Sci

MDPI

Systematic Review

Epibionts and Epiphytes in Seagrass Habitats: A Global Analysis of Their Ecological Roles

Nicoletta Marsiglia [1], Mar Bosch-Belmar [1,2,3,*], Francesco Paolo Mancuso [1,2] and Gianluca Sarà [1,2]

[1] Laboratory of Ecology, Department of Earth and Marine Sciences (DiSTeM), University of Palermo, 90128 Palermo, Italy; nicoletta.marsiglia@unipa.it (N.M.); francesco.mancuso@unipa.it (F.P.M.); gianluca.sara@unipa.it (G.S.)
[2] National Biodiversity Future Center (NBFC), 90128 Palermo, Italy
[3] Consorzio Nazionale Interuniversitario per le Scienze del Mare (CoNISMa), Piazzale Flaminio 9, 00196 Rome, Italy
* Correspondence: mariadelmar.boschbelmar@unipa.it

Abstract: Seagrass ecosystems support complex biological interactions that shape marine community structure and ecosystem functioning. Thanks to their structural complexity, they support heterogeneous communities and interact with associated benthic invertebrates and fish populations, establishing complex relationships that influence the performance and fitness of the involved organisms. This study, through a systematic review, investigated the existing potential biotic interactions between seagrasses and epibionts–epiphytes on a global scale. We created a complex search string and ran it in the online databases Scopus and Web of Science, yielding a total of 62 final outcomes spanning from 1984 to 2024. Our results revealed both positive and negative effects of different biotic interactions among these habitat formers and their associated symbionts. The review showed that the most studied interactions referred to *Posidonia oceanica* (Delile, 1813) L. and *Zostera marina* (Linnaeus, 1753), which provide refuge and habitat to different epiphytes and epibionts. The reviewed studies highlighted the importance of epiphytes, their potential role in seagrass growth, nutrient dynamics, and their implications for light absorption, while epibionts enhance canopy structure and can protect seagrasses from predation, but potential drawbacks remain poorly understood. Understanding and preserving these intricate biotic interactions is critical to ensuring the long-term functionality and resilience of seagrass ecosystems in a continuously changing environment.

Keywords: biotic interaction; seagrasses; symbionts; epiphytes; epibionts; functioning; systematic review

Academic Editor: Panagiota Katikou

Received: 20 November 2024
Revised: 9 March 2025
Accepted: 25 April 2025
Published: 8 May 2025

Citation: Marsiglia, N.; Bosch-Belmar, M.; Mancuso, F.P.; Sarà, G. Epibionts and Epiphytes in Seagrass Habitats: A Global Analysis of Their Ecological Roles. *Sci* **2025**, *7*, 62. https://doi.org/10.3390/sci7020062

1. Introduction

Biotic interactions are one of the main factors influencing the distribution and abundance of species worldwide [1,2]. Among these, the interaction between habitat-forming species and their associated biodiversity plays a fundamental role in ecosystem functioning [2,3]. The performance, abundance, and distribution of these structuring species may affect the dynamics of biotic interactions such as predation and competition, and may influence the effect of abiotic stress (such as thermal stress) in the associated community [4–7]. As such, widely distributed habitat formers like trees, corals, and canopy macroalgae sustain extremely rich and varied communities [8,9]. Particularly, seagrasses are marine flowering plants that provide important shallow-water ecosystems all around the world. A wide variety of organisms, including fish and invertebrates with significant commercial value, find food and refuge under their massive canopies and the organic matter that they deposit in sediments [10].

Seagrasses are highly productive, habitat-forming species found worldwide, creating densely populated meadows that offer a variety of important ecosystem services. These services vary significantly among seagrass species, including (i) raising the pH and O_2 levels in the surrounding water column during the day, which benefits calcifying organisms such as corals [11–13]; (ii) protecting the coast from erosion through wave attenuation [13]; (iii) providing a range of feeding and nursery grounds, particularly for juvenile fish and marine invertebrates [13]; (iv) absorbing nutrients such as nitrogen and phosphorus, thereby improving water quality [13]; and (v) efficiently sequestrating and fixing carbon into the sediment, making them important blue carbon ecosystems and thus mitigating climate change [13–15]. Their ecosystem services are considered highly valuable, with some estimations suggesting their contribution to ecosystems may rival those of coral reefs and tropical forests in certain contexts, in terms of carbon sequestration and coastal protection [16]. Healthy and productive seagrass meadows are thus important for ensuring a good environmental state of marine waters, especially in coastal regions [13]. In shallow waters, seagrasses grow in a range of sediment types and often offer the only solid substrate that macroalgae may attach to. According to Kitada et al. [17], their presence can increase the surface area of the bottom suitable for colonization by epiphytic or epibenthic diatoms by a factor of 5 to nearly 19. The overall primary production of the seagrass ecosystem is substantially increased by offering additional suitable substrate to photosynthetic organisms [18].

Different studies examining interactions between seagrasses, epiphytes, epibionts, and grazers date back to the early 1990s [19–21]. At that time, these relationships were considered complex and poorly understood. Since then, our understanding has improved. One of the key aspects of these interactions is the colonization of leaves by epiphytes and epibionts. Seagrasses are now recognized as providing substrate for different epibionts and epiphytes, with which they can have both positive and negative interactions. Seagrasses and the epiphytic algae that develop on their leaves are closely linked, as are the invertebrate herbivores that feed on these epiphytes [20,22,23]. The leaves of seagrasses facilitate mesograzers [20,22,23]. Their biotic interactions with epiphytes, epibionts, and mesograzers influence biodiversity, primary productivity, and ecosystem functionality [20]. The diversity of seagrass-associated communities varies along natural environmental gradients, such as light availability, nutrient levels, temperature, and hydrodynamics, significantly affecting the growth and survival of host plants. Also, the composition and productivity of communities that live in interaction with seagrasses leaves vary with abiotic and biotic factors [20]; for example, variations in nutrient and light availability, mechanical disturbance, such as turbulence and currents, that can lead to leaf abrasion and damage, salinity, and seagrass desiccation, or biotic factors, such as the presence of grazer, that remove large portions of seagrass leaves with attached algal epiphytes or periphyton grazers, remove only loosely adhering diatoms, and possibly algal sporelings, but leave the leaves intact [20], or they influence the growth rate, age, and morphology of seagrass leaves, chemical exchanges (nutrient, DOC), and competition for space with other algae or sessile fauna [20].

Seagrass communities worldwide are threatened by the combined effects of local anthropogenic stressors and global climate change [23–25], facing both top-down effects that alter grazer population and behaviour and bottom-up effects that directly impact seagrass performance and, consequently, their associated communities and consumers. As recently reported by Chen et al. [26], different drivers of climate change, such as marine heatwaves or high-intensity cyclones, can negatively impact on seagrass health and their associated epifauna. This impact has been shown in terms of reducing canopy growth rates and increasing detachment processes, provoking spatial meadow fragmentation and finally causing seagrass and associated biodiversity loss. In addition, physical disturbance, herbivory, and light and nutrient availability are all factors influencing seagrass functioning [25,27,28]. Eutrophication can promote excessive epiphyte proliferation, reducing seagrass growth and modifying the structure of associated communities [24]. For this reason, it is essential to study the key biotic interactions between seagrasses and their associated communities, as well as their roles in habitat functioning and the ecosystem services they provide.

The purpose of this systematic review was to compile and analyze existing research on biotic interactions between seagrasses and their symbionts across different geographical regions. This review aimed to provide an overview of the biotic interactions between these habitat-forming species and their associated epibionts and epiphytes, highlighting the benefits and drawbacks of different types of interactions. Understanding the various types of biotic interactions and studying how they can influence the performance of the species involved is crucial in the current and future context of climate change, and may help to assess how these relationships influence ecosystem functioning and resilience under stressful conditions.

2. Materials and Methods

This systematic review was performed by applying the Preferred Reporting Items for Systematic Reviews and Meta-Analyses (PRISMA) guidelines proposed by Liberati et al. [29–31].

2.1. Search Strategy

The PRISMA method was applied to explore one main research question: (1) what are the biotic interactions between seagrasses or phanerogams and their epibionts–epiphytes? And a secondary question, what are the advantages and disadvantages of different types of biotic interactions (symbiosis, mutualism, and commensalism) between these organisms? To answer these questions, a literature search was conducted using the PICO (Population, Intervention, Comparison, and Outcomes) approach to define our keywords. The PICO elements were as follows: population of interest (P)—biotic (species) components; intervention (I)—all different types of biotic interactions between epibionts, epiphytes, and habitat-forming organisms, such as seagrasses and phanerogams; comparator (C)—different responses of communities to different types of biotic interaction; and outcomes (O)—species' complex interactions, and the advantages and disadvantages of the biotic interactions between seagrasses and epiphytes–epibionts. Based on these PICO elements, the following research string was developed: (biotic interaction OR commensalism OR mutualism OR symbiosis) AND (epiphyt* OR epibiont* OR symbiont*) AND (seagrass* OR phanerogam*). The initial search was carried out on 18 December 2023, and was repeated on 26 June 2024 on Elsevier's Scopus (www.scopus.com) and Clarivate Web of Science (www.webofknowledge.com) databases.

2.2. Study Selection

The results were reported according to the PRISMA guidelines, following four steps: (1) identification, (2) screening, (3) eligibility, and (4) inclusion. The identification step involved identifying records through database searching and removing duplicates. The screening step consisted in reviewing papers by title and abstract, and based on the inclusion/exclusion criteria, determining whether they would proceed to the next screening phase. The eligibility and inclusion steps were guided by a set of selection criteria, involving a more detailed assessment at the full-text level. The inclusion criteria encompassed studies focusing on the following:

(1) The biotic interactions between seagrasses and epibionts, mobile fauna, and epiphytes;
(2) The effects of these biotic interactions on the host.

The exclusion criteria included the following:

(1) Off-topic studies;
(2) Non-English-language publications;
(3) Incomplete book chapters.

Data were extracted from the selected records using a structured matrix. This matrix included information such as publication date, habitat details (location, country, latitude and longitude), species characteristics (taxonomic order and species), specific details of biotic interactions, types of biotic interactions (mutualism, commensalism, symbiosis), seagrass role, advantages and disadvantages of the biotic interactions, and additional comments.

