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RECEIVED 28 September 2023

ACCEPTED 29 November 2023

PUBLISHED 19 December 2023

CITATION

Gibbons EG and Quijón PA (2023)
Macroalgal features and their influence on
associated biodiversity: implications for
conservation and restoration.
Front. Mar. Sci. 10:1304000.
doi: 10.3389/fmars.2023.1304000

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Macroalgal features and their influence on associated biodiversity: implications for conservation and restoration

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Studies examining the relationship between seaweeds and the diversity of associated organisms have been attempted far less than those focusing on the influence of terrestrial plants. That is troublesome considering the growing number of studies reporting the decline or local loss of macroalgae because of ocean warming and climate change. Since the fate of macroalgae will have an influence on associated organisms, this brief overview examined the different roles played by macroalgae, making the distinction between morphological features associated with individual seaweed species and those associated with populations or habitats. Most studies at both (individual and population) levels have identified positive relationships between morphological features such as structural complexity (including fractal dimensions) and invertebrate biodiversity, and the abundance of various faunistic groups. Some of these relationships are stronger than others, often with complex outcomes, suggesting that the current and future ecological benefits provided by macroalgae are strongly species- and habitat-dependent. While the displacement or local-scale loss of seaweeds may continue because of climate change, the features identified here may become useful in light of conservation and restoration efforts.

KEYWORDS

seaweeds, biodiversity, abundance, conservation, restoration, climate change

1 Introduction

Many macroalgal species function as ecosystem engineers or foundation species (*sensu* Marzinelli et al., 2016) and are therefore central to restoration and sustainability goals (Ellison et al., 2005; Marzinelli et al., 2016). These macroalgae create direct or indirect food sources (Tano et al., 2016), space suitable for attachment, growth, or reproduction (Gallardo et al., 2021), refuge from predators (Best et al., 2014), and altered (often ameliorated) physical conditions for marine invertebrates (Brawley and Adey, 1981; Christie et al., 2003; Schmidt and Scheibling, 2006; Best et al., 2014; Schaal et al., 2016; Tano et al., 2016; Gallardo et al., 2021; El-Khaled et al., 2022) and vertebrates (e.g., Norderhaug et al., 2005), including seabirds and mammals (Lorentsen et al., 2010;

Christensen-Dalsgaard et al., 2017). Despite their importance, studies addressing the biodiversity associated with marine macroalgae have been attempted considerably less than those associated with terrestrial plants (Parker et al., 2001; Goodsell et al., 2004; Best et al., 2014; Gallardo et al., 2021). However, there is a need for these studies given ongoing climate events and anthropogenic disturbances, which are resulting in accelerated loss of species across coastal habitats worldwide (Bates and DeWreede, 2007). In this changing scenario, quantifying the contribution of macroalgae to biodiversity, both as individual algae or as clumps, beds, or populations, is undeniably important (Bates and DeWreede, 2007; El-Khaled et al., 2022).

Several macroalgal morphological or structural features have been directly or indirectly associated with the colonization and use of macroalgae by infaunal and epifaunal organisms (Bates and DeWreede, 2007; Duarte et al., 2020). However, these features have not been thoroughly explored in the context of biodiversity levels and their change in a warming ocean (Chemello and Milazzo, 2002). An examination of these features at the individual and population levels is not only important from a research perspective. It may also help conservation efforts, particularly in the case of macroalgal species that are threatened or are experiencing long-term declines (Lilley and Schiel, 2006; Marzinelli et al., 2014; Tummon Flynn et al., 2019). For those species, evidence showing their contribution to biodiversity and the features that enhance biodiversity levels, can support claims calling for their further protection and restoration (Marzinelli et al., 2014; Buršić et al., 2019; El-Khaled et al., 2022). Therefore, the goal of this minireview was to examine whether macroalgae influence biodiversity, and to identify the characteristics of individual seaweeds, or seaweed populations, that have an influence on any aspect of biodiversity. For this review, “biodiversity” was quantified using various measures, including species richness, diversity and/or species evenness, and biomass and abundance of organisms, among other metrics.

The influence of macroalgae on biodiversity is outlined in Table 1 and includes a compilation of 62 published studies (as of November 2023) deemed representative rather than comprehensive of those addressing seaweed-biodiversity relationships. We focused primarily on physical or structural features, including fractal dimensions (e.g. Davenport et al., 1996; Tokeshi and Arakaki, 2012) when measured, but did not account for a distinct branch of studies on algal chemical products (e.g. Hay and Fenical, 1996). These chemical products have evolved from the interaction between seaweeds, consumers, hosts, or colonizers (often as defenses against herbivory) at every coastal region and latitude (see e.g., Amsler, 2008 and Amsler et al., 2014). Their influence on species interactions and biodiversity has been comprehensively reviewed by other authors (Amsler, 2008 and chapters and references therein; Ianora et al., 2006; Hay, 2009; and Sotka et al., 2018, among others). Studies focusing primarily on aquatic plants outside of the realm of marine macroalgae were not considered either. For instance, species such as *Zostera marina* often overlap and interact with various marine macroalgae (Richard and Quijón, 2023). However, they belong into a distinct group of flowering plants with root systems, which has been examined by other authors (e.g., Hansen et al.,

2010) and was deemed beyond the scope of this minireview. The articles examined here were obtained using search engines such as OneSearch and Google Scholar, networks (e.g., ResearchGate), and cross-listed references within articles and other online resources. Key words used in these searches included “seaweed” or “algae” or “kelp,” “rhodoliths”, “biodiversity” or “diversity” “invertebrates” or “epifauna” or “infauna”, and various combinations among them. Our review uses rather loosely the terms algae and seaweeds, but in all instances, we are referring to marine macroalgae. Likewise, our review includes studies on algae identified as “foundation species” or “ecosystem engineers”, but these terms were not used as keywords given their widely known importance (e.g., Dayton, 1985; Stachowicz, 2001; Ellison et al., 2005) and much broader influence, often above the level of communities.

