including among others light availability and attenuation (see Minguito-Frutos et al., 2023). The behavior and physiology of seagrasses is often dictated by their ability to photosynthesize and grow in the presence of algal shading (Brun et al., 2003), their efficiency during nutrient uptake (Alexandre et al., 2021), their ability to avoid harmful effects mediated by changes in the sediment (e.g., pH; Mvungi et al., 2012), and their response to indirect interactions with epiphytes (e.g., Irlandi et al., 2004). It follows that drastic changes in local algae and algal beds are likely to alter the fitness of seagrasses, in the same way that has been repeatedly demonstrated for algal-coral interactions (e.g., Carpenter et al., 2008; Anton et al., 2020). In a warming ocean, the outcome of seagrass-algal interactions is equally important, yet the mechanisms mediating their dynamics have not gathered the same attention. This article aimed to explore mechanisms and local outcomes from the examination of the literature available on seagrass-macroalgal interactions. Assuming such interactions continue to increase in frequency and possibly in severity, as most forecasts suggest, their examination may help predict likely future scenarios and aid on the prioritization of conservations efforts (Nordlund et al., 2018; He and Silliman, 2019).

This Mini review examined 46 peer-reviewed articles, deemed representative from geographic regions where seagrass and macroalgal beds coexist and their interactions have been documented. Some coastal areas are known to support extensive seagrass meadows and macroalgae (e.g., sites in Kenya and other coastal areas in Africa; e.g., Coppejans et al., 1992), but as this overview suggests, they are still affected by a geographic gap in the literature (see Figure 1). The articles summarized in Table 1, with their key features and outcomes, were found using relevant keywords such as "seagrass," "macroalgae," "seaweed," "seagrass interactions,"' and "algal-seagrass interactions," among others, from databases, networks, and search engines available to us (e.g., OneSearch, Google Scholar, ResearchGate), and through examination of cross-references within multiple articles. Although we loosely use the term alga or algae in Table 1, we are in all cases referring to any type of marine macroscopic algae (macroalgae) or seaweed, excluding any forms of microalgae that may be associated with, for instance, blooms. The same applies to the paragraphs below detailing and discussing the results of the brief overview.

2 The overwhelming frequency of negative interactions

Nearly 80% of the studies examining interactions between seagrasses and macroalgae have found evidence of negative interactions, with a clear imbalance against seagrasses: most of these studies found that macroalgae had direct or indirect negative effects on seagrasses (e.g., Ceccherelli and Cinelli, 1997; Ceccherelli and Campo, 2002; Alexandre et al., 2017, 2021; Bittick et al., 2018; among several others). Nonetheless, a few studies have also found negative impacts of seagrasses on macroalgae (Davis and Fourqurean, 2001; Alexandre et al., 2017; Menicagli et al., 2021). Harmful effects on seagrasses were often associated with losses on a competition for light (De Villele and Verlaque, 1995; Dumay et al., 2002; Irlandi et al., 2004; Hessing-Lewis et al., 2011; Zribi et al., 2023) or through light reduction via shading (Hauxwell et al., 2001, 2003; Liu et al., 2005; Eklöf et al., 2006; Lamote and Dunton, 2006; Huntington and Boyer, 2008; Van Katwijk et al., 2010; Homer et al., 2011; Mvungi et al., 2012; Hessing-Lewis et al., 2015; Han et al., 2016; Correia et al., 2022a). Shading by macroalgae has also been associated with the creation of unfavorable biogeochemical conditions (Hauxwell et al., 2001; Van Katwijk et al., 2010; Mvungi et al., 2012; Hessing-Lewis et al., 2015). As a result, seagrass under chronically reduced light conditions have experienced a decline in biomass (Eklöf et al., 2006; Huntington and Boyer, 2008; Hessing-Lewis et al., 2011, 2015; Han et al., 2016), shoot density (Hauxwell et al., 2003; Huntington and Boyer, 2008; Hessing-Lewis et al., 2011, 2015), canopy height (Correia et al., 2022a), leaf elongation rates (Zribi et al., 2023), metabolic efficiency (Irlandi et al., 2004), photosynthetic efficiency (De Villele and Verlaque, 1995; Liu et al., 2005; Lamote and Dunton, 2006; Mvungi et al., 2012; Zribi et al., 2023), and growth rates (Hauxwell et al., 2001; Huntington and Boyer, 2008; Homer et al., 2011). In addition, due to algal growth, some seagrasses have seen their vegetative development modified (De Villele and Verlaque, 1995; Dumay et al., 2002; Van Katwijk et al., 2010; Hessing-Lewis et al., 2011) or have been harmed with a decline in shoot density (Ceccherelli and Cinelli, 1997; Taplin et al., 2005), shoot biomass (Taplin et al., 2005), metabolic efficiency and, ultimately, survival rates (De Villele and Verlaque, 1995; Hauxwell et al., 2001; Martínez-Lüscher and Holmer, 2010; Homer et al., 2011).