2.3. Data Extraction

The initial search identified 378 records (scientific papers), with 147 records from Web of Science and 231 from Scopus. After removing 145 duplicates, 233 records remained for further screening. The screening process was conducted in three stages. In the first two stages, the title and abstract were reviewed, resulting in the exclusion of 143 records, leaving 90 records for full-text evaluation. In the third stage, full-text screening resulted in the exclusion of 11 additional records, while 79 were assessed for exclusion based on specific reasons. Ultimately, 62 records were included in the systematic review. The identification and selection process is illustrated in Figure 1.

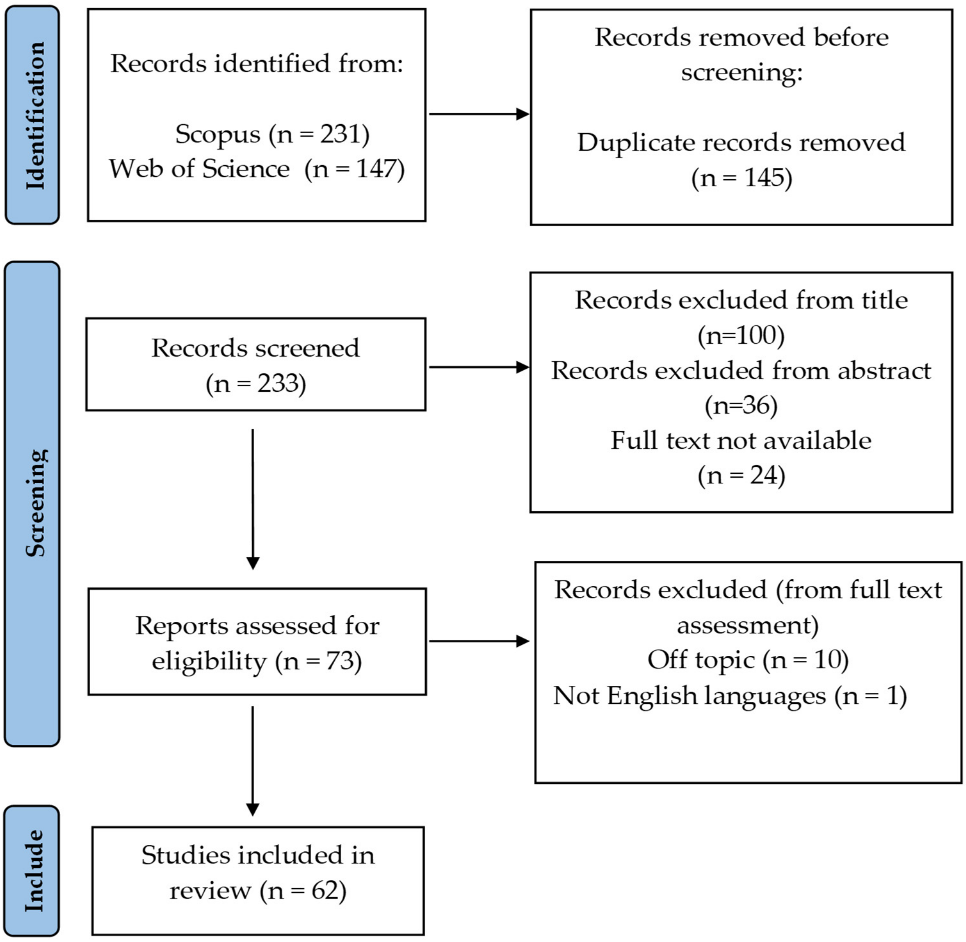

Figure 1. PRISMA 2020 flow diagram illustrating the systematic review process for literature selection.

3. Results

The selected records spanned from 1984 to 2024, with the highest number of studies occurring between 1999 and 2006, averaging 4 records per year during this period (Figure 2). From the 62 peer-reviewed papers analyzed, 106 interactions between seagrasses and their symbionts were identified and examined.

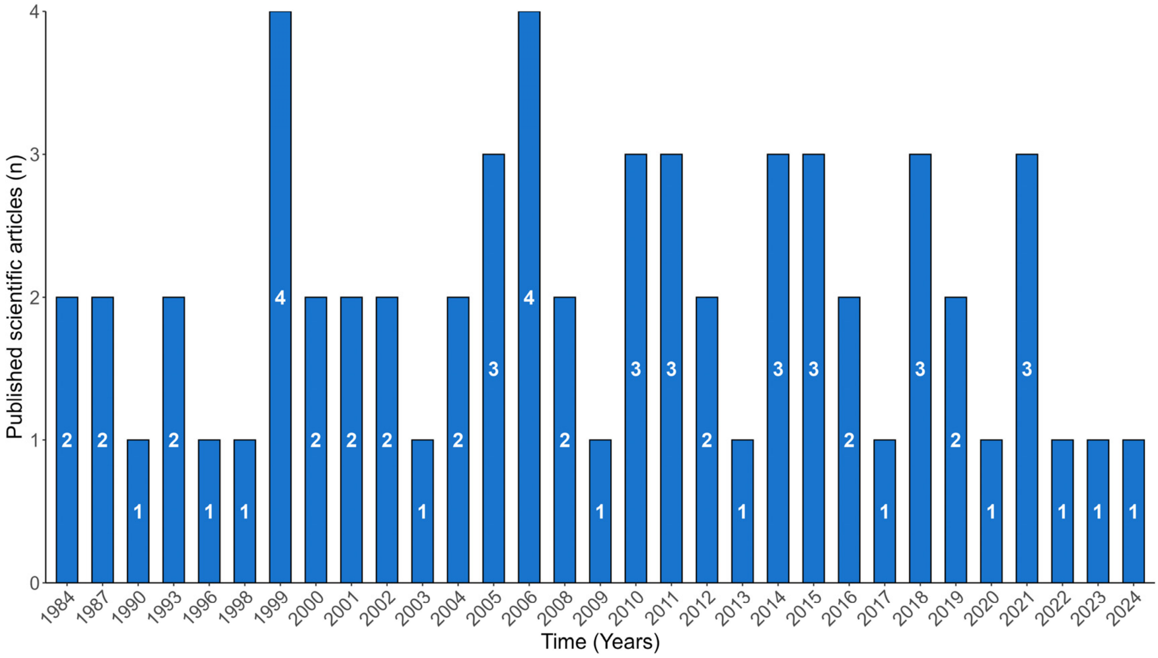

Figure 2. Temporal trend of scientific published articles on the existing interactions among seagrasses and their epiphytes and epibionts at a global scale included in the systematic review.

The analyzed studies focused on seagrasses or vegetal foundation species of the order Alismatales, such as *Posidonia oceanica*, *P. australis* (Hook, 1858), *P. sinuosa* (Cambridge & J.Kuo), *Cymodocea nodosa* ((Ucria) Ascherson, 1870), *C. rotundata* (Ascherson & Schweinfurth, 1870), *Zostera marina*, *Z. capricorni* (Aschers, 1876), and *Z. caespitosa* (Miki, 1932) species. These species cover a worldwide distribution, with 55% of the studied cases concentrating on the Mediterranea Sea (Figure 3). Most studies examined biotic interactions among epibionts–epiphytes–seagrass or grazers–epiphytes–seagrass, focusing on the roles of epiphytes, epibionts, and grazers in their interactions with seagrasses and considering both the advantages and disadvantages of these interactions.

Regarding the impact of seagrass on epiphytes, the studies reported varied and sometimes contained conflicting information. Some papers indicated that seagrasses may negatively affect epiphytes by inhibiting their growth through the release of chemical compounds such as phenolics [22,32]. Others suggested that seagrasses are not simply inert substrates for microalgal attachment, but rather they influence community composition by altering competitive interactions between different microalgal groups [32,33]. Additionally, some papers highlighted the role of seagrasses as refuges from predators [22,34].

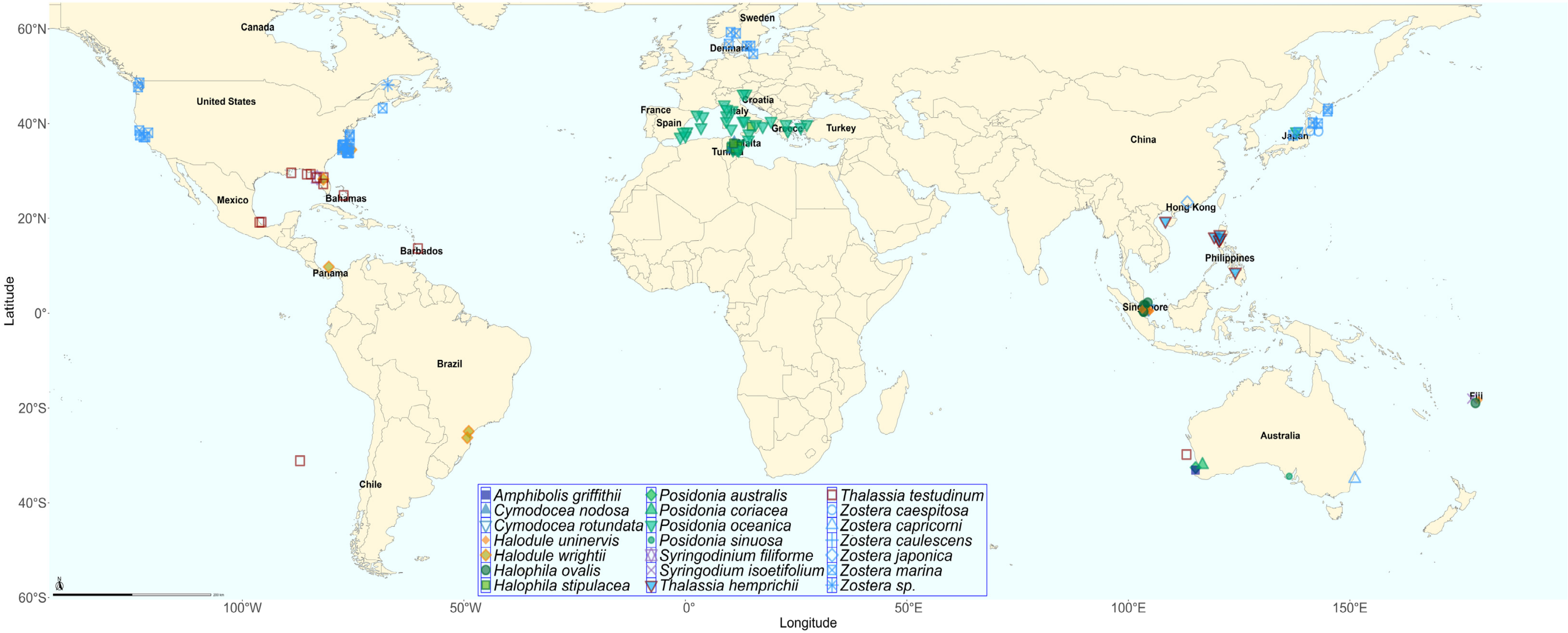

Figure 3. Case studies (n = 106) geographic location and main seagrass species involved in the biotic interactions. Each marker shape represents a different seagrass species identified in the review, while different colours group species by genus.