2 The influence of individual seaweed features

Out of the studies compiled in Table 1, a large majority suggests that seaweed’s structural complexity (measured for instance as branching, physical rugosity or fractal dimensions) contributes to various metrics of invertebrate diversity and abundance. Higher structural complexity has been causally linked with increased invertebrate biodiversity (Chemello and Milazzo, 2002; Frame et al., 2007; Schaal et al., 2016; Mancuso et al., 2023a), species richness (Gee and Warwick, 1994; Duarte et al., 2020), and organisms’ abundance (Russo, 1990; Davenport et al., 1996; Chemello and Milazzo, 2002; Frame et al., 2007; Schaal et al., 2016; Dijkstra et al., 2017; Duarte et al., 2020). The reported influence of complexity is variable, resulting in increases of nearly 58% in Shannon-Wiener diversity (Chemello and Milazzo, 2002) to increases in biodiversity levels ranging between 52% and 115%, depending on the time of year (Schaal et al., 2016). Algal complexity has also resulted in increases that ranged from 40% (Dijkstra et al., 2017) to an almost eight-fold increase in abundance (Chemello and Milazzo, 2002). Consistent with this, seaweed’s fractal dimensions have been also shown to have an influence on invertebrate abundance and taxon richness (Mancuso et al., 2023a) regardless of host identity (Veiga et al., 2014). However, some studies have also found mixed results, with strong positive correlations between community structure and algal complexity features such as holdfast diameter and frond length, and negative correlations with features such as the number of stipes (Velasco-Charpentier et al., 2021).

A few studies have found that algal structural complexity had little influence on e.g. invertebrate species richness (Russo, 1990; Dijkstra et al., 2017) or abundance (Russo, 1990; Lenzo et al., 2023), while others have found that these relationships change temporarily. According to Da Rocha et al. (2006), similar assemblages could be associated with structurally different macroalgae, but complexity still have an influence on the biology of the dominant groups of invertebrates. Due to life cycles, macroalgal morphological features change seasonally (Leite and Turra 2003; Mancuso et al., 2023b) and this has prompted studies examining the influence of these changes on associated epifaunal

TABLE 1 A summary of studies identifying relationships between macroalgae or their features and various aspects of coastal organism biodiversity levels. In addition to location and type of habitat, seaweed species and features, responses measured, target taxa (or groups of taxa) and reported effects on biodiversity are presented for 62 studies (reference #s are organized alphabetically by authors' last names and are identified in the footnote of this Table).

Location	Habitat	Seaweed(s)/ feature(s)	Measured response	Target taxa	Effect on faunal diversity	#
US/CA	Kelp forests	<i>M. pyrifera</i> , understory algae/ Canopy, density, shade	Other seaweeds, sessile invertebrate diversity	Invertebrate communities	Canopy of kelp in multiple sites influenced other algae and invertebrate diversity and abundance. Indirect facilitation processes.	1
Canada/BC	Intertidal seaweed system	<i>A. leptophyllum</i> , <i>A. japonicus</i> , others/Species & functional richness, functional composition	Small epifaunal species composition, functional groups	Amphipods, copepods	Invertebrate composition and diversity were related to seaweed identity in simple monocultures (functional composition).	2
US/CA	Mid- high intertidal	<i>M. papillatus</i> , <i>C. columbiana</i> , <i>P. limitata</i> / Identity, richness, total cover	Invertebrate species richness, abundance	Amphipods, isopods	Richness and abundance were higher in polycultures than in monocultures. Richness increased with cover. Densely branched algae held highest density.	3
Croatia	Coralline turf/ intertidal	<i>C. officinalis</i> / Within-habitat biodiversity	Invertebrate density, taxonomic groups	Amphipods, polychaetes	<i>Corallina officinalis</i> supported a high diversity of invertebrates.	4
Germany	Rocky shore, tidal flats	<i>S. muticum</i> , <i>H. siliquosa</i> , other/complexity & invasive status	Epibiota species richness	Gastropods, amphipods	Diversity was correlated with algal complexity, regardless of native non-native status.	5
Spain	Rocky intertidal habitats	<i>Sargassum muticum</i> and <i>Laminaria ochroleuca</i> / structural complexity and habitat position	Density, taxa abundance, and diversity	Gastropods, malacostracenanematodes	When comparing mid to low shore position, there was significant differences in number of taxa with less in the mid shore than low.	6
Brazil	Euphotic and mesophotic	Rhodolith beds/ Structural characteristics of zones	Macroinvertebrates spp. diversity, abundance	Polychaeta, crustacea	Euphotic rhodolith beds supported twice the abundance and number of taxa than mesophotic.	7
Italy	Rocky plateau	<i>S. vulgare</i> , <i>C. spinosa</i> , <i>D.</i> <i>fasciola</i> / Branching, ramuli, leaves, algal and stem width	Mollusk abundance, diversity	Neotaenio-glossa	More complex plants had higher abundances and richness. Structural complexity was related to degree of branching, width, and log of stem width.	8
Australia	Fringing reef	<i>Sargassum</i> /Canopy size	Epifaunal abundance and biomass	Crustaceans and molluscs	There was a positive correlation between canopy size & associated epifaunal community.	9
Norway	Kelp forests	<i>iliolatenreal</i> Distribution on lamina, stipe & holdfast	Mobile invertebrate diversity, abundance	Amphipods, gastropods	Holdfasts hosted highest number of species, while stipes had the highest abundance. Lamina had the lowest diversity and abundance.	10
Brazil	Rocky beach	<i>Sargassum polyceratium</i> , others, sediments/ Physical structure	Shannon-Wiener index, density, and genera richness	Nematodes	No significant difference in phytal nematofauna between habitats but dominant genera in each suggests that complexity influence organism biology	11
South Georgia	Subtidal habitat	<i>Macrocystis pyrifera</i> , <i>Desmarestia menziesi</i> , others/ Fractal dimensions	Abundance & biomass	Copepods, peracarids, bivalves	The most complex algae (by fractal dimensions), supported highest abundance and biomass.	12
Australia	Intertidal sheltered shore	<i>Corallina</i> , <i>Hormosira</i> , <i>Enteromorpha</i> /Fractal dimensions and emersion	Abundance	Copepods	Most complex algae had highest abundance and when emerged had the lowest rates of migration.	13
US/ ME/NH	Rocky subtidal	Native: <i>S. latissima</i> , <i>Ulva</i> sp.... Introduced: <i>B. hamifera</i> .../ Structural complexity, height	Meso-invertebrate abundance, richness	Amphipods	Seaweed complexity accounted for 93% of abundance & 71% spp. richness. Introduced algae were more complex & enhanced density.	14