Seagrass-macroalgal negative interactions have also resulted from the competition for nutrients (Ceccherelli and Cinelli, 1997; Davis and Fourqurean, 2001; Homer et al., 2011; Alexandre et al., 2017, 2021). While a few studies found that seagrass nutrient uptake rates were negatively affected by the presence of algae (Alexandre et al., 2017, 2021), at least one study has found that seagrass could also harm the nutrient uptake of macroalgae (Alexandre et al., 2017). Other studies have found that has a result of nutrient competition, seagrasses have been affected by a reduction in growth rates (Homer et al., 2011), shoot density (Ceccherelli and Cinelli, 1997), and short-shoot size (Davis and Fourqurean, 2001). The alternative outcome (i.e., a reduction in macroalgal growth and thalli size) has been documented in one study only (Davis and Fourqurean, 2001). Partially related phenomena, such as algal decomposition, have been found to account for several indirect impacts on seagrasses (Homer and Nielsen, 2007; Han et al., 2016). Algal decomposition increased nitrogen and reduced carbon content of seagrasses, rapidly impacting their C:N ratio (Han et al., 2016). The same factor has been shown to increase sulfide pools in the sediment, invading seagrass roots and indirectly causing a decline in their growth rates (Homer and Nielsen, 2007).

A frequent focus of studies documenting negative interactions is the role of sudden macroalgal blooms on seagrasses (Nelson and Lee, 2001; Brun et al., 2003; Cummins et al., 2004; Stafford and Bell, 2006; Sugimoto et al., 2007; Hessing-Lewis et al., 2011, 2015; Olyarnik and Stachowicz, 2012; Bittick et al., 2018; Santos

FIGURE 1
Map outlining the geographic distribution of the 46 studies used in the Mini review and summarized in Table 1. The numbers correspond to those cited at the bottom of Table 1.

et al., 2020). These studies have found that as a result of a bloom, seagrasses have experienced declines in shoot density (Nelson and Lee, 2001; Sugimoto et al., 2007; Hessing-Lewis et al., 2011, 2015; Olyarnik and Stachowicz, 2012; Bittick et al., 2018), shoot height (Sugimoto et al., 2007; Hessing-Lewis et al., 2011), shoot production (Olyarnik and Stachowicz, 2012), seedling density (Sugimoto et al., 2007), foliage cover (Santos et al., 2020), elongation rates (Brun et al., 2003), biomass (Hessing-Lewis et al., 2011, 2015; Olyarnik and Stachowicz, 2012), growth rates (Sugimoto et al., 2007), and survival rates (Olyarnik and Stachowicz, 2012). Additionally, more persistent macroalgal blooms have increased seagrass fragmentation (Santos et al., 2020) and in some instances have allowed macroalgae to replace seagrass (Stafford and Bell, 2006). Decomposition following algal blooms has also been linked to a decrease in seagrass biomass (Cummins et al., 2004). A few additional studies have reported negative seagrass-algal interactions but have not conclusively identified the causing or mediating mechanisms (Ceccherelli and Campo, 2002; Taplin et al., 2005; Martínez-Lüscher and Holmer, 2010; Thomson et al., 2013; Kalokora et al., 2021; Menicagli et al., 2021; Firth et al., 2023).