3.1. Seagrasses and Epiphytes–Epibionts Communities

All seagrasses presented different epiphytic species on their leaves (Figure 4). Studies reported that *Z. marina* mainly presented green and brown algae, filamentous and encrusting diatoms (mainly *Cocconeis scutellum* (Ehrenberg, 1838)), and filamentous algae (mainly *Delesseria sanguinea*). In contrast, *Posidonia oceanica* supports a broader range of epiphyte species, including epiphytic diatoms (*Amphiprora constricta* (Ehrenberg, 1843), *Climacosphenia moniligera* (Ehrenberg, 1943), *Asteromphalus flabellatus* (Brèbisson) Greville, 1859), and cyanobacteria (*Oscillatoria* sp., *Anabaena* sp., and *Pseudanabaena* sp.)) [35]. *Thalassia testudinum* hosts periphyton, epiphytic cyanobacteria, and diatoms, with the genus *Cocconeis* being particularly dominant [36]. In *Halophila stipulacea*, interactions with different filamentous red algae species have been identified (e.g., *Pseudoceramium tenerrimum* ((Martens) Barros-Barreto & Maggs, 2023), *Dasya corymbifera* (Agardh, 1841), *Polysiphonia tenerrima* (Kutzing, 1843), *Spyridia filamentosa* ((Wulfen) Harvey, 1833), and *Wrangelia penicillata* (Agardh, 1828)), as well as coarsely branched species like *Chondria pygmaea* (Garbary & Vandermeulen, 1990) and *Laurencia* sp. [37].

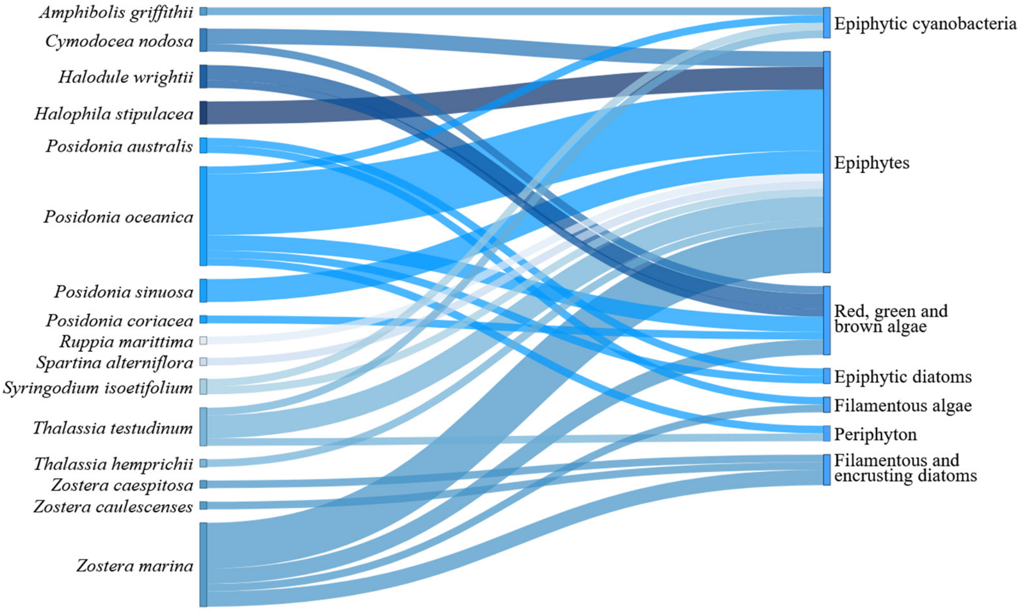

Figure 4. Interactions between seagrass species and their relative epiphytes reported in the analyzed case studies. The fluxes in the width of the bars are representative of the number of studies. Seagrass colours identify species belonging to the same genus.

Regarding epibiont interactions with seagrasses (Figure 5), amphipods and polychaetes were the most reported taxa. The most studied seagrasses were *Zostera marina*, *Posidonia oceanica*, and *Thalassia testudinum* (Banks ex König, 1805). Among them, studies on *Z. marina* focused on its interaction with different epibionts, including molluscs (*Rissoa* sp., *Rissoa membranacea* (Adams, 1800), *Littorina littorea* (Linnaeus, 1758), *Theodoxus fluviatilis* (Linnaeus, 1758), and *Radix baltica* (Linnaeus, 1758)), crustaceans (mainly *Gammarus locusta* (Linnaeus, 1758), *Gammarus oceanicus* (Segerstråle, 1947), and *Idotea balthica* (Pallas, 1772)), amphipods (*Microdeutopus gryllotalpa* (Costa, 1853)), and different species of decapods, nudibranchs, polychaetes, isopods, turbellarians, and sea anemones. Reported epibionts for *Posidonia oceanica*, however, included different species of amphipods (*Apherusa chiereghini* (Giordani Soika, 1950), *Dexamine spiniventris* (Costa, 1853), *Gammarus* spp.)), molluscs (*Jujubinus striatus* (Linnaeus, 1758), *Bittium reticulatum* (Costa, 1778)), sea anemones, decapods, and different species of other marine invertebrates. Meanwhile, *Thalassia testudinum* hosted amphipods, crustaceans (*Tozeuma carolinense* (Kingsley, J.S. 1878)), gastropods (*Turbo* *castanea* (Gmelin, 1971)), decapods (*Pagurus maclaughlinae* (Garcìa-Gomez, 1982), *Thor manningi* (Chace, 1972)), bivalves (*Modiolus americanus* (Leach, 1815)), and protozoan ciliates (e.g., *Lagotia expansa* (Levinson, 1893), *Metafolliculina andrewsi* (Hadzi, 1938), *Parafolliculina tristanensis* (Dons, 1948), *Acineta tuberosa* (Pallas, 1766)).

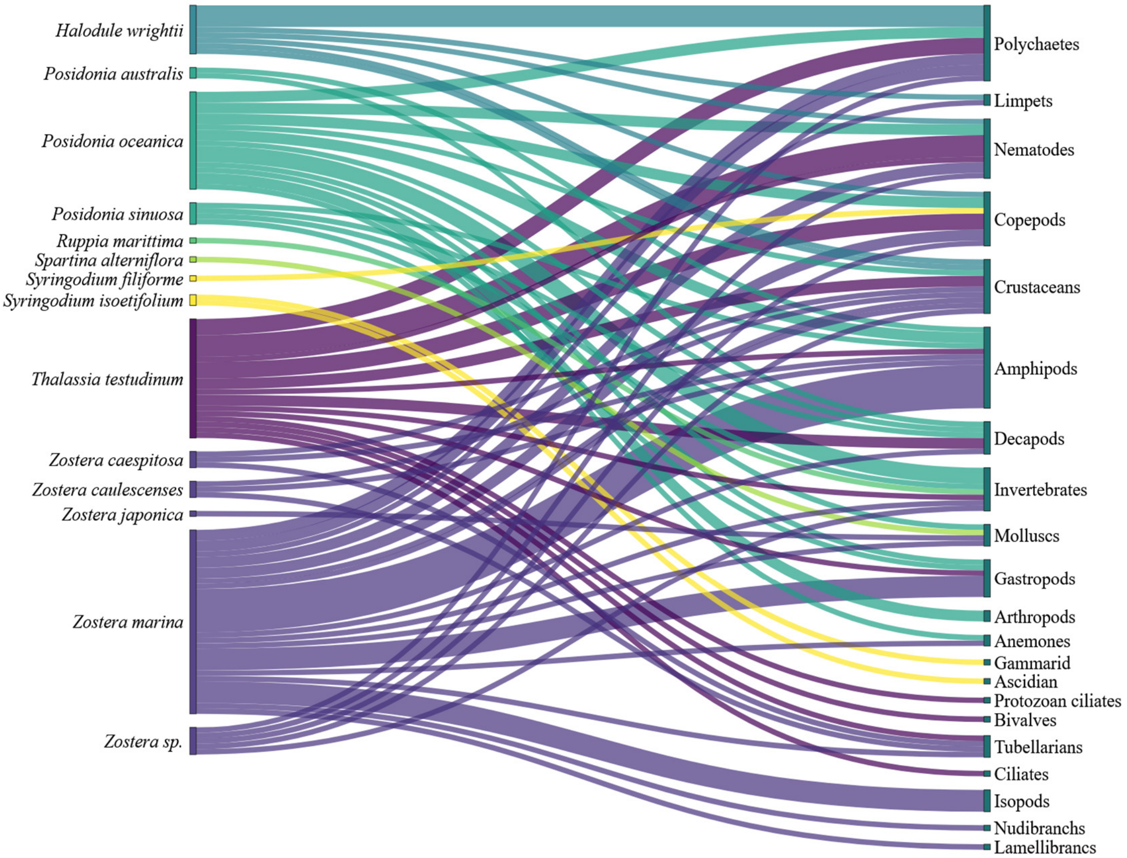

Figure 5. Interactions between seagrass species and their relative epibionts reported in the analyzed case studies. The fluxes in the width of the bars are representative of the number of studies. Seagrass colours identify species belonging to the same genus. Labels for high taxonomic groups, such as phyla, reflect studies where a lower taxonomic level was not specified.

Studies focused on macrofauna associated with seagrasses (Figure 6) showed that *Z. marina* was mainly associated with crabs (*Carcinus maenas* (Linnaeus, 1758)), brittles stars, fish (*Nerophis ophidion* (Linnaeus, 1758), *Syngnathus typhle*, *Micrometrus minimus* (Gibbons, 1854), *and Paralabrax clathratus* (Girard, 1854)), and pen clam (*Atrina rigida*, (Lightfoot, 1786)). *Posidonia oceanica* leaves interacted with and hosted fish (*Sarpa salpa* (Linnaeus, 1758)), different mollusc species, and sea urchins (*Paracentrotus lividus* (Lamarck, 1816)), while, among *T. testudinum* leaves, sea urchins (*Lytechinus variegatus* (Lamarck, 1816), fish (*Lagodon rhomboides* (Linnaeus, 1766)), crustaceans, turtles, waterflow, and dugongs were the main taxa reported.