(Continued)

TABLE 1 Continued

Location	Habitat	Seaweed(s)/ feature(s)	Measured response	Target taxa	Effect on faunal diversity	#
Brazil	Estuary	<i>G. domingensis</i> , <i>S. filiformis</i> , <i>G. cuneata</i> , <i>D. ciliolateata</i> ,/ Habitat complexity index	Mollusk composition, richness, diversity, abundance	Gastropods, bivalves.	Habitat complexity was positively correlated with mollusk abundance & richness.	15
Italy	Algal assemblages	<i>P. crispa</i> , <i>P. oceanica</i> / Leaves and rhizomes	Sessile invertebrate abundance, diversity, phenotype richness	Invertebrates	<i>P. crispa</i> 's holobionts, leaves & rhizomes had highest abundances, while its mats had higher Simpson diversity & phenotype richness.	16
US/CA	Rocky intertidal	<i>S. multicum</i> , <i>Z. farlowii</i> , <i>Others and turf-forming algae</i>	Species richness and density per algal weight unit	Ostracods	Structurally complex algae held more ostracods. Turf-forming algae held more richness.	17
US/CA	Rocky reefs, subtidal	Rhodoliths/Rhodoliths beds vs crushed rhodolith sands	Invertebrate density and abundance	Tanaids	Rhodolith beds supported higher abundance than the less complex crushed rhodolith beds.	18
Spain	Rocky subtidal bar	<i>H. scoparia</i> , <i>H. filicina</i> , <i>C. fragile</i> , <i>C. bursa</i> , <i>S. coronipifolius</i> .../ Soft or hard calcareous thallus	Invertebrate species richness, abundance	Annelids, Arthropods, Molluscs	Higher biodiversity was found in hard than soft algae, possibly due to the structure of the thalli and the microhabitats it provides.	19
England	Intertidal zone	<i>Chondrus crispus</i> , <i>Laurencia pinnatifida</i> , <i>others</i> / Fractal dimensions	Macro- & meiofauna abundance and richness	Copepods/nematodes	Changes in thallus structure affected meiofauna more than macrofauna. Complex substrate results in increased diversity.	20
Spain	Lower intertidal	<i>B. bifurcate</i> , <i>S. muticum</i> , <i>others</i> / Presence of invasive species	Epifaunal abundance, richness, diversity	Gastropods, isopods	<i>B. bifurcate</i> held the highest diversity whereas <i>S. polyschides</i> held the highest biomass of epifauna.	21
French Polynesia	Coral reef-lagoon	<i>L. kotschyannum</i> /Branch density, thallus rugosity, interstitial volume	Assemblage abundance	Crustaceans	Host morphology was most important in defining cryptofaunal assemblages.	22
Australia	Subtidal rocky coasts	<i>E. radiata</i> / Habitat configuration	Invertebrate density, species richness	Assemblages	Invertebrate assemblages, but not spp. richness, differed between <i>E. radiata</i> mono-specific and interspersed strands and clumped strands.	23
US/CA	Rocky mid-intertidal	<i>P. fastigiata</i> Size	Invertebrate richness, abundance	Copepods, amphipods	Higher biodiversity was positively associated with seaweed size.	24
US/ME	Rocky shore, tidepools	<i>U. lactuca</i> , <i>C. rubrum</i> , <i>C. crispus</i> , <i>C. officinalis</i> , <i>L. digitata</i> ... mimics/ Degree of branching	Amphipod density	Amphipods	Branched algae had the highest densities, possibly due to the higher amount of habitable space available between fronds.	25
Australia	Rhodolith beds	<i>H. rupestre</i> , <i>Lithothamnion</i> , <i>others</i> /Foliose vs fruticose forms	Cryptofaunal abundance	Polychaeta	Minor or no differences in assemblages. Higher rhodolith diversity not correlated with cryptofauna.	26
UK	Kelp beds	Artificial kelp holdfast/ Complexity of holdfast	Invertebrate diversity richness, abundance	Amphipods, gastropods	Holdfast complexity was associated with species richness, diversity & abundance.	27
Scotland	Intertidal zone	<i>Cladophora rupestris</i> , <i>Laminaria digita</i> , and <i>Fucus serratus</i> /Fractal dimensions and emersion	Abundance	Copepods, amphipods, bivalves	Most complex macroalgae had higher abundance of invertebrates. Emersion only affected the least complex seaweed, causing an increase in abundance.	28
US/CA	Kelp forests	<i>Egrecia menziesii</i> / Algal cover, canopies at multiple sites	Algal cover/ richness,	Other algae, invertebrate benthos	<i>Egrecia</i> kelp has both positive and negative effects on benthic biodiversity in stressful and non-stressful habitats, respectively.	29

(Continued)