3 Evidence of seaweed-seagrass positive and neutral interactions

Although negative interactions dominate the relationships between seagrasses and macroalgae, there are instances in which positive interactions have been also documented (Ceccherelli and Cinelli, 1999; Ceccherelli and Campo, 2002; Irlandi et al., 2004; Hessing-Lewis et al., 2011; Alexandre et al., 2017; Pereda-Briones et al., 2019; Kalokora et al., 2021; Correia et al., 2022a; Emmclan et al., 2022). While most of these studies have shown that seagrasses could benefit from the presence of macroalgae (Ceccherelli and Campo, 2002; Irlandi et al., 2004; Hessing-Lewis et al., 2011; Pereda-Briones et al., 2019; Kalokora et al., 2021; Emmclan et al., 2022), a couple of studies found the opposite, i.e., a benefit primarily toward the macroalgae (Ceccherelli and Cinelli, 1999; Alexandre et al., 2017; Correia et al., 2022a). The presence of macroalgae has been causally associated with increased seagrass shoot density (Ceccherelli and Campo, 2002), enhanced growth (Kalokora et al., 2021) positive changes in seagrass morphology (Ceccherelli and Campo, 2002; Emmclan et al., 2022), and added protection from low-tide associated stressors, excessive epiphyte cover, hydrodynamic disturbance, and ocean warming (Irlandi et al., 2004; Hessing-Lewis et al., 2011; Pereda-Briones et al., 2019). Meanwhile, the presence of seagrasses has been shown to enhance nutrient uptake in macroalgae (Alexandre et al., 2017), increase macroalgal density (Correia et al., 2022a), and provide protection against currents, tides, and hydrodynamic disturbance (Ceccherelli and Cinelli, 1999). Most of these positive interactions have been reported from off-shore, more marine-influenced zones (Ceccherelli and Cinelli, 1999; Hessing-Lewis et al., 2011), and have taken place between species of the families Zosteraceae (Ceccherelli and Campo, 2002; Hessing-Lewis et al., 2011; Alexandre et al., 2017) and Ulvaceae (Hessing-Lewis et al., 2011; Alexandre et al., 2017; Emmclan et al., 2022).

TABLE 1 A compilation of studies assessing the interactions between seagrasses and macroalgae, identifying studies with numbers (#), and providing details on location, approach [observational (O) or experimental (E)], time span, species, main design features, main responses measured, and main results reported.

#	Location	Approach/time span	Seagrass	Alga	Design	Response	Main results
1	Portugal	E 0.5 hr.	*Z. noltei, Z. marina and C. nodosa*	*U. rotundata, D. dichotama, C. decorticatum*	Incubation of species individually and combined at increasing nutrient levels	Percent ^{15}N enrichment of tissues	In most combinations, seagrass had higher N surge uptake than seaweed. This suggested that uptake interaction effects can be positive or negative
2	FL/USA	E 13 mo.	*T. testudinum*	*Anadyomene* sp.	Incubation of species individually and combined at various nutrient levels	Nutrient uptake rate	Individual seagrass and algae had similar NH_3 surge uptake, but seagrass had a higher PO_4 uptake, and its PO_4 uptake decreased in the presence of algae
3	CA/USA	E 10 wk.	*Z. marina*	*Ulva* sp.	Algal additions (6 different densities)	Shoot density, blade growth rate and epiphyte load	With higher algal abundance, shoot density and epiphyte loads declined linearly or non-linearly.
4	Spain	E 1 yr.	*Z. noltii*	*U. rigida*	Algal shading measured in lab and field experiments	Seagrass growth and internal C, N and P, DOC alga-seagrass transfer	Shading reduced (not consistently) elongation rates and gross production. However, some algal DOC was transferred to seagrass
5	Italy	E 14 mo.	*C. nodosa* and *Z. noltei*	*C. racemosa*	Algal presence and absence	Shoot density and flower reproductive shoot density	With algae: *C. nodosa* shoot density declined while *Z. noltei* density rose. Flower/reproductive shoot density was significantly higher
6	Italy	E 13 mo.	*C. nodosa*	*C. taxifolia*	Nutrient addition and neighbor presence/removal	Blade/shoot density and blade/leaf size	With alga: No effect on seagrass or algal density. Co-occurring species had larger leaf size than individual species
7	Italy	E 13 mo. / 10 wk.	*P. oceanica*	*C. taxifolia*	Exposure of algae to 10-100% seagrass densities and control and mimic canopies	Algal blade length	With seagrass: Positive effects were greatest at site where seagrass density was lower. Shading entailed a cost
8	Italy	E 13 mo.	*C. nodosa*	*C. taxifolia*	Nutrient control/addition and neighbor presence/removal	Shoot/blade density and length	Algae and seagrass were not affected by either treatment. Where co-occurring, both species were larger in size
9	USA	O 5 mo.	*T. testudinum, S. filiform, others*	Drift algae (various spp)	Five estuaries: sites with more than 50% seagrass cover were assessed	Abiotic conditions, algal biomass, and seagrass cover, abundance and morphometrics	Drift algae was found to be most dense when associated with high percent cover of seagrasses with intermediate canopy heights
10	Australia	E 12 wk.	*R. megacarpa* and two others	*E. intestinalis*	Algal addition vs natural, exclusion and fenced controls	Seagrass biomass and benthic invertebrate structure	Macroalgae began to decompose after 3 mo. causing dramatic declines in seagrass biomass and infauna
11	FL/USA	E 4 mo.	*T. testudinum*	*H. incrassata*	Algal removal, addition (2×) and seagrass removal	Changes in growth rate and biomass	With seagrass: algae thalli size and growth rate decreased. With algae: no impact on seagrass
12	France	O 1 yr.	*P. oceanica*	*C. taxifolia*	Two sites: with and without algae	# of adult and intermediate leaves per shoot, width of adult and intermediate leaves, other leaf measures	Algae invaded sparse seagrass on early spring, causing a decline in #, width, and longevity of leaves. In the longer-term, dense seagrass beds were the most resistant