3.2. Detected Interactions

Studies highlighted both the benefits and drawbacks of biotic interactions between seagrasses and symbionts (Figure 7). The majority of case studies (70.8%) reported positive interactions among seagrasses and their symbionts, and just one reported a negative effect of epibionts on their host. For example, most of the studies focused on the positive role of epiphytes growing on seagrasses as a food source for epifauna and herbivores [22,37–40]. Epiphytes also improve the primary production of the system, protect seagrasses from desiccation caused by tidal and wind action, and, finally, improve biodiversity, supporting epifauna community (Figure 7a) [32,38,39]. Among them, diatoms and microalgae not only represent a source of food, but also improve the system's primary production and biodiversity [32,33,41], while cyanobacteria mainly provide food for epifauna [42]. Despite the many positive roles of epiphytes for their hosts and the associated macrofauna, they also can negatively affect their surrounding environment (Figure 7b). They can limit light, significantly reducing seagrass growth and photosynthesis, but also reducing nutrient exchange between phanerogams and the water column [32].

Epibionts living on seagrasses are organisms playing significant roles (Figure 8), increasing the physical complexity of the canopy, protecting seagrass from predation, and finally providing a very important trophic link between seagrasses and secondary consumers, such as fish and decapod crustaceans [43]. Thus, epibionts such as invertebrates and crustaceans, act as trophic mediators: they transform organic matter of plant origins into edible matter for higher trophic level organisms, facilitating the transfer of energy and nutrients from the vegetative environment to marine trophic networks [32]. Moreover, invertebrates and suspension-feeding bivalves contribute to increasing the complexity of seagrass canopies [44] through a combination of factors, including sediment enrichment, enhanced water quality, and trophic interactions that promote biodiversity [44–47]. Despite their importance, only 17.7% of 62 published articles focus on the role of epibionts in seagrass functioning, while the majority (82.3%) emphasize epiphytes. This imbalance highlights the need for more research into the ecological contributions of epibionts.

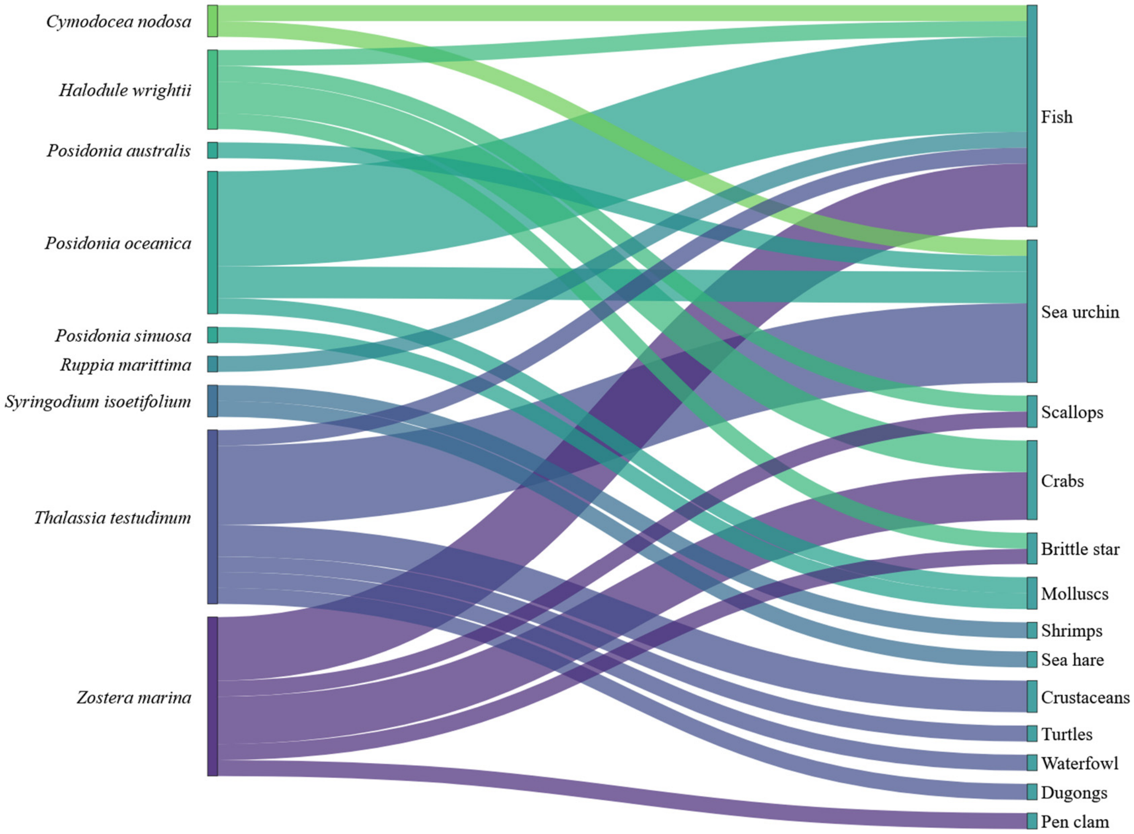

Figure 6. Interactions between seagrass and macrofauna reported in the analyzed case studies. The fluxes in the width of the bars are representative of the number of studies. Seagrass colours identify species belonging to the same genus.

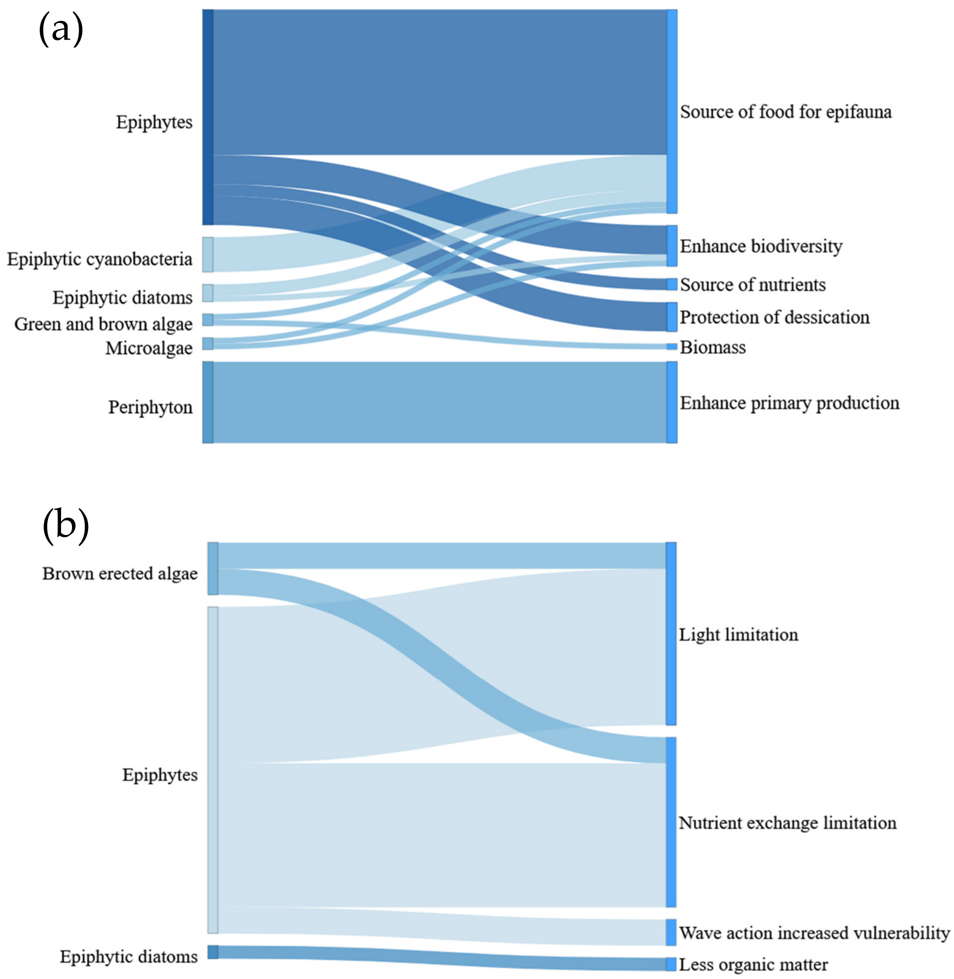

Figure 7. Positive (**a**) and negative (**b**) roles of epiphytes interacting with seagrasses. The fluxes in the width of the bars are representative of the number of studies.

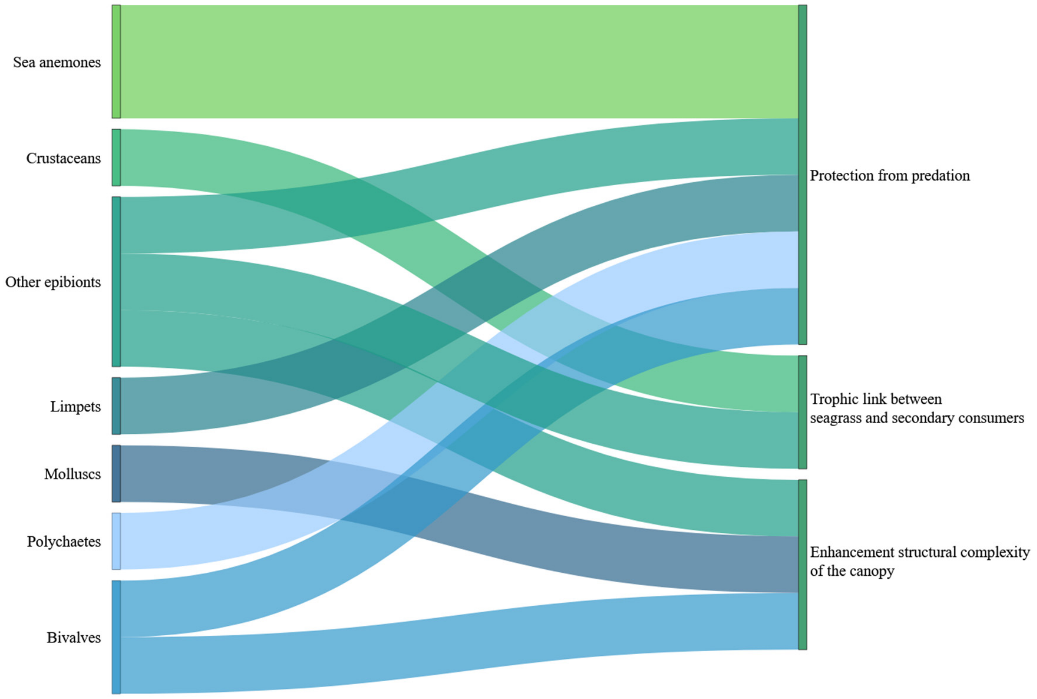

Figure 8. Positive roles of epibionts interacting with seagrasses. The fluxes in the width of the bars are representative of the number of studies.