TABLE 1 Continued

Location	Habitat	Seaweed(s)/ feature(s)	Measured response	Target taxa	Effect on faunal diversity	#
			invertebrate diversity			
England	Mid-shore rock pool	<i>Coralline officinalis</i> , <i>Cladophora rupestris</i> , others/ Degree of branching	Density, abundance, diversity	Ostracod	Results show that structural complexity affects epifaunal communities in space and time	30
US/CA	Kelp forests	<i>M. pyrifera</i> / Canopy in physical gradient	Invertebrate density, diversity, interactions	Epibionts, communities	Canopies of kelp along a physical gradient influenced epibionts, invertebrate density, diversity, and some of their trophic interactions.	31
Chile	Rocky intertidal shore	Coralline algal turf/ Habitat characteristics	Taxonomic richness and abundance	Polychaetes	Froned density and amount of sediment were the best variables to explain assemblage differences.	32
Brazil	Sandy beach	<i>Sargassum</i> /Biomass	Density	Gastropoda	There were variations in seaweed biomass and epifauna density throughout the year.	33
Italy	Shallow coastal areas	Native & invasive seaweeds/ PUAs & structural complexity	Meio- & microphytobenthic communities	Diatoms, copepods, macrofauna.	Invasive algae supported less diversity than native species. PUAs & structural complexity could not predict differences in meiobenthic assemblages.	34
New Zealand	Intertidal rocky shores	<i>Hormosira banksii</i> / Presence or absence of dominant habitat-forming seaweed	Epifaunal abundance, species richness	Amphipods, Micro-snails copepods	Removal of dominant seaweed caused a decline in epifaunal species richness and abundance.	35
Spitsbergen	Arctic benthic communities	<i>L. digitata</i> , <i>A. aff. Flagellate</i> , etc./Abiotic and biotic factors	Invertebrate and species abundance, and invertebrate density	Bryozoa and Crustacea	Low diversity in shallow algae due to ice/ waves. Thallus morphology influenced epifauna, which was lower when compared to other regions.	36
Australia	Rocky intertidal	Invasive: <i>C. fragile fragile</i> Native: <i>C. fragile tasmanicum</i> .../Branching, thallus & holdfast S:A	Epifauna taxonomic richness, abundance	Gastropods, gammarid amphipods	Invasive seaweed's holdfasts hold highest taxa richness. Branching was correlated with taxa and abundance on native but not invasive seaweeds.	37
Italy	Temperate rocky coast	<i>Cystoseira montagnei</i> / Habitat size	Richness, evenness, structure, composition, trophic guilds	Gastropods	Abundance, richness, and H' increased with patch-size. Best explanatory algal features were algal surface, thallus volume & biomass.	38
Italy	Intertidal habitat	<i>E. amentacea</i> & <i>Laurencia</i> / Structural complexity	Species richness, H' index, Pielou's evenness	Amphipods	The most and least complex algae had more density and diversity, respectively. Due to allelochemicals.	39
Italy	Shallow rocky shore	<i>Gongolaria montagnei</i> / Fractal analysis	Abundance and species richness	Molluscs	Fractal dimensions of algae change during its vegetative cycle, and these changes have the ability to alter assemblages of organisms using the algae.	40
Australia	Shallow rocky reefs	<i>P. comosa</i> , <i>E. radiata</i> / Structural complexity	Commercial species _{relative} abundance, biomass	Abalone, sea urchins, fish	<i>P. comosa</i> supported higher density of abalone and urchins than <i>E. radiata</i> . This seems related to alga's complexity or chemical cues.	41
Australia	Exposed, rocky reefs	<i>P. comosa</i> , <i>E. radiata</i> , <i>S. vestitum</i> /Extant native vs transplanted plants	Epifaunal number of taxa, individuals	Crustaceans, mollusks	Algae had different assemblages. Transplanted algae supported lower diversity than undisturbed algae but supported considerable diversity.	42
Russia	Red algae zone	<i>C. truncates</i> , <i>P. extensum</i> , others/ Presence of algae species	Taxon richness	Bryozoans	Zonation found in epibenthic organisms in the red algae zone. Differences in assemblages between sites could be due to hydrology and sediments.	43

(Continued)

TABLE 1 Continued

Location	Habitat	Seaweed(s)/ feature(s)	Measured response	Target taxa	Effect on faunal diversity	#
Brazil	Sandstone reefs	Rhodoliths/Complexity of microhabitats	Faunal richness and diversity (meiofauna and macrofauna)	Nematoda, polychaetes	Rhodoliths complex microhabitats supported higher richness and diversity than bare sediment.	44
Antarctic	Subtidal	<i>D. menziessi</i> , <i>A. utricularis</i> , others/Chemical defenses	Amphipod densities	Amphipods, sea stars	Seaweed with high density of amphipods developed deterrents. Amphipods used habitats as refuges.	45
Chile	Subtidal forests	<i>Macrocystis pyrifera</i> / Holdfast size	Invertebrate species richness, diversity	Crustaceans, echinoderms	Species richness, diversity & abundance increased with size of holdfasts (up until a threshold)	46
US/VA	Seagrasses, algal assemblage	<i>Z. marina</i> , <i>R. maritima</i> , drift algae, green and red algae/ Seaweed richness, composition	Epifaunal density	Isopods, amphipods	In mixed habitats, epifauna abundance was higher on seaweeds than seagrasses. Plant composition was more influential than plant diversity.	47
US/VA	Estuarine Seagrass/ seaweeds	<i>G. verrucosa</i> , <i>Ulva</i> spp., <i>C. rubrum</i> , <i>S. filiformis</i> / Diversity and surface area	Motile epifauna density, diversity/ evenness, biomass	Amphipods	Plant diversity influenced Simpson diversity. Plant surface enhanced biomass & abundance, but reduced evenness & Simpson diversity.	48
US/CA	Nearshore systems	<i>Sporolithon australe</i> / Rhodoliths	Cryptofaunal abundance, taxon richness	Polychaetes, crustaceans	Living rhodolith habitats had higher diversity than dead rhodolith beds and bare sand.	49
US/HI	Reef platform	<i>P. japonica</i> , <i>D. crenulate</i> , <i>T. ornate</i> , <i>G. fastigiata</i> .../ Surface area, biomass, S: B ratio	Epifaunal amphipod abundance	Amphipods	Abundance was correlated with seaweed S:A and biomass. Amphipod abundance or richness were not correlated with S:A.	50
France	Rocky shore	<i>L. digitata</i> , <i>P. palmata</i> , <i>M. stellatus</i> , <i>E. elongate</i> / Structural complexity	Invertebrate, abundance, richness	Amphipods, gastropods	Algal complexity was correlated with abundance, richness & diversity. More complex assemblages supported higher epifaunal diversity.	51
Canada, NS	Subtidal rocky reef	<i>C. fragile</i> , <i>L. longicuris</i> , <i>L. digitata</i> /Fronds, holdfasts, thalli	Epifaunal abundance	Gastropods	Assemblages on fronds and holdfasts differ among algae. Diversity on the fronds was also different.	52
Greenland	Arctic benthic communities	<i>Clathromorphum</i> sp., <i>S. longicuris</i> , etc./Kelp beds vs coralline algae	Invertebrate species diversity	Mixed	Interstitial communities in rhodolith habitats are different and more diverse than in kelp beds.	53
Australia	Temperate artificial rocky reefs	<i>E. radiata</i> , artificial kelp/ Density, patch size, position	Epifaunal secondary productivity, richness, diversity, structure	Epifauna	Patch size had positive effect on richness. Mimic patch edges had higher richness than center, their size influenced diversity in centrally located habitats.	54
Costa Rica	Shallow subtidal	Rhodoliths/ Aggregation level	Macrofauna richness. Abundance, H', composition.	Crustaceans, polychaetes, mollusks	Moderately and highly aggregated rhodoliths had highest richness. Highest abundance and H' found at moderately aggregated rhodoliths.	55
Brazil	Benthic habitats	Rhodolith beds/ Nodule densities and morphology	Macrofaunal diversity	Annelida, Crustacea, Mollusks	Density was similar between high- and low-density rhodolith beds. Density and trophic richness were higher on nodules compared to sediments below.	56
Tanzania	Rocky, soft sediment seaweeds	<i>T. conoides</i> , <i>S. aquifolium</i> / Seagrass & seaweed combinations	Epifaunal abundance, biomass, taxa richness	Crustaceans, Annelids	Seaweed richness was correlated with epifaunal abundance, richness & biomass. Seaweeds had also higher biodiversity and fish than seagrasses.	57
New Zealand	Rocky subtidal	Brown and laminarian algae/ Thallus width, growth forms	Mobile epifauna density	Amphipods, isopods	Thallus width and density were inversely related. Thallus width and isopod shape were related. algal fine structured growth was related with abundance.	58