(Continued)

TABLE 1 (Continued)

#	Location	Approach/time span	Seagrass	Alga	Design	Response	Main results
13	France/ Italy	O 1 yr.	*P. oceanica*	*C. taxifolia and C. racemoseosa*	Three levels of interactions assessed as well as two sites without seagrass	# of adult and intermediate leaves, leaf biometry, A coefficient and leaf index	Interaction modified seagrass vegetative development but not the # of leaves per shoot or belowground tissue production
14	Zanzibar, Tanzania	E 11 wk.	*E acoroides*. T. hemprichii	*E. denticulatum*	Off-bottom farm pots over seagrass beds	Seagrass soot density, length, and leaf growth	Seaweed farming reduced above-ground seagrass biomass by 40%.
15	Malaysia	O Unspecified	Hydrochari-taceae	*U. reticulata*	Two sites: with and without algae	Morphometry of shoots	With algae: seagrass had higher leaf dimensions and metabolite contents
16	England	E 4 yr.	*Z. marina*	*S. muticum*	Seagrass with and without macroalgae	Seagrass shoot density, dry weight, phenolic compounds	With algae, seagrass density and phenolic contents decreased but experienced no effect on nutrient
		E 3-4 wk.				Nutrient partitioning, photosynthetic ability/growth	Partitioning
17	Australia	O/E 3 mo.	*P. australis* and *Z. capricorni*	*C. taxifolia*	Algal transplants in sparse and dense seagrass beds	Seagrasses grow rate	Alga did not affect the growth of *P. australis* but may have contributed to decline of *Z. capricorni*
18	China	E 6 wk.	*Z. marina*	*U. pertusa*	Algal addition and removal, nutrient addition and control	Seagrass N and C contents, morphology and structure	Algal addition reduced below-ground biomass. Nutrients lowered above/below ground biomass ratio
19	MA/USA	E ~3 mo.	*Z. marina*	Various algae (canopies)	Two sites: high and low land derived N rates. Algal removal and addition.	Shoot density and growth rate	With higher algal canopy height: seagrass grew less and its loss increased. Without algae: seagrass density and aboveground net production rose
20	MA/USA	O 1 yr.	*Z. marina*	*C. vagabunda* and *G. tikvahiae*	Four sites: Two with low land-derived N loads and two with higher N loads	Shoot density, aboveground biomass, leaf, rhizome and root features and production	Algal biomass was highest in estuaries with high N load, where seagrass nearly disappeared. At estuaries with low N-load, loss was minor
21	OR/USA	O 5 yr.	*Z. marina*	Ulvoid algae	Monitoring of four estuaries	Algal biomass and seagrass patterns	Southern estuaries had 30× algal biomass, but seagrass decline lacked clear temporal patterns. Main drivers: sea upwelling and local conditions
22	OR/USA	E 4 mo.	*Z. marina*	*U. linza* and *U. lactuca*	Algal control, removal, addition and mimics. Also, nutrient control and addition	Seagrass shoot density, shoot and sheath length	Lab: seagrass had strong negative response to nutrient and algal addition. Field: only weak evidence of negative responses in seagrass
23	OR/USA	E 22 mo.	*Z. marina*	*U. linza* and *U. lobata*	Pulse addition and removal of algae	Seagrass density and biomass	Algal blooms did not trigger seagrass biomass declines in marine area. Experimental algal addition affected seagrass in riverine areas only
24	Denmark	E 4 wk.	*Z. marina*	*G. vermiculo-phylla*	Temperature manipulation, macroalgae additions (1× and 2.25×) and control	Seagrass growth and mortality	Independently, algal cover had no effect on seagrass, but a negative (non-significant) effect was detected at the highest temperature