4. Discussion

Our systematic review revealed complex interactions between seagrasses and their symbionts (epibionts–epiphytes), emphasizing both the benefits and drawbacks for habitat-forming species, as well as the indirect contribution of these biotic interactions to the community structure and functioning.

4.1. Seagrass-Epiphytes Interactions

Seagrasses offer numerous advantages to symbionts, including serving as refuges, providing a substrate for epiphytes and epibionts, and offering a strategic position for acquiring food and light. However, seagrasses can also inhibit the growth of epiphytes by releasing chemical compounds such as phenolics, which have an inhibitory effect on microalgae and bacteria [48]. These dual interactions highlight the complexity of seagrass–epiphyte relationships.

Spatial and temporal variability in epiphyte communities in host organisms has been widely studied [49–51]. Seagrass leaves serve as a dynamic substratum for both sessile epifauna and epiphytes [32], and their morphological traits can influence symbiont position and types of interaction. Variations in epiphyte diversity may be influenced by the seagrass species, leaf length, growth rate or turnover, surrounding environment, and availability and spatio-temporal distribution of epiphyte propagules. In addition, epiphyte colonization and community structure have been found to be influenced by local light and temperature conditions [52], grazing pressure, and/or nutrient concentration [53,54]. Moreover, water motion and the variety of algal propagules influence epiphyte growth, and colonization processes in general [55,56].

The impact of epiphytes on seagrasses is one of the most extensively studied topics in the scientific literature [22,32,36,57,58]. Among their many roles, epiphytes contribute significantly to these interactions by shielding seagrass leaves from predators. Seagrass leaves and stems provide substrate where grazer–epiphyte interactions take place, hosting a wide diversity of grazers, including fish, molluscs, and crustaceans. While gastropods are particularly effective at controlling epiphyte biomass, filter-feeding molluscs are considered important herbivores in filtering phytoplankton [59]. Filer-feeders transform suspended material by changing particle size distributions in the water column and by converting particulate material into dissolved constituents or biomass via metabolism processes [32]. Peterson and Heck [45] proposed that bivalves could establish positive feedback loops in aquatic ecosystems. Suspension-feeding bivalves consume phytoplankton, assimilating organic matter while simultaneously excreting ammonium as a metabolic byproduct through excretion and diffusion across gill membranes. This released ammonium serves as a readily available nitrogen source for primary producers, such as seagrasses and macroalgae, enhancing their growth and photosynthetic efficiency. The increased plant biomass, in turn, can support further phytoplankton production by stabilizing sediments and enhancing nutrient retention, thereby reinforcing the feedback cycle. Although their role in grazing the propagules of epiphytes is little known, it is insignificant compared to the grazing activity of gastropods [32].

Grazing is a crucial process in seagrass ecosystems for three main reasons: it influences the productivity of the seagrass communities [10]; it may affect the species composition of seagrass epiphytes [60]; and it provides a major trophic link for the cycling of nutrients [10,38]. Grazers can help control epiphytic biomass and productivity, thus reducing the potential negative effects of these on host organisms. This regulation can occur through different trophic levels, impacting seagrass ecosystems. The assemblage of small invertebrates living in seagrass beds can provide top-down control of epiphytes by directly grazing on epiphytic algae, while nutrient concentration, a bottom-up factor, can affect epiphytes and seagrasses differently [61]. The addition of nutrients can lead to either higher or lower seagrass productivity, with significant decreases often attributed to human-induced nutrient enrichment in coastal water. Excess nutrients can lead to an increase in phytoplankton biomass and the growth of epiphytes on seagrass leaves, consequently reducing light penetration in the water column and limiting light availability at the leaf surface. Both effects can negatively impact seagrass performance and growth [62]. Excess nutrients can lead to an increase in phytoplankton biomass and the growth of epiphytes on seagrass leaves, consequently reducing light penetration in the water column and limiting light availability at the leaf surface. Both effects can negatively impact seagrass performance and growth.

According to Richardson (1980) and Penhale and Smith (1977) [63,64], one of the key protective roles of epiphytes is the reduction in possible macrophyte desiccation during low water levels via the entrapment and retention of moisture by diverse epiphytic algae species. It was shown by Trocine et al. (1981) [65] that epiphytes also protect *Halophila engelmannii*, *Syringodium filiforme*, and *Halodule wrightii* from UV radiation damage. While *H. wrightii* and *S. filiforme* showed varying tolerances and photo-repair mechanisms, *H. engelmannii* was intolerant of ultraviolet radiation [20]. The pattern that epiphytes often follow when colonizing seagrass blades may have additional positive effects on the host plant. The distal parts of blades are the oldest and typically the most densely epiphytes due to seagrasses' basal leaf development. Both sea urchins (Ott and Maurer 1977) and parrotfish (Lobel and Ogden 1981) like to eat these tips. It is believed that removing senescent and heavy epiphyte leaf tips selectively will improve light penetration through the seagrass canopy and inflict no harm on the seagrass (Ott and Mauer 1977; Lobel and Ogden 1981). As a result, epiphytes may cause direct grazing to shift to senescent leaf tissue from the seagrasses' primary photosynthetic (i.e., more basal) tissue [20].

A key element of seagrass–epiphyte interactions is related to the nutrient exchange between them (microalgae and seagrasses) [22]. Indeed, the population of bacteria on *Zostera marina* may be supported almost entirely by carbon obtained directly from seagrass photosynthesis [66]. Seagrasses swing in response to wave action and currents, which may play a significant role in producing steep chemical diffusion gradients, eliminating potential growth-inhibiting substances, and clearing accumulated sediments [25]. This movement improves the nutrient exchange and growth of epiphytes [13]. Importantly, epiphytes form a boundary layer around seagrass leaves, as documented by Orth and van Montfrans (1984) [22], which can influence oxygen and nutrient diffusion. While this microenvironment can enhance localized exchanges, it can also act as a barrier, reducing the availability of nutrients and oxygen from bulk water to the seagrass tissues. This effect may impact the photosynthetic efficiency and overall health of seagrasses, especially in environments where water movement is limited. The competition for light and nutrients between epiphytes and seagrasses has been well documented (Cebrián et al., 1999) [57], and its implications vary with leaf age and environmental conditions. Cebrian et al. (1999) observed that epiphyte biomass follows a sigmoidal accrual pattern along the lifespan of *Posidonia oceanica* leaves, with older leaves supporting significantly higher loads. The increased epiphytic load can exacerbate shading effects, leading to a reduction in seagrass productivity. Moreover, epiphytes can absorb up to 30% of incident light on older leaves, potentially decreasing photosynthetic efficiency. Given that older *P. oceanica* leaves already experience reduced productivity, this additional light attenuation may further constrain their metabolic performance.

Despite all these positive effects, the presence of epiphytes on seagrass leaves may also entail negative effects, such as limiting light absorption, leading to decreased growth of seagrasses [32,57,67] and reducing photosynthetic rates [36,58,68]. They can compete for nutrients in the water column, and may also increase the susceptibility of seagrasses to leaf loss when subjected to physical forces such as wave action [54]. Additionally, the diffusion barrier created by epiphytes may reduce metabolic efficiency by limiting the exchange of dissolved gases and nutrients between seagrasses and their surrounding environment, further impacting seagrass performance [69].

The results showed that epiphytes represent overall a source of food for epifaunal organisms and play an important role in the trophodynamics of seagrass communities. They can enhance primary production thanks to periphyton, contributing significantly to the overall productivity of seagrass meadows [52,70]. Moreover, they can reduce water movement and protect littoral seagrasses in the low tide from desiccation and insolation [71], contributing to the biodiversity of these systems, and helping to determine the composition of mobile assemblages. The total primary production of the systems is increased by photosynthetic epiphytes [72], and this productivity can equal or surpass that of farmed terrestrial ecosystems [73].

4.2. Seagrass–Epibionts Interactions

Marine epibionts are organisms living on the leaves of seagrasses, contributing to primary production, increasing canopy physical complexity, and facilitating nutrient cycling. Despite their importance, only 17.7% of 62 published articles focus on the role of epibionts in seagrass functioning, while the majority (82.3%) focus on epiphytes.

Epibionts contribute significantly to seagrass communities by providing a food source for heterotrophic fauna [32,62,74]. Meiofauna associated with seagrasses often exploit epiphytic algae on seagrass blades, as suggested by Lewis and Hollingworth [75]. These interactions can enhance nutrient regeneration and support higher trophic levels. Coull and Bell [76] suggested that these epibionts may play an integral role as nutrient regenerators and food for higher trophic levels in shallow waters. Epibionts can also increase the physical complexity and tridimensionality of seagrass canopy habitats [43]. By adding structural layers to seagrass leaves, epibionts can modify water flow, enhance habitat heterogeneity, and create microhabitats for various organisms. However, their impact depends on the type and abundance of epibionts, as excessive growth may compete with seagrasses for light and nutrients, potentially leading to negative effects [75,76].