(Continued)

TABLE 1 Continued

Location	Habitat	Seaweed(s)/ feature(s)	Measured response	Target taxa	Effect on faunal diversity	#
Portugal	Rocky shore	Annual species; <i>Chondracanthus teedii</i> , <i>Codium tomentosum</i> , others/ Biomass and fractal measures	Abundance and taxa richness	Molluscs, crustaceans, polychaetas.	Biomass & fractal area of macroalgae had the biggest influence on shaping associated epifaunal communities.	59
Portugal	Intertidal rocky pools	Native and invasive seaweeds/ Macroalgal complexity	Taxa richness and abundance	Mixed epifauna	Abundance increased with algae's dry weight & fractal dimension, independent of algae identity, affected abundance & richness.	60
Chile	Subtidal subantarctic kelp forest	<i>Lessonia flavicans</i>	Species richness, abundance, community structure	Macrobenthic communities	Diversity and community structure correlated positively and negatively with distinct features of algal structural complexity	61
Sweden	Shallow hard bottoms	<i>F. vesiculosus</i> / Presence or absence	Invertebrate biomass, abundance, richness	Gastropods, bivalves	The presence of <i>F. vesiculosus</i> was positively associated with the biomass but not the species richness of invertebrates.	62

Table reference numbers (#): Arkema et al. (2009)¹, Bates and DeWreede (2007)², Best et al. (2014)³, Buršič et al. (2019)⁴, Buschbaum and Chapman (2006)⁵, Cacabelos et al. (2010)⁶, Cerqueira Veras et al. (2020)⁷, Chemello and Milazzo (2002)⁸, Chen et al. (2020)⁹, Christie et al. (2003)¹⁰, Da Rocha et al. (2006)¹¹, Davenport et al. (1996)¹², Davenport et al. (1999)¹³, Dijkstra et al. (2017)¹⁴, Duarte et al. (2020)¹⁵, El-Khaled et al. (2022)¹⁶, Frame et al. (2007)¹⁷, Gabara et al. (2018)¹⁸, Gallardo et al. (2021)¹⁹, Gee and Warwick (1994)²⁰, Gestoso et al. (2012)²¹, Glanz (2021)²², Goodsell et al. (2004)²³, Gunill (1982)²⁴, Hacker and Steneck (1990)²⁵, Harvey and Bird (2008)²⁶, Hauser et al. (2006)²⁷, Hooper and Davenport (2006)²⁸, Hughes (2010)²⁹, Hull (1997)³⁰, Karr (2011)³¹, Kelaher and Castilla (2005)³², Leite and Turra (2003)³³, Lenzo et al. (2023)³⁴, Lilley and Schiel (2006)³⁵, Lippert et al. (2001)³⁶, Lutz et al. (2019)³⁷, Mancuso et al. (2021)³⁸, Mancuso et al. (2023a)³⁹, Mancuso et al. (2023b)⁴⁰, Marzinelli et al. (2014)⁴¹, Marzinelli et al. (2016)⁴², Mikhaylova et al. (2019)⁴³, Neves and Costa (2022)⁴⁴, Núñez-Pons et al. (2012)⁴⁵, Ojeda and Santelices (1984)⁴⁶, Parker (1998)⁴⁷, Parker et al. (2001)⁴⁸, Robinson (2015)⁴⁹, Russo (1990)⁵⁰, Schaal et al. (2016)⁵¹, Schmidt and Scheibling (2006)⁵², Schoenrock et al. (2018)⁵³, Shelamoff et al. (2020)⁵⁴, Solano-Barquero et al. (2022)⁵⁵, Stelzer et al. (2021)⁵⁶, Tano et al. (2016)⁵⁷, Taylor and Cole (1994)⁵⁸, Torres et al. (2015)⁵⁹, Veiga et al. (2014)⁶⁰, Velazco-Charpentier et al. (2021)⁶¹, Wikstrom and Kautsky (2007)⁶².

assemblages (Hull, 1997; Leite and Turra 2003; Torres et al., 2015; Mancuso et al., 2023b). For instance, changes in fractal dimensions during the algal vegetative cycle have resulted in changes in associated gastropod communities (Mancuso et al., 2023b) and the timing of peak abundances of ostracod populations (Hull, 1997). The latter author, for example, found that ostracod densities in the most complex alga (*Ceramium nodulosum*) peaked in February, whereas in the least complex alga (*Chondrus crispus*) they peaked in December (Hull, 1997). Meanwhile, the seasonal variation in biomass of a different seaweed (*Sargassum* spp) appeared to be unrelated with the seasonal variation of its own associated epifauna (Leite and Turra 2003). Yet another study (Torres et al., 2015) found that a combination of two of the macroalgal features cited above (fractal area and biomass) were the best predictors of associated epifaunal assemblages.