(Continued)

TABLE 1 (Continued)

#	Location	Approach/time span	Seagrass	Alga	Design	Response	Main results
25	Denmark	E 3 wk.	*Z. marina*	*C. rubrum* and *C. linum*	Algal additions (1× and 2×) and control	Seagrass growth rates, water oxygen concentrations and sediment H_2S concentrations	After 3 wk. combined effects of water column anoxia and high H_2S invasion caused significant reductions in seagrass growth rates
26	Australia	E 5 wk.	*H. ovalis*	*G. comosa*	Seagrass exposed to 3 algal densities at 3 temperatures	Seagrass biomass and other measurements	Strong negative effect on seagrass. Temperature effect was additive and synergic. Building up of pore water DS mediates negative effect.
27	CA/USA	O/E 3 mo.	*Z. marina*	*Gracilariopsis* sp.	Algal addition (2 densities), removal and control	Seagrass number and density, sediment properties, shoot density and growth rate	Significant negative relationship between seagrass shoot density and algal biomass
28	FL/USA	O 1 yr.	*T. testudinum*	Drift algae	Algae removal and control	Seagrass cover and residence time	High drift algae cover reduced seagrass above-ground biomass by 3 mo. But not afterwards.
		E 1 wk-6 mo.	*T. testudinum*	*Laurencia* sp., Ceramium sp. and *Polysiphonia* sp.	Algal addition/removal and control. Epiphyte removal	Seagrass above and below-ground biomass and shoot density and growth rates	Drift algae did not affect seagrass growth, but epiphytes did and because they were reduced by drift algae, there was evidence of a positive effect
29	Zanzibar, Tanzania	O 2 mo.	*T. hemprichii*	*Halimeda spp.*	Comparison of sites with distinct cover of seagrass and algae	Seagrass and algal growth and production rates	Low and mid algal cover enhanced seagrass growth, while presence of seagrass reduced the productivity of algae but raised $CaCO_3$ content
30	TX/USA	E 5 wk.	*T. testudinum*	Drift algae	3 light treatments and control	Fluorescence parameters, chlorophyll indices and	Seagrass fluorescence quantum yield declined when exposed to chronic reduction in irradiance by drift
		E 4 wk.	*T. testudinum*	Drift algae	Algal addition and removal	sediment H_2S	algae and increase in sediment porewater H_2S: Physiological stress due to light deprivation
31	Brazil	E 2 yr.	*R. maritima*	*Rhizoclonium spp and drift algae*	Addition of drift algae on seagrass meadows	Seagrass above and below ground biomass, and demographic parameters	Impacts on seagrass biomass, shoot height and density, and rhizome length
32	Taiwan	E n.d.	*T. hemprichii*	*Enteromorpha and Ulva spp.*	Comparison of seagrass with/without Ulvoid algae	Seagrass Photosynthetic performance	Shading reduced photosynthetic performance and reduced inorganic C uptake
33	FL/USA	E 3 yr.	*T. testudinum*	*Laurencia* sp. and *Dictyota* sp.	Algal presence and absence, sea urchin addition	Biomass and shoot density	Algae did not affect seagrass biomass, but there was synergy between urchin grazing and algae on seagrass shoot density
34	Denmark	E 3 wk.	*Z. marina*	*G. vermiculo-phylla*	Algal additions (high, low, and control) at various temperatures	Seagrass net photosynthesis and dark respiration.	Algae reduced seagrass survival but not dark respiration rates. At high temperature, algae also reduced seagrass net photosynthesis
35	Italy	E 2 yr.	*C. nodosa*	*C. cylindracea*	Neighbor control/addition, sedimentation and various types of plastics	Seagrass performance	Algae made seagrass allocate more biomass to fine roots. Seagrass reduced algal performance. HD polyethene plastics and sedimentation shifted interaction from competitive to neutral