The most commonly reported epibionts interacting with seagrasses included sea anemones, hydroids, bryozoans, and polychaetas [77]. Some species of sea anemones, for instance, can form dense aggregations and patterns of high local abundance, with area dimensions ranging from less than 1 mm to more than 1 m [44,78,79]. They may therefore be an important driver of the complexity of the habitat, providing shelter and resources for many associated organisms, including fish and decapod crustaceans. Despite their toxic nematocysts, which can impair prey performance, sea anemones play an essential role in the ecological dynamics of seagrass habitats [79–82]. Suspension-feeding bivalves in coastal systems play a crucial role in nutrient cycling. They exhibit robust interactions with the water column above them through filtering particles and excreting phosphate and ammonium (NH_4^+) [45], facilitating nutrient remineralization, which supports plant growth. According to Dame et al. [83], bivalve aggregates may create a positive feedback loop where suspension-feeding bivalves consume particulate nitrogen (as phytoplankton) and rapidly remineralize it into ammonium. This, in turn, enhances nutrient availability and promotes seagrass productivity. Furthermore, organic deposits linked to bivalves can further enhance phosphorus release in anaerobic conditions, underscoring their importance in nutrient dynamics. The composition of epibiont communities may act as a predictor of environmental conditions and water quality [84]. Any disruption of these species, caused by the presence and accumulation of potentially harmful compounds in the water, could impact these communities and, in turn, higher trophic levels.

Overall, epiphytes and epibionts are considered sensitive indicators of "natural" and long-term environmental variation as their biomass corresponds to changes in nutrient conditions [26,85]. They may respond to environmental changes more quickly than the seagrasses themselves [85].

5. Gaps in Knowledge and Study Limitations

Despite significant progress, research remains skewed toward epiphytes over epibionts, leaving the functional roles of organisms such as bivalves and sea anemones underexplored. Inconsistencies persist regarding epiphyte impacts on seagrass: while some findings highlight chemical defences and potential benefits (e.g., increased biodiversity, food for grazers), others emphasize harmful competition for light and nutrients. The threshold at which epiphytes shift from beneficial to detrimental is still unclear, especially under stressors like marine heatwaves and eutrophication. Moreover, the dynamics of epiphyte colonization and community composition remain poorly understood across spatial and temporal scales, particularly in the face of climate-driven stressors. Additionally, the cumulative effects of multiple anthropogenic pressures on seagrass–symbiont interactions remain insufficiently quantified.

Our work has highlighted important insights into seagrass–symbiont interactions and their responses to environmental changes. However, these insights do not consider studies published in languages other than English, nor those found in non-indexed (grey) studies, from which further details might be gleaned. Additionally, the prevalence of qualitative studies has precluded the inclusion of quantitative data on the effects of interactions between species. Given that our study aimed to provide a comprehensive overview of these interactions, we had to take into account the limitations imposed by this approach.

6. Conclusions

Although some gaps remain, our systematic review underscores the multifaceted roles that epiphytes and epibionts play in seagrass ecosystems. The literature analysis demonstrates the predominantly beneficial roles of these symbionts, with around 70% of studies reporting positive effects. Beyond boosting overall biodiversity and primary production, these symbionts contribute to nutrient recycling, provide additional habitat complexity, and can serve as sensitive indicators of water quality and environmental change. While epiphytes offer crucial feeding opportunities for diverse grazers, they may also intensify competition for light and nutrients, highlighting the nuanced balance within seagrass meadows. Epibionts, similarly, enhance canopy structure and can protect seagrasses from predation, but potential drawbacks remain poorly understood. Ultimately, these interactions have direct implications for ecosystem services such as carbon sequestration, habitat provisioning, and fishery productivity. Understanding and preserving these intricate relationships is critical to ensure the long-term functionality and resilience of seagrass ecosystems in a changing world.

7. Future Directions

Further research on seagrass–symbiont interactions is crucial for understanding how changes in the strength of these interactions can impact the ecological functions of seagrass meadows, and how these effects may evolve under changing environmental conditions, such as those driven by climate change. Biotic interactions between seagrasses and their symbionts can play a dual role, either enhancing seagrass resilience or exacerbating environmental stressors, thereby affecting the stability of ecosystem services such as carbon sequestration, habitat provision, and nutrient cycling. To fully grasp these dynamics, long-term studies are needed to assess the spatial and temporal variability of epiphyte and epibiont communities, particularly in response to climate-driven stressors. A key research priority is to determine the threshold at which epiphyte accumulation begins to negatively impact seagrass photosynthesis and productivity, providing critical insights for conservation and management efforts. Additionally, investigating the combined effects of multiple stressors—such as eutrophication, rising temperatures, and habitat fragmentation—through multifactorial experiments and predictive modelling will be crucial in forecasting the future of seagrass ecosystems under increasing anthropogenic pressures. Advancements in monitoring technologies, including high-resolution imaging, acoustic sensors, and artificial intelligence-based tools, offer promising opportunities to track epiphyte and epibiont dynamics with unprecedented accuracy. In summary, understanding these interactions is critical for guiding biodiversity conservation efforts and ensuring the long-term sustainability of these ecologically and economically valuable marine ecosystems.

Author Contributions: Conceptualization, N.M., M.B.-B., F.P.M. and G.S.; data collection and analysis, N.M.; writing—original draft preparation, N.M.; writing—review and editing, M.B.-B., F.P.M. and G.S.; funding acquisition, G.S. All authors have read and agreed to the published version of the manuscript.

Funding: This study was funded under the National Recovery and Resilience Plan (NRRP), Mission 4 Component 2 Investment 1.4—Call for tender No. 3138 of 16 December 2021, rectified by Decree n.3175 of 18 December 2021 of the Italian Ministry of University and Research funded by the European Union—NextGenerationEU. Project code CN_00000033, Concession Decree No. 1034 of 17 June 2022, adopted by the Italian Ministry of University and Research, CUP B73C22000790001, Project title "National Biodiversity Future Center—NBFC". Additional funding was received from the European Union's Horizon Europe Research and Innovation Programme ACTNOW project "Advancing understanding of Cumulative Impacts on European marine biodiversity, ecosystem functions and services for human wellbeing"—G.A. nº 101060072.

Institutional Review Board Statement: Not applicable.

Informed Consent Statement: Not applicable.

Data Availability Statement: All articles included in this review are available in the public databases Scopus and WoS.

Conflicts of Interest: The authors declare no conflicts of interest.

References

1. Jones, C.G.; Lawton, J.H.; Shachak, M. Organisms as Ecosystem Engineers. *Oikos* **1994**, *69*, 373–386. [CrossRef]
2. Stelling-Wood, T.P.; Poore, A.G.B.; Hughes, A.R.; Everett, J.D.; Gribben, P.E. Habitat Traits and Predation Interact to Drive Abundance and Body Size Patterns in Associated Fauna. *Ecol. Evol.* **2023**, *13*, e10771. [CrossRef]
3. Teagle, H.; Hawkins, S.J.; Moore, P.J.; Smale, D.A. The Role of Kelp Species as Biogenic Habitat Formers in Coastal Marine Ecosystems. *J. Exp. Mar. Biol. Ecol.* **2017**, *492*, 81–98. [CrossRef]
4. Bertness, M.D.; Gaines, S.D.; Hay, M.E.; Stachowicz, J.J.; Grosholz, E. Marine Community Ecology. In *Marine Community Ecology*; Sinauer Associates: Sunderland, MA, USA, 2001; Volume 47, p. 332. ISBN 10.2307/3069148.
5. Klecka, J.; Boukal, D.S. The Effect of Habitat Structure on Prey Mortality Depends on Predator and Prey Microhabitat Use. *Oecologia* **2014**, *176*, 183–191. [CrossRef] [PubMed]
6. Romero, G.Q.; Gonçalves-Souza, T.; Vieira, C.; Koricheva, J. Ecosystem Engineering Effects on Species Diversity across Ecosystems: A Meta-Analysis. *Biol. Rev.* **2015**, *90*, 877–890. [CrossRef] [PubMed]
7. Wright, J.T.; Gribben, P.E. Disturbance-Mediated Facilitation by an Intertidal Ecosystem Engineer. *Ecology* **2017**, *98*, 2425–2436. [CrossRef]
8. Lapointe, L.; Bourget, E. Influence of Substratum Heterogeneity Scales and Complexity on a Temperate Epibenthic Marine Community. *Mar. Ecol. Prog. Ser.* **1999**, *189*, 159–170. [CrossRef]