While the studies cited above examined seaweed structural complexity at the individual level, others have focused on the complexity of specific traits of seaweeds (e.g., thallus and holdfast morphology). Such traits specifically include blades' surface area or density (Gunill, 1982; Russo, 1990; Parker et al., 2001; Kelaher and Castilla, 2005), degree of branching or number of blade branches (Hacker and Steneck, 1990; Chemello and Milazzo, 2002; Lutz et al., 2019), thallus characteristics (i.e., the morphology of full seaweeds) (Taylor and Cole, 1994; Schmidt and Scheibling, 2006; Gallardo et al., 2021), and holdfast characteristics (Ojeda and Santelices, 1984; Hauser et al., 2006; Schmidt and Scheibling, 2006; Lutz et al., 2019). The first features (seaweed surface area and density) have been found to have the strongest relationships with invertebrate assemblages (Kelaher and Castilla, 2005). These features have been shown to contribute to significant increases in invertebrate diversity (Gunill, 1982), from two to ten-fold increases in abundance (Russo,

1990; Gunill, 1982), and up to a 15-fold increase in biomass (Parker et al., 2001). Exceptions have been found, though, where surface area was shown to reduce invertebrate diversity and evenness (Parker et al., 2001).

Physiological features of seaweed thalli have also been linked with significant changes in invertebrate biodiversity (Gallardo et al., 2021) and density levels (Taylor and Cole, 1994). For example, comparing soft and hard thalli, Gallardo et al. (2021) reported a 20–50% increase in biodiversity levels in hard thalli species when compared to soft thalli species. Likewise, Taylor and Cole (1994) showed an inverse relationship between thallus width and invertebrate densities, with a density increase of nearly 300% from the widest to the narrowest thallus. Such a surprising relationships can be explained by the finely structured thinner thalli, which led to a higher small-scale structural complexity that favored epifaunal density (Taylor and Cole, 1994). The branching of the thalli also supported a higher number of taxa and individuals (Lutz et al., 2019), and higher overall abundances and biodiversity levels (Hacker and Steneck, 1990; Chemello and Milazzo, 2002). For example, the degree of branching increased the density of amphipods, among the most common epifaunal groups associated with seaweeds (e.g., Tummon Flynn et al., 2021), from ~2 individuals/100mL interstitial volume on seaweeds with large leathery thalli, to ~22 individuals/100mL interstitial volume on coarsely branched thalli (Hacker and Steneck, 1990).

Structural complexity has also been linked to a prominent group of red coralline algae, the Rhodoliths (Harvey and Bird, 2008; Stelzer et al., 2021; Neves and Costa, 2022). They create a porous habitat that enhances individual and bed physical complexity (Gabara et al., 2018; Cerqueira Veras et al., 2020),

supporting significantly higher diversities than non-living beds or adjacent bare sediments (Robinson, 2015; Stelzer et al., 2021; Neves and Costa, 2022), or even some kelp beds (Schoenrock et al., 2018). Along with complexity, the depth (shallow or deep, in tropical or polar latitudes, respectively; Mikhaylova et al., 2019; Cerqueira Veras et al., 2020) and density of these beds also contribute to biodiversity. Counter examples include studies where different rhodolith forms are only weakly associated with species assemblages (Harvey and Bird, 2008), or host morphology was the most important in determining cryptofaunal assemblages associated with crustose coralline algae (Glanz, 2021). Lastly, regarding macroalgae that have holdfasts, it has been found that taxa richness (Lutz et al., 2019), number of species, species diversity, and abundance (Ojeda and Santelices, 1984; Hauser et al., 2006) all significantly increased in relation with holdfast structural complexity. For example, Hauser et al. (2006) found increases of nearly 170%, 250% and 260% in invertebrate species richness, diversity, and abundance, respectively, from the least to the most complex holdfasts of artificial kelps under comparison. Similarly, Lutz et al. (2019) found that a species of non-indigenous green alga (*Codium fragile* spp. *Fragile*), which possessed more complex holdfasts than native conspecifics (*C. fragile*), held twice the species richness. However, it is noteworthy that at least two studies have found no differences in invertebrate taxa (Schmidt and Scheibling, 2006) and assemblages (Lutz et al., 2019) in relation to the holdfast complexity, for kelp and green algae, respectively.

3 The influence of seaweed habitat features

In addition to features associated with individual seaweeds, several studies have focused on how the structure or makeup of entire seaweed communities (or habitats) contribute to invertebrate diversity. Various aspects of invertebrate communities, including biodiversity, have been associated with seaweed diversity and/or species richness (Parker, 1998; Bates and DeWreede, 2007; Best et al., 2014; Tano et al., 2016), seaweed identity and species composition (Parker, 1998; Lilley and Schiel, 2006; Wikstrom and Kautsky 2007; Bates and DeWreede, 2007; Marzinelli et al., 2016), seaweed assemblage structure (Goodsell et al., 2004; Frame et al., 2007), seaweed habitat size (Shelamoff et al., 2020; Chen et al., 2020; Mancuso et al., 2021), and habitat position in relation to tide level (Davenport et al., 1999; Hooper and Davenport, 2006; Cacabelos et al., 2010; Loke and Todd, 2016). The first of these features, seaweed species richness, has often been correlated with higher invertebrate species richness (Parker, 1998; Best et al., 2014). For instance, Best et al. (2014) found that while habitats with higher algal species richness had ~9% higher animal species richness, they tend to have lower animal abundance. At least two articles have found this association to be weak (Parker, 1998; Bates and DeWreede, 2007) and claimed that seaweed species composition (rather than richness) correlated better with increases in invertebrate diversity. With regards to the structure of seaweed assemblages, Goodsell et al. (2004) did not find causal effects on

species richness, but the makeup of invertebrate communities was significantly different among distinct algal habitat configurations. Likewise, Frame et al. (2007) found that the abundance of ostracods was closely associated with the structural complexity of various algae, while their highest species richness was associated with turf-forming algae.