(Continued)

TABLE 1 (Continued)

#	Location	Approach/time span	Seagrass	Alga	Design	Response	Main results
36	Sweden	E 1 wk.	*Z. marina*	*U. intestinalis*	Seagrass photosynthesis under Ulva and pH changes	Photosynthetic capacity	Ulva lowered light and enhanced pH reducing seagrass photosynthesis ability
37	WA/USA	E 13 mo.	*Z. marina*	*U. obscura*	Algal removal and control	Seagrass shoot density and algal biomass.	Natural algal blooms caused a loss in seagrass. While controls lost 54% shoots, areas with algal removal lost only 12%
38	CA/USA	E 38 mo.	*Z. marina*	*Ulva* sp.	Algal removal, addition and control	Seagrass biomass	Algal addition reduced seagrass shoot biomass by up to 90% and for up to 9 mo
39	Spain	E 3 mo.	*P. oceanica*	*C.cylindracea L. lallemandii*	3 temperature treatments and presence/absence of algae	Seagrass seedling survival, development and biomass	Presence of both algae ameliorated impact of high temperature and seagrass
40	FL/USA	O 6 yr.	Anadyomene	Algal blooms	Percent cover	Seagrass foliage cover and fragmentation level	Algal blooms reduced seagrass foliage cover and increased levels of seascape fragmentation
41	FL/USA	E 15 mo.	*H. wrightii*	*C. prolifera*	Seagrass presence and absence	Seagrass above and below-ground biomass	Algae may replace seagrasses by overgrowth or competition. Disturbance-related bare areas may allow algae to replace seagrass by space preemption
42	Japan	E n.d.	*Z. marina*	*Ulva* sp.	Seagrass transplantation, seagrass seeding and control	Seagrass shoot density and length. Volume of *Ulva* sp.	Ulvoid accumulation caused a decline in seagrass shoot and seedling density and was correlated with.
		E 13 mo.			Algal addition of 2 canopy heights and control	Seagrass survival rate and leaf elongation rate of seagrass	the decline in other various seagrass measurements
43	FL/USA	E 6 mo.	*H. wrightii*	*C. prolifera*	Plots set at 2 depths with seagrass, algae or both	Shoot/frond density and above- and belowground biomass	Without algae: seagrass shoot density and biomass were higher during growing season. Instead, algae were unaffected by seagrass
44	Denmark	E 1 mo.	*Z. marina*	*G. vermicu-lophylla*	Addition of invasive alga on seagrass exp. Plots	Seagrass above- and below-ground biomass	The invasive alga reduced native seagrass above-ground biomass
45	Wadden Sea	O 6 mo.	*Z. marina* and *Z. nolteii*	*Gracilaria*, Ulva, others	Monitoring of sparsely and densely vegetated plots at two locations	Seagrass seed density and biomass	In both locations, seagrass biomass declined over winter. Seed density was higher in reference area and in densely vegetated plots
		E 5 mo.	*Z. marina* and *Z. nolteii*	*Gracilaria*, Ulva, and others	Seagrass transplants to sites with and without algae	Survival, cover, reproductive shoots and seed density	Macroalgae negatively impacted seagrass seed producing shoot survival
46	Tunisia	E 3 mo.	*C. nodosa*	*C. linum*	Addition of low, moderate and high algal cover	Structural, morphological, and physiological variables	With rising algal cover, leaf elongation rates and biomass declined while leaf chlorophyll and carotenoid concentrations increased