9. Bruno, J.F.; Boyer, K.E.; Duffy, J.E.; Lee, S.C.; Kertesz, J.S. Effects of Macroalgal Species Identity and Richness on Primary Production in Benthic Marine Communities. *Ecol. Lett.* **2005**, *8*, 1165–1174. [CrossRef]
10. Jiménez-Ramos, R.; Brun, F.G.; Vergara, J.J.; Hernández, I.; Pérez-Lloréns, J.L.; Egea, L.G. Nutrient Enrichment and Herbivory Alter Carbon Balance in Temperate Seagrass Communities. *Mar. Pollut. Bull.* **2024**, *206*, 116784. [CrossRef]
11. Greve, T.M.; Borum, J.; Pedersen, O. Meristematic Oxygen Variability in Eelgrass (*Zostera marina*). *Limnol. Oceanogr.* **2003**, *48*, 210–216. [CrossRef]
12. Ricart, A.M.; Ward, M.; Hill, T.M.; Sanford, E.; Kroeker, K.J.; Takeshita, Y.; Merolla, S.; Shukla, P.; Ninokawa, A.T.; Elsmore, K.; et al. Coast-Wide Evidence of Low PH Amelioration by Seagrass Ecosystems. *Glob. Change Biol.* **2021**, *27*, 2580–2591. [CrossRef]
13. Brodersen, K.E.; Kühl, M. Effects of Epiphytes on the Seagrass Phyllosphere. *Front. Mar. Sci.* **2022**, *9*, 821614. [CrossRef]
14. Duarte, C.M.; Middelburg, J.J.; Caraco, N. Major Role of Marine Vegetation on the Oceanic Carbon Cycle. *Biogeosciences* **2005**, *2*, 1–8. [CrossRef]
15. Fourqurean, J.W.; Duarte, C.M.; Kennedy, H.; Marbà, N.; Holmer, M.; Mateo, M.A.; Apostolaki, E.T.; Kendrick, G.A.; Krause-Jensen, D.; McGlathery, K.J.; et al. Seagrass Ecosystems as a Globally Significant Carbon Stock. *Nat. Geosci.* **2012**, *5*, 505–509. [CrossRef]
16. Boutar, L.; Espinosa, F.; Bazairi, H. Reconstruction of Cymodocea Nodosa's Dynamivs as Tool to Examine the Conservation Status of a Mediterranean Declared Marine Proteced Area. *Mediterr. Mar. Sci.* **2021**, *23*, 754–765. [CrossRef]
17. Kitada, S.; Nakajima, K.; Hamasaki, K.; Shishidou, H.; Waples, R.S.; Kishino, H. Rigorous Monitoring of a Large-Scale Marine Stock Enhancement Program Demonstrates the Need for Comprehensive Management of Fisheries and Nursery Habitat. *Sci. Rep.* **2019**, *9*, 5290. [CrossRef]
18. Spicer, M.E.; Woods, C.L. A Case for Studying Biotic Interactions in Epiphyte Ecology and Evolution. *Perspect. Plant Ecol. Evol. Syst.* **2022**, *54*, 125658. [CrossRef]
19. Van Montfrans, J.; Wetzel, R.; Orth, R.J. Epiphytes-Grazer Relationships in Seagrass Meadows: Consequences for Seagrass Growth and Production. *Estuaries* **1984**, *7*, 289–309. [CrossRef]
20. Howard, R.K.; Edgar, G.J.; Hutchings, P.A. Faunal Assemblages of Seagrasses Beds. In *Biology of Seagrasses: A Treatise on the Biology of Seagrasses with Special Reference to the Australian Region*; Elsevier: Amsterdam, The Netherlands, 1989; pp. 536–564.
21. Robertson, A.I.; Mann, K.H. Population Dynamics and Life History Adaptations of Littorina Neglecta Bean in an Eelgrass Meadow (*Zostera marina* L.) in Nova Scotia. *J. Exp. Mar. Biol. Ecol.* **1982**, *63*, 151–171. [CrossRef]
22. Bass, A.V.; Falkenberg, L.J. Seasonal Effects and Trophic Pressure Shape the Responses of Species Interactions in a Tropical Seagrass Meadow to Marine Heatwaves. *Oikos* **2024**, *2024*, e10382. [CrossRef]
23. Orth, R.J.; Van Montfrans, J. Epiphyte—Segrass Relationships with an Emphasis on the Role of Micrograzing: A Review. *Aquat. Bot.* **1984**, *18*, 43–69. [CrossRef]
24. Orth, R.J.; Carruthers, T.J.B.; Dennison, W.C.; Duarte, C.M.; Fourqurean, J.W.; Heck, K.L.; Hughes, A.R.; Kendrick, G.A.; Kenworthy, W.J.; Olyarnik, S.; et al. A Global Crisis for Seagrass Ecosystems. *Bioscience* **2006**, *56*, 987–996. [CrossRef]
25. Waycott, M.; Duarte, C.M.; Carruthers, T.J.B.; Orth, R.J.; Dennison, W.C.; Olyarnik, S.; Calladine, A.; Fourqurean, J.W.; Heck, K.L.; Hughes, A.R.; et al. Accelerating Loss of Seagrasses across the Globe Threatens Coastal Ecosystems. *Proc. Natl. Acad. Sci. USA* **2009**, *106*, 12377–12381. [CrossRef] [PubMed]
26. Chen, Y.Y.; Edgar, G.J.; Fox, R.J. The Nature and Ecological Significance of Epifaunal Communities within Marine Ecosystems. *Oceanogr. Mar. Biol.* **2021**, *59*, 585–719. [CrossRef]
27. Duarte, C.M. Seagrass Depth Limits. *Aquat. Bot.* **1991**, *40*, 363–377. [CrossRef]
28. Estes, J.A.; Peterson, C.H. Marine Ecological Research in Seashore and Seafloor Systems: Accomplishments and Future Directions. *Mar. Ecol. Prog. Ser.* **2000**, *195*, 281–289. [CrossRef]
29. Moher, D.; Liberati, A.; Tetzlaff, J.; Altman, D.G. Preferred reporting items for systematic reviews and meta-analyses: The PRISMA Statement. *Open Med.* **2009**, *3*, e123–e130.
30. Liberati, A.; Altman, D.G.; Tetzlaff, J.; Mulrow, C.; Gøtzsche, P.C.; Ioannidis, J.P.A.; Clarke, M.; Devereaux, P.J.; Kleijnen, J.; Moher, D. The PRISMA Statement for Reporting Systematic Reviews and Meta-Analyses of Studies That Evaluate Health Care Interventions: Explanation and Elaboration. *PLoS Med.* **2009**, *6*, 339. [CrossRef] [PubMed]
31. Hutton, B.; Salanti, G.; Caldwell, D.M.; Chaimani, A.; Schmid, C.H.; Cameron, C.; Ioannidis, J.P.A.; Straus, S.; Thorlund, K.; Jansen, J.P.; et al. The PRISMA Extension Statement for Reporting of Systematic Reviews Incorporating Network Meta-Analyses of Health Care Interventions: Checklist and Explanations. *Ann. Intern. Med.* **2015**, *162*, 777–784. [CrossRef]
32. Jernakoff, P.; Brearley, A.; Nielsen, J. Factors Affecting Grazer-Epiphyte Interactions in Temperate Seagrass Meadows. *Oceanogr. Mar. Biol.* **1996**, *34*, 109–162.
33. Pinckney, J.L.; Micheli, F. Microalgae on Seagrass Mimics: Does Epiphyte Community Structure Differ from Live Seagrasses? *J. Exp. Mar. Biol. Ecol.* **1998**, *221*, 59–70. [CrossRef]
34. Jephson, T.; Nyström, P.; Moksnes, P.O.; Baden, S.P. Trophic Interactions in *Zostera marina* Beds along the Swedish Coast. *Mar. Ecol. Prog. Ser.* **2008**, *369*, 63–76. [CrossRef]

35. Ugarelli, K.; Chakrabarti, S.; Laas, P.; Stingl, U. The Seagrass Holobiont and Its Microbiome. *Microorganisms* **2017**, *5*, 81. [CrossRef] [PubMed]
36. Mabrouk, L.; Ben Brahim, M.; Hamza, A.; Mahfoudhi, M.; Bradai, M.N. A Comparison of Abundance and Diversity of Epiphytic Microalgal Assemblages on the Leaves of the Seagrasses *Posidonia oceanica* (L.) and *Cymodocea nodosa* (Ucria) Asch in Eastern Tunisia. *J. Mar. Biol.* **2014**, *2014*, 1–10. [CrossRef]
37. Horner, S.M.J. Similarity of Epiphyte Biomass Distribution on *Posidonia* and Artificial Seagrass Leaves. *Aquat. Bot.* **1987**, *27*, 159–167. [CrossRef]
38. Klumpp, D.W.; Salita-Espinosa, J.T.; Fortes, M.D. Feeding Ecology and Trophic Role of Sea Urchins in a Tropical Seagrass Community. *Aquat. Bot.* **1993**, *45*, 205–229. [CrossRef]
39. Michael Martin-Smith, K. Abundance of Mobile Epifauna: The Role of Habitat Complexity and Predation by Fishes. *J. Exp. Mar. Biol. Ecol.* **1993**, *174*, 243–260. [CrossRef]
40. Mabrouk, L.; Ben Brahim, M.; Jebara, A.; Jribi, I. Comparison of Epiphyte Algal Assemblages on the Leaves of Marine Seagrasses *Posidonia oceanica* (L.) Delile, *Cymodocea nodosa* (Ucria) Asch, and the Lessepsian *Halophila stipulacea* (Forssk.) Asch in Chebba (East of Tunisia). *Mar. Ecol.* **2021**, *42*, e12642. [CrossRef]
41. Michael, T.; Shin, H.W.; Spafford, D.; Michael, T.S.; Hanna, R.; Spafford, D.C. A Review of Epiphyte Community Development: Surface Interactions and Settlement on Seagrass. *J. Environ. Biol.* **2008**, *29*, 629–638.
42. Yamamuro, M. Importance of Epiphytic Cyanobacteria as Food Sources for Heterotrophs in a Tropical Seagrass Bed. *Coral Reefs* **1999**, *18*, 263–271. [CrossRef]
43. Nakaoka, M.; Toyohara, T.; Matsumasa, M. Seasonal and Between-Substrate Variation in Mobile Epifaunal Community in a Multispecific Seagrass Bed of Otsuchi Bay, Japan. *Mar. Ecol.* **2001**, *22*, 379–395. [CrossRef]
44. Brooker, R.M.; Feeney, W.E.; Sih, T.L.; Ferrari, M.C.O.; Chivers, D.P. Comparative Diversity of Anemone-Associated Fishes and Decapod Crustaceans in a Belizean Coral Reef and Seagrass System. *Mar. Biodivers.* **2019**, *49*, 2609–2620. [CrossRef]
45. Peterson, B.J.; Heck, K.L. Positive Interactions between Suspension-Feeding Bivalves and Seagrass—A Facultative Mutualism. *Mar. Ecol. Prog. Ser.* **2001**, *213*, 143–155. [CrossRef]
46. Wang, L.; Zhang, W.; Gladstone, S.; Ng, W.-K.; Zhang, J.; Shao, Q. Effects of Isoenergetic Diets with Varying Protein and Lipid Levels on the Growth, Feed Utilization, Metabolic Enzymes Activities, Antioxidative Status and Serum Biochemical Parameters of Black Sea Bream (*Acanthopagrus schlegelii*). *Aquaculture* **2019**, *513*. [CrossRef]
47. Heck, K.L.; Valentine, J.F. Plant-Herbivore Interactions in Seagrass Meadows. *J. Exp. Mar. Biol. Ecol.* **2006**, *330*, 420–436. [CrossRef]
48. Mannino, A.M.; Micheli, C. Ecological Function of Phenolic Compounds from Mediterranean Fucoid Algae and Seagrasses: An Overview on the Genus Cystoseira Sensu Lato and *Posidonia oceanica* (L.) Delile. *J. Mar. Sci. Eng.* **2020**, *8*, 19. [CrossRef]
49. Saunders, J.E.; Attrill, M.J.; Shaw, S.M.; Rowden, A.A. Spatial Variability in the Epiphytic Algal Assemblages of *Zostera marina* Seagrass Beds. *Mar. Ecol. Prog. Ser.* **2003**, *249*, 107–115. [CrossRef]
50. Johnson, M.P.; Edwards, M.; Bunker, F.; Maggs, C.A. Algal Epiphytes of *Zostera marina*: Variation in Assemblage Structure from Individual Leaves to Regional Scale. *Aquat. Bot.* **2005**, *82*, 12–26. [CrossRef]
51. Vanderklift, M.A.; Lavery, P.S. Patchiness in Assemblages of Epiphytic Macroalgae on *Posidonia Coriacea* at a Hierarchy of Spatial Scales. *Mar. Ecol. Prog. Ser.* **2000**, *192*, 127–135. [CrossRef]
52. Drake, L.A.; Dobbs, F.C.; Zimmerman, R.C. Effects of Epiphyte Load on Optical Properties and Photosynthetic Potential of the Seagrasses *Thalassia testudinum* Banks Ex König and *Zostera marina* L. *Limnol. Oceanogr.* **2003**, *48*, 456–463. [CrossRef]
53. Gil, M.; Armitage, A.R.; Fourqurean, J.W. Nutrient Impacts on Epifaunal Density and Species Composition in a Subtropical Seagrass Bed. *Hydrobiologia* **2006**, *569*, 437–447. [CrossRef]
54. Prado, P.; Alcoverro, T.; Martínez-Crego, B.; Vergés, A.; Pérez, M.; Romero, J. Macrograzers Strongly Influence Patterns of Epiphytic Assemblages in Seagrass Meadows. *J. Exp. Mar. Biol. Ecol.* **2007**, *350*, 130–143. [CrossRef]
55. Lavery, P.S.; Reid, T.; Hyndes, G.A.; Elven, B.R.V. Effect of Leaf Movement on Epiphytic Algal biomass of Seagrass Leaves. *Mar. Ecol. Prog. Ser.* **2007**, *338*, 97–106. [CrossRef]
56. Kendrick, G.A.; Burt, J.S. Seasonal Changes in Epiphytic Macro-Algae Assemblages Between Offshore Exposed and Inshore Protected *Posidonia sinuosa* Cambridge et Kuo Seagrass Meadows, Western Australia. *Bot. Mar.* **1997**, *40*, 77–85. [CrossRef]
57. Cebrián, J.; Enríquez, S.; Fortes, M.; Agawin, N.; Vermaat, J.E.; Duarte, C.M. Epiphyte Accrual on *Posidonia oceanica* (L.) Delile Leaves: Implications for Light Absorption. *Bot. Mar.* **1999**, *42*, 123–128. [CrossRef]
58. Fong, J.M.; Lai, S.; Yaakub, S.M.; Ow, Y.X.; Todd, P.A. The Diet and Feeding Rates of Gastropod Grazers in Singapore's Seagrass Meadows. *Bot. Mar.* **2018**, *61*, 181–192. [CrossRef]
59. Rindi, F.; Maltagliati, F.; Rossi, F.; Acunto, S.; Cinelli, F. Algal Flora Associated with a *Halophila stipulacea* (Forssksl) Ascherson (Hydrocharitaceae, Helobiae) Stand in the Western Mediterranean. *Oceanol. Acta* **1999**, *22*, 421–429. [CrossRef]
60. Andrade, A.R.; Paula, C.A.; Leite, F.P.P.; Costa, T.M.; Machado, G.B.O. The Role of Food Value on Host Use by the Herbivorous Amphipod Sunamphitoe Pelagica. *J. Exp. Mar. Biol. Ecol.* **2024**, *574*, 152007. [CrossRef]