Macroalgae often form patches, beds, or habitats of limited dimensions. The size of these patches has been positively correlated with invertebrate species richness, abundance, and biomass (Shelamoff et al., 2020; Mancuso et al., 2021). The former author found that a decrease in seaweed patch size reduced animal species richness by 50%, while reducing Shannon-Wiener diversity by 20%, from the largest to the smallest patch (Shelamoff et al., 2020). Similarly, Chen et al. (2020) found that canopy volume in conjunction with algal weight, had a strong correlation with invertebrate abundance and biomass. Variation in biotic and abiotic factors due to differences in geographic location often accounts for part of these relationships. However, studies conducted in high (including polar) latitudes, follow the general trend observed in warmer coasts: bed size and structural complexity favors higher invertebrate diversity (Lippert et al., 2001; Schoenrock et al., 2018). Harsh physical conditions (including ice and wave stress) frequently limit overall diversity in shallow compared to deep habitats, increasing the likelihood of unstable, more fluctuating communities and favoring the development of barren habitats (Lippert et al., 2001; Mikhaylova et al., 2019). Despite that, most evidence suggests that the food, habitat, and refuge associated with complex seaweed beds also favors stability and ultimately local biodiversity (e.g., Lippert et al., 2001; Núñez-Pons et al., 2012; Mikhaylova et al., 2019). Locally, large seaweed beds, particularly kelp forests, display interesting (complex) relationships between canopies, physical conditions and species interactions and diversity. Karr (2011) found that *Macrocystis pyrifera* kelp forests most directly exposed to swell, supported larger density and diversity (and different assemblages) than less exposed forests. The same author suggested that kelp canopy's functional role was a nursery habitat for fish, that indirectly altered trophic interactions (Karr, 2011).

The role played by seaweed beds has also been associated with the presence or absence of certain species, including the giant kelp referred to above (Karr, 2011). For example, large canopies of giant kelp have strong direct and indirect effects on other seaweeds, and ultimately on invertebrate diversity and community structure (e.g., Arkema et al., 2009). As stated above, the influence of "foundation species" (Dayton, 1985; Stachowicz, 2001) exceeds community-level metrics such as biodiversity. Such influence is strong, but as described by Hughes (2010) for the brown alga *Egregia menziesii*, is also complex and varies with local physical conditions and spatial scale. When these key species are artificially removed or lost, they cause strong changes over multiple species and trophic levels (Ellison et al., 2005; Castorani et al., 2018; Montie and Thomsen, 2023). For example, Lilley and Schiel, 2006 found that when a dominant habitat forming seaweed species was removed, the period following removal (up to two years afterwards), was characterized by a significant decrease in the number of invertebrate taxa. In fact, two

years after these experiments, removal plots had ~40% less taxa than control (non-removal) plots (Lilley and Schiel, 2006). Effects on different trophic levels resulting from kelp harvesting in Norway have been reported by Lorentsen et al. (2010) and Christensen-Dalsgaard et al. (2017). Likewise, Perälä et al. (2023) have highlighted the negative influence of the harvesting of *Laminaria hyperborea* forests from the Northeast Atlantic on the survival of Atlantic cod and European lobsters. All those results are closely related with those documented by Wikstrom and Kautsky (2007), who showed that in the absence of a common seaweed, the biomass of associated invertebrates was significantly lower. In addition, Marzinelli et al. (2016) focused on a related aspect with practical implications for biodiversity: these authors found that when transplanted seaweed species are brought into an area, they often support less diversity than the same species in their “undisturbed” condition.

Many macroalgae and the habitats they create are associated with intertidal systems, and therefore, are exposed to periodic emersion. Not surprisingly, several studies have examined how macroalgal structural complexity influences associated assemblages in relation with their position across the intertidal gradient (Davenport et al., 1999; Hooper and Davenport, 2006; Cacabelos et al., 2010). In sheltered shorelines of South Australia, the periodic emersion of three species of macroalgae caused a significant reduction in associated epifaunal numbers. However, macroalgal structural complexity ameliorated these reductions: for organisms associated with the simplest alga (*Enteromorpha*) 44 times as many animals were present when submerged than when emersed, a ratio strikingly higher than the one measured in animals associated with the most complex algae (*Corallina*) for which the submerged to emersed ratio was only 1.8 (Davenport et al., 1999). The reduced losses observed in complex algae was partially attributed to water retention which likely prevents desiccation potential effects. However, trends like these are not necessarily consistent across studies. Hooper and Davenport (2006) compared three macroalgae of distinct structural complexity (as measured by fractal dimensions) and although the most complex alga had the richest associated communities, there were no differences in terms of epifaunal emigration levels during low tide emersion.