Study numbers are linked to authorship in the footnote. References: [1] Alexandre et al. (2017); [2] Alexandre et al. (2021); [3] Bittick et al. (2018); [4] Brun et al. (2003); [5] Ceccherelli and Campo (2002); [6] Ceccherelli and Cinelli (1997); [7] Ceccherelli and Cinelli (1999); [8] Ceccherelli and Sechi (2002); [9] Correia et al. (2022a); [10] Cummins et al. (2004); [11] Davis and Fourqurean (2001); [12] De Villele and Verlaque (1995); [13] Dumay et al. (2002); [14] Eklöf et al. (2006); [15] Emmclan et al. (2022); [16] Firth et al. (2023); [17] Glasby (2013); [18] Han et al. (2016); [19] Hauxwell et al. (2001); [20] Hauxwell et al. (2003); [21] Hessing-Lewis and Hacker (2013); [22] Hessing-Lewis et al. (2015); [23] Hessing-Lewis et al. (2011); [24] Höffle et al. (2011); [25] Homer and Nielsen (2007); [26] Homer et al. (2011); [27] Huntington and Boyer (2008); [28] Irlandi et al. (2004); [29] Kalokora et al. (2021); [30] Lamote and Dunton (2006); [31] Lanari et al. (2018); [32] Liu et al. (2005); [33] Maciá (2000); [34] Martínez-Lüscher and Holmer (2010); [35] Menicagli et al. (2021); [36] Mvungi et al. (2012); [37] Nelson and Lee (2001); [38] Olyarnik and Stachowicz (2012); [39] Pereda-Briones et al. (2019); [40] Santos et al. (2020); [41] Stafford and Bell (2006); [42] Sugimoto et al. (2007); [43] Taplin et al. (2005); [44] Thomson et al. (2013); [45] Van Katwijk et al. (2010); [46] Zribi et al. (2023).

A few additional studies have also documented neutral seagrass-macroalgal interactions (Maciá, 2000; Ceccherelli and Sechi, 2002; Irlandi et al., 2004; Hessing-Lewis et al., 2011; Höffle et al., 2011; Glasby, 2013; Hessing-Lewis and Hacker, 2013; Alexandre et al., 2017; Menicagli et al., 2021; Firth et al., 2023). The results of these studies showed no significant effects of macroalgal presence on seagrass nutrient uptake rates (Alexandre et al., 2017), nutrient partitioning (Firth et al., 2023), shoot density (Ceccherelli and Sechi, 2002), growth (Irlandi et al., 2004; Höffle et al., 2011; Glasby, 2013), and biomass (Maciá, 2000; Hessing-Lewis et al., 2011). Likewise, seagrasses have been demonstrated to have only a minor influence (whether positive or negative) on macroalgae nutrient uptake rates (Alexandre et al., 2017) and blade density (Ceccherelli and Sechi, 2002). An interesting observational study found that the lack of seagrass responses to high fluctuations of macroalgal production at a given site was due to the mediation of tides and local currents (Hessing-Lewis and Hacker, 2013). In addition, an experimental study found that the interaction between seagrass and macroalgae could be shifted from competitive to neutral in the presence of high-density polyethylene plastics and sedimentation (Menicagli et al., 2021). These neutral interactions were most often found between species of the genus *Zostera* (Hessing-Lewis et al., 2011; Höffle et al., 2011; Hessing-Lewis and Hacker, 2013; Alexandre et al., 2017) and the families Ulvaceae (Hessing-Lewis et al., 2011; Hessing-Lewis and Hacker, 2013; Alexandre et al., 2017) and Caulerpaceae (Ceccherelli and Sechi, 2002; Glasby, 2013; Menicagli et al., 2021).