61. Touchette, B.W.; Burkholder, J.M. Review of Nitrogen and Phosphorus Metabolism in Seagrasses. *J. Exp. Mar. Biol. Ecol.* **2000**, *250*, 133–167. [CrossRef]
62. Ibarra-Obando, S.E.; Heck, K.L.; Spitzer, P.M. Effects of Simultaneous Changes in Light, Nutrients, and Herbivory Levels, on the Structure and Function of a Subtropical Turtlegrass Meadow. *J. Exp. Mar. Biol. Ecol.* **2004**, *301*, 193–224. [CrossRef]
63. Richardson, F.D. Ecology of *Ruppia maritima*, L. in New Hampshire (U.S.A.) Tidal Marshes. *Rhodora* **1980**, *82*, 403–439.
64. Penhale, P.A.; Smith, J.R. Excretion of Dissolved Organic Carbon by Eelgrass (Zostera) and Its Epiphytes. *Limnol. Oceanogr.* **1977**, *22*, 400–407. [CrossRef]
65. Trocine, R.P.; Rice, J.D.; Wells, G.N. Inhibition of Seagrass Photosynthesis by Ultraviolet B. *Plant Physiol.* **1981**, *68*, 74–81. [CrossRef] [PubMed]
66. Wahl, M.; Goecke, F.; Labes, A.; Dobretsov, S.; Weinberger, F. The Second Skin: Ecological Role of Epibiotic Biofilms on Marine Organisms. *Front. Microbiol.* **2012**, *3*, 292. [CrossRef]
67. Heck, K.L. Seagrass Ecosystems: A Careerlong Quest to Understand Their Inner Workings. *Gulf Caribb. Res.* **2019**, *30*, II. [CrossRef]
68. Hovel, K.A.; Warneke, A.M.; Virtue-Hilborn, S.P.; Sanchez, A.E. Mesopredator Foraging Success in Eelgrass (*Zostera marina* L.): Relative Effects of Epiphytes, Shoot Density, and Prey Abundance. *J. Exp. Mar. Biol. Ecol.* **2016**, *474*, 142–147. [CrossRef]
69. Fong, C.W.; Lee, Y.; Wu, R.S.S. The Effects of Epiphytic Algae and Their Grazers on the Intertidal Seagrass *Zostera japonica*. *Aquat. Bot.* **2000**, *67*, 251–261. [CrossRef]
70. Valdez, S.R.; Zhang, Y.S.; van der Heide, T.; Vanderklift, M.A.; Tarquinio, F.; Orth, R.J.; Silliman, B.R. Positive Ecological Interactions and the Success of Seagrass Restoration. *Front. Mar. Sci.* **2020**, *7*. [CrossRef]
71. Borowitzka, M.A.; Lavery, P.S.; Van Keulen, M. Epiphytes of Seagrasses. In *Seagrasses: Biology, Ecology and Conservation*; Springer: Heidelberg, Germany, 2006; pp. 441–461. ISBN 140202942X.
72. Borum, J.; Duarte, C.M.; Krause-Jensen, D.; Greve, T.M. *European Seagrasses: An Introduction to Monitoring and Management*; Monitoring and Managing of European Seagrasses [EU Project]; The M&M Project: Cumbria, UK, 2004; ISBN 8789143213.
73. Crespo, E.; Lozano, P.; Blasco, J.; Moreno-Garrido, I. Epiphyte Toxicity Bioassay for Ecotoxicological and Coastal Monitoring. *Environ. Monit. Assess.* **2014**, *186*, 4647–4654. [CrossRef]
74. Lewis, J.B.; Hollingworth, C.E. Leaf Epifauna of the Seagrass *Thalassia testudinum*. *Mar. Biol.* **1982**, *71*, 41–49. [CrossRef]
75. Coull, B.C.; Bell, S.S. Perspectives of Marine Meiofaunal Ecology. In *Ecological Processes in Coastal and Marine Systems*; Livingston, R.J., Ed.; Springer: Boston, MA, USA, 1979; Volume 10, pp. 189–216.
76. Guilini, K.; Weber, M.; De Beer, D.; Schneider, M.; Molari, M.; Lott, C.; Bodnar, W.; Mascart, T.; De Troch, M.; Vanreusel, A. Response of Posidonia Oceanica Seagrass and Its Epibiont Communities to Ocean Acidification. *PLoS ONE* **2017**, *12*, e0181531. [CrossRef] [PubMed]
77. Colombara, A.M.; Quinn, D.; Chadwick, N.E. Habitat Segregation and Population Structure of Caribbean Sea Anemones and Associated Crustaceans on Coral Reefs at Akumal Bay, Mexico. *Bull. Mar. Sci.* **2017**, *93*, 1025–1047. [CrossRef]
78. Dixon, A.K.; McVay, M.J.; Chadwick, N.E. Demographic Modelling of Giant Sea Anemones: Population and Effects of Mutualistic Anemonefish in the Jordanian Red Sea. *Mar. Freshw. Res.* **2017**, *68*, 2145–2155. [CrossRef]
79. Titus, B.M.; Daly, M.; Macrander, J.; Del Rio, A.; Santos, S.R.; Chadwick, N.E. Contrasting abundance and Contribution of Clonal Proliferation to the Population Structure of the Corkscrew Sea Anemone *Bartholomea annulata* in the Tropical Western Atlantic. *Invertebr. Biol.* **2017**, *136*, 62–74. [CrossRef]
80. Chadwick, N.E.; Ďuriš, Z.; Horkà, I. Biodiversity and Behavior of Shrimps and Fishes Symbiotic with sea Anemones in the Gulf of Aqaba, Northern Red Sea. In *The Improbable Gulf: History, Biodiversity, and Protection of the Gulf of Aqaba (Eilat)*; Magnes Press: Jerusalem, Israel, 2008; pp. 209–223.
81. Briones-Fourzán, P.; Pérez-Ortiz, M.; Negrete-Soto, F.; Barradas-Ortiz, C.; Lozano-Álvarez, E. Ecological Traits of Caribbean Sea Anemones and Symbiotic Crustaceans. *Mar. Ecol. Prog. Ser.* **2012**, *470*, 55–68. [CrossRef]
82. Feeney, W.E.; Brooker, R.M.; Johnston, L.N.; Gilbert, J.D.J.; Besson, M.; Lecchini, D.; Dixson, D.L.; Cowman, P.F.; Manica, A. Predation Drives Recurrent Convergence of an Interspecies Mutualism. *Ecol. Lett.* **2019**, *22*, 256–264. [CrossRef]
83. Dame, R.F.; Wolaver, T.G.; Libes, S.M. The Summer Uptake and Release of Nitrogen by an Intertidal Oyster Reef. *Neth. J. Sea Res.* **1985**, *19*, 265–268. [CrossRef]
84. Giovannetti, E.; Montefalcone, M.; Morri, C.; Bianchi, C.N.; Albertelli, G. Early Warning Response of *Posidonia oceanica* Epiphyte Community to Environmental Alterations (Ligurian Sea, NW Mediterranean). *Mar. Pollut. Bull.* **2010**, *60*, 1031–1039. [CrossRef]
85. Piazzi, L.; Balata, D.; Ceccherelli, G. Epiphyte Assemblages of the Mediterranean Seagrass Posidonia Oceanica: An Overview. *Mar. Ecol.* **2016**, *37*, 3–41. [CrossRef]