Abstract: Macroalgae are the source of many harmful allelopathic compounds, which are synthesized as a defense strategy against competitors and herbivores. Therefore, it can be predicted that certain species reduce aquaculture performance. Herein, the allelopathic ability of 123 different taxa of green, red, and brown algae have been summarized based on literature reports. Research on macroalgae and their allelopathic effects on other animal organisms was conducted primarily in Australia, Mexico, and the United States. Nevertheless, there are also several scientific reports in this field from South America and Asia; the study areas in the latter continents coincide with areas where aquaculture is highly developed and widely practiced. Therefore, the allelopathic activity of macroalgae on coexisting animals is an issue that is worth careful investigation. In this work, we characterize the distribution of allelopathic macroalgae and compare them with aquaculture locations, describe the methods for the study of macroalgal allelopathy, present the taxonomic position of allelopathic macroalgae and their impact on coexisting aquatic competitors (Cnidaria) and herbivores (Annelida, Echinodermata, Arthropoda, Mollusca, and Chordata), and compile information on allelopathic compounds produced by different macroalgae species. This work gathers the current knowledge on the phenomenon of macroalgal allelopathy and their allelochemicals affecting aquatic animal (competitors and predators) worldwide and it provides future research directions for this topic.

Keywords: aquatic animals; allelopathy; allelochemicals; chemical defense; defense strategy; plant defense; species interactions

1. Introduction

Aquaculture has rapidly grown over the past few decades and is now the fastest-growing food sector worldwide [1]. The global aquaculture production in 2015 was approximately 106 million tons, which represents approximately 163 billion US dollars [2]. The global population has been increasing and is expected to reach ~10 billion in the middle of the 21st century [3]. The corresponding increase in food demand is driving the expansion of aquaculture [4]. The pressure on these food sectors to maximize production and reduce losses is also expected to increase [2].

A popular method to increase aquaculture production is to enrich farming tanks with macroalgae species. Macroalgae as a food source believed to be an ideal candidate for growth in fishponds because they provide high biomass production and protein content [5]. Additionally, the environment of the ponds is improved by macroalgae through the balance
of pH levels [6]. Different macroalgal species have been integrated into land-based integrated multi-trophic aquacultures (IMTA) for biomass production [7]. The high amount of protein from macroalgae represents valuable feed for animal species with high commercial value [5,7]. However, studies on this topic rarely mention that allelopathic macroalgae can negatively affect and even exterminate both competitors and predators by secreting a broad range of harmful and toxic substances such as acetogenins, alkaloids, aromatic compounds, fluorotannins, polyphenols, terpenes, and amino acids [8].

Macroalgal allelopathy refers to the effects of substances produced by the microalgae on target organisms [9]. These effects can be related to the growth, health, origin, or population biology of the donor and target organisms [8,9]. The allelopathic activity of macroalgae is a complex process. It is considered that its level depends on the production of active allelopathic compounds and their effective escalation to accompanying organisms [10]. Macroalgae are mainly benthic organisms firmly attached to the seabed, which forces them to compete for substrates, nutrients, and light with other benthic organisms. There are also unattached forms of macroalgae [11], which can influence the development of planktonic organisms. Kersen [11] showed that the unattached forms of Furcellaria lumbricalis and Coccotylus truncatus can be considerably denser than their respective attached forms. Therefore, their deleterious effects on other organisms can be stronger than those of benthic algae. Nevertheless, their allelopathic activities have not been sufficiently investigated.

Studies related to the impact of macroalgae on other organisms have mainly focused on marine environments [8,12,13]. However, freshwater and brackish macroalgae can also achieve rapid biomass increase, which can result in algal blooms [14–16]. Moreover, macroalgae from freshwater and brackish ecosystems can negatively affect the growth of photoautotrophs [17,18]. Nevertheless, there is little research on the impact of these organisms on coexisting aquatic animals. Macroalgae in marine environments belong to three groups: Ulvophyceae, Chlorophyta (green algae), Florideophyceae, Rhodophyta (red algae), and Phaeophyceae, Ochrophyta (formerly Phaeophyta; brown algae), whereas those from freshwater include mainly Ulvophyceae, Chlorophyta and Charophyceae, Charophyta [19]. Macroalgae with confirmed allelopathic activity against other heterotrophic organisms are shown in Figure 1.

Figure 1. Examples of allelopathic green algae (A): Codium fragile (a), Halimeda tuna (b), Ulva sp. (c); red algae. (B): Ceramium rubrum (a), Grateloupia sp. (b), Polysiphonia sp. (c); brown algae. (C): Dictyota sp. (a), Padina sp. (b), Sargassum sp. (c).
Recently, research on the allelopathy phenomenon has increased significantly [8,13,20]; however, to the best of our knowledge, no published review has revealed the negative effects of macroalgae on coexisting competitors and predators. In this work, we (i) characterize the distribution of allelopathic macroalgae and compare them with aquatic locations, (ii) describe the methods for the study of macroalgae allelopathy, (iii) present the taxonomic position of allelopathic macroalgae and their impact on coexisting animal competitors (Cnidaria species) and herbivores (Annelida, Echinodermata, Mollusca, and Chordata species), and (iv) compile information on allelopathic compounds produced by different macroalgae species. This work gathers the current knowledge on the phenomenon of macroalgal allelochemicals affecting aquatic competitors and herbivores worldwide and it provides future research directions for this topic.

2. Distribution of Allelopathic Macroalgae and Aquaculture Locations

In this work, the allelopathic effect of green algae (Chlorophyta, Ulvophyceae), red algae (Rhodophyta, Florideophyceae), and brown algae (Ochrophyta, Phaeophyceae) was investigated against different aquatic animals. Allelopathic activity has been reported for a total of 123 taxa, including 37 green algae (30%), 45 red algae (37%), and 41 brown algae (33%). The allelopathic ability of 11 different genera of Chlorophyta, 28 genera of Rhodophyta, and 13 genera of Ochrophyta has been reported (Figure S1, Table S1). The allelopathic activity of macroalgae has most often been studied in Chlorophyta from the genera *Caulerpa*, *Chlorodesmis*, and *Ulva*. *Hypnea* sp. has been the most frequently studied among Rhodophyta for allelopathy. Among the allelopathic Ochrophyta, *Dictyota* sp. and *Lobophora* sp. have been the most frequently studied. The least numerous studies for allelopathic ability have been conducted for organisms belonging to *Anadyomene*, *Codium*, *Penicillus*, and *Rhaphia* (green algae); *Asparagopsis*, *Callophyllus*, *Centroceras*, *Ceramium*, *Chondria*, *Chondriopsis*, *Chondrophyccus*, *Crassiphycus*, *Delisea*, *Dermomena*, *Digenea*, *Endosiphonia*, *Peyssonnelia*, *Phacelocarpus*, *Plocamium*, *Polysiphonia*, *Tayloriella*, *Tichocarpus*, and *Yuzurua* (red algae); and *Canistrocarpus*, *Desmarestia*, *Dictyopteris*, *Dilophus*, *Ecklonia*, *Laminaria*, and *Sphacelaria* sp. (brown algae).

Research on macroalgae and their allelopathic effects on other organisms has been primarily conducted in Australia, Mexico, and the United States (Figure 2). Nevertheless, a few scientific investigations have been conducted in South America and Asia in areas coinciding with aquaculture activity (Figure 2). In most areas, all three phyla were tested. However, the studies in some regions focused only on one macroalgae phylum. *Chlorodesmis fastigiata* is the most studied green algae, accounting for 30.4% of all tested organisms of this phylum [21–26]. In studies on brown algae, *Dictyota bartayresiana* dominates, accounting for 12.5% of the total studies [22,24,27], whereas in red algae, *Galaxaura filamentosa* is the most widely investigated, with studies accounting for 13.6% [22–24].
Furthermore, several researchers have reported the negative effects of macroalgae on Mol-
4. Taxonomic Position of Allelopathic Macroalgae and Their Impact on Coexisting Competitors and Herbivores

Macroalgae are major competitors for the light and space for corals and other benthic organisms from the Cnidaria phylum on tropical reefs [43]. Competition can occur through direct and indirect physical and chemical mechanisms reviewed in detail by Chadwick and Morrow [44]. Macroalgae can produce inhibitory compounds affecting corals and epibionts that compete for light or space [9]. Globally, many coral reefs have been damaged, and areas with reduced coral cover and increased macroalgal abundance have been widely identified [45]. Despite the well-documented negative correlation between macroalgae and coral recruitment, the mechanisms through which macroalgae affect this recruitment have received little attention.

In addition, macroalgal allelopathy has an important and as-yet unrecognized role in structuring temperate shallow marine communities of herbivores: Annelida