4 Drift algae

Although macroalgae are often anchored to the seafloor, evidence of interactions between seagrasses and macroalgae was also examined for a smaller (representative) complement of drift algae. We found no clear indication that drift algae were more often responsible for negative interactions (as in the study by Lanari et al., 2018) than anchored algae. Similarly, cases of positive interactions were found to occur with both anchored (Ceccherelli and Cinelli, 1999; Ceccherelli and Campo, 2002; Alexandre et al., 2017) and drifting macroalgae (Irlandi et al., 2004; Hessing-Lewis et al., 2011; Alexandre et al., 2017; Correia et al., 2022a; Emmclan et al., 2022). Interestingly, neutral interactions were more frequently found with drifting macroalgae (Maciá, 2000; Irlandi et al., 2004; Hessing-Lewis et al., 2011; Höffle et al., 2011; Hessing-Lewis and Hacker, 2013) than anchored forms (Ceccherelli and Sechi, 2002; Glasby, 2013). The latter results may be due to the shorter residence of drift algae on or around seagrasses, or possibly due to the seagrass' clonal nature, that potentially minimized the effects by these "transient" macroalgae (Irlandi et al., 2004). When found, positive interactions were often context-dependent and species-dependent. For example, *Caulerpa taxifolia* was found to have negative effects on *Posidonia oceanica* (De Villele and Verlaque, 1995) and *Cymodocea nodosa* (Ceccherelli and Campo, 2002) while having a positive impact on traits like the shoot density of *Zostera noltei* (Ceccherelli and Campo, 2002). More research addressing context (habitat) and species dependency is clearly necessary, as local complements of species change as a result of climate events.

5 Some implications in the face of climate change

The evidence examined shows that interactions between seagrasses and macroalgae are predominantly negative and that seagrass species are most often at a competitive disadvantage. Extreme weather events resulting from climate change may increase the frequency and severity of floods and surface runoff (e.g., Chegwidden et al., 2020), which could change even further the balance of interactions between these primary producers. Increasing rates of eutrophication (Nazari-Sharabian et al., 2018) may account for some of these changes, as many of the articles reviewed, explicitly or not, point toward interactions between algae and seagrass that have been mediated by changing nutrient levels (Hauxwell et al., 2001, 2003; Ceccherelli and Campo, 2002; Ceccherelli and Sechi, 2002; Hessing-Lewis et al., 2015; Han et al., 2016; Alexandre et al., 2017, 2021). Macroalgae have been shown to be at a competitive advantage for nutrient acquisition, with only one study finding a neutral interaction when facing a nutrient load increase (Ceccherelli and Sechi, 2002). Rising ocean temperatures likely add to this imbalance: evidence of interactions taking place at different temperatures (e.g., Martínez-Lüscher and Holmer, 2010; Höffle et al., 2011; Homer et al., 2011) suggests that the negative effects of seaweeds and rising temperatures on seagrasses are either additive or synergistic.

Macroalgae seem generally more resistant to rising temperatures and, in some cases, can also take advantage of increased nutrient availability (Höffle et al., 2011; Duarte et al., 2018). Meanwhile, seagrass species become quickly stressed (and harmed), as they are generally more vulnerable to rising temperatures and the rapid growth of macroalgae (Martínez-Lüscher and Holmer, 2010; Höffle et al., 2011; Homer et al., 2011). This is concerning given that most climate change forecasts (see Bindoff et al., 2019) predict an increase in water temperatures and therefore more frequent increases in macroalgal biomass (Cressey, 2017; Gobler et al., 2017). Beyond changes associated with macroalgae and warming, various other co-occurring anthropogenic factors have already been found to be directly or indirectly responsible for seagrass decline or loss (Orth and Moore, 1983; Walker and McComb, 1992; Short and Wyllie-Echeverria, 1996; Orth et al., 2006; Waycott et al., 2009), making negative cumulative effects plausible, and the outcome of seagrass-algal interactions even more complex (see review by Pirotta et al., 2022). Even though the negative prospects for seagrass are unmistakable, Bennett et al. (2022) has highlighted the considerable resilience of these primary producers and the research by Kendrick et al. (1999, 2002) suggests that seagrass losses are not irreversible. In addition, and unlike other (more controversial) environmental issues, there seems to be a unified view in the public discourse addressing the role played by current conservation efforts (Nordlund et al., 2018; Unsworth et al., 2019): in the face of a changing ocean, these efforts are critical for protecting existing seagrass meadows and, where possible, for reversing some alarming seagrass losses.

Author contributions

MR: Data curation, Formal analysis, Investigation, Methodology, Writing – original draft, Writing – review & editing. PQ: Conceptualization, Formal analysis, Funding acquisition, Investigation, Methodology, Supervision, Writing – original draft, Writing – review & editing.

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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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Supplementary material

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