4 Implications for conservation, restoration, and monitoring

As the bulk of the information summarized in Table 1 indicates, most research to date shows that macroalgae and the habitats they create contribute to an increase in at least some measure of biodiversity. While those increases range widely from weak to very strong, and the influence of non-native seaweeds or other factors add an additional level of complexity (e.g., Veiga et al., 2016; Lutz et al., 2019; Ndhlovu et al., 2021; Lenzo et al., 2023), seaweeds generally improve rather than hinder associated communities. The most consistent promoter of faunal diversity seems to be the complexity of identifiable features within a seaweed itself (e.g., branching or holdfast morphology; Hacker and Steneck, 1990; Hauser et al., 2006; Lutz et al., 2019; Velasco-Charpentier et al.,

2021) or the complexity achieved by the presence of several individuals or species coming together into a discernable habitat (Best et al., 2014; Tano et al., 2016). Algal structural complexity-biodiversity relationships have also been examined using fractal dimensions, and the outcome of several key studies have provided added support to these relationships (e.g., Mancuso et al., 2023b). However, some of this research has also identified exceptions and highlighted outcome variations, partly due to the strong influence of organisms’ size and spatial scale on fractal dimensions (e.g., Gee and Warwick, 1994). Among the above refereed studies, tide distribution or seasonal variation associated with life cycles, in addition to various concurrent factors (e.g., Ndhlovu et al., 2021) suggest that algal structural complexity is one but not the sole predictor of associated biodiversity levels (Torres et al., 2015).

From a conservation and restoration point of view, such features gain relevance in coastal areas where seaweeds and seaweed habitats are in decline, or otherwise where lasting populations of rare, threatened, or endangered species of seaweeds can be found. Given the importance of these species, some of them coined foundation species (*sensu* Wikström and Kautsky, 2007; Dijkstra et al., 2017; El-Khaled et al., 2022) or ecosystem engineers (Schmidt and Scheibling, 2006; Schaal et al., 2016; Shelamoff et al., 2020), their loss likely entails escalating changes on associated communities. Based on most of the evidence reviewed here, such changes are most likely detrimental to diversity or abundance metrics (Ellison et al., 2005; Norderhaug et al., 2005; Marzinelli et al., 2016). Conserving or restoring by protecting, planting, or transplanting key seaweed species is complex, resource intensive, and provides variable levels of success due to many unaccounted factors (Marzinelli et al., 2016; Whitaker et al., 2023). However, when facing the accelerated loss or displacement of seaweed species caused by climate change (see Bindoff et al., 2019), they represent the best approach for protecting the ecological services they provide and a diversity of reliant organisms that otherwise may be lost as well. The results of this review also suggest that the monitoring of estuarine or coastal fauna should focus heavily on the sampling of seaweed habitats, particularly those holding complex species- or bed-related features. As highlighted above, such features generally contribute to richer associated communities (Christie and Kraufvelin 2004; Frame et al., 2007; Shelamoff et al., 2020; Mancuso et al., 2023a) by providing shelter against harsh physical conditions (e.g., the brown alga *Phyllospora comosa* in exposed rocky reefs of Australia; Marzinelli et al., 2016), or refuge against predators (e.g., a variety of the red alga *Chondrus crispus* in sedimentary bottoms of Atlantic Canada; Tummon Flynn et al., 2020).

Our call for surveys that include the careful examination of seaweed habitats applies to every type of organism. However, our review incidentally found that meiofaunal groups warrant further attention (see e.g., Da Rocha et al., 2006; Veiga et al., 2016), and a particular group among macrofaunal organisms, the amphipods, has been the most recurrently found, sampled, and studied in relation to seaweed characteristics (Table 1). Similar conclusions were highlighted in Christie et al. (2009)’s review of organisms associated with macrophytes, including macroalgae. These authors

showed that amphipod abundances were dynamic (due to dispersal, colonization, and behavior) but consistently among the highest. Likewise, complex interactions between chemically defended macroalgae and amphipods have been documented in multiple regions, including Antarctic habitats (Brawley, 1992; Núñez-Pons et al., 2012). It follows that in a scenario of further seaweed declines due to climate change, amphipods (and the consumers relying on these small crustaceans for food) will be among the most directly affected. Considering the plausibility of monitoring, we argue that among the macrobenthic taxa associated with macroalgae, amphipods may be among the species to be studied as recurrent users of rugose habitats such as those provided by many morphologically complex algae.

This overview made also evident a potential geographic gap: most of the studies examined were conducted in warm, low-mid latitudes, such as southern U.S.A., the Mediterranean coasts or Australia (Hacker and Steneck, 1990; Russo, 1990; Taylor and Cole, 1994; Lutz et al., 2019; Shelamoff et al., 2020), although a representative number of studies from high (including polar) latitudes have been also considered (e.g., Lippert et al., 2001; Núñez-Pons et al., 2012; Velasco-Charpentier et al., 2021). Often, the diverse complement of seaweeds found in low-mid latitude regions support rich associated communities, making the influence of features such as physical complexity potentially more evident. The lower representation of higher latitude (potentially less diverse) seaweed-invertebrate communities may mask additional relationships in those regions, and merits further examination. Similarly, there was a relatively high number of studies conducted in rocky shores (e.g., Taylor and Cole, 1994; Buschbaum and Chapman, 2006; Schaal et al., 2016; Dijkstra et al., 2017) in comparison to those conducted in sedimentary habitats. Despite obvious differences, physical complexity of seaweeds or seaweed morphological features remained consistently related with biodiversity levels. Still, distinct ecosystems warrant further attention and open a potential venue for future comparative studies to help us better understand how these relationships operate. As forecasted (Bindoff et al., 2019), climate events will continue to displace and locally exclude seaweed species, so knowledge on the seaweed features that contribute the most to the biodiversity of associated organisms should quickly transition to practice. Ultimately, ongoing seaweed losses should be matched by further monitoring, conservation, and restoration efforts.

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EG: Data curation, Formal analysis, Investigation, Writing – original draft, Writing – review and editing. PQ: Conceptualization, Formal analysis, Funding acquisition, Investigation, Supervision, Writing – original draft, Writing – review and editing.

Funding

The author(s) declare financial support was received for the research, authorship, and/or publication of this article. A CGS-M fellowship (EG) and a Discovery grant (PQ) both from the Natural Sciences and Engineering Research Council of Canada (NSERC) provided support during the preparation of this Minireview.

Acknowledgments

We thank Paula Tummon Flynn and K. Devon Lynn (UPEI), and two reviewers for their feedback on earlier versions of this manuscript.

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.

The author(s) declared that they were an editorial board member of *Frontiers*, at the time of submission. This had no impact on the peer review process and the final decision.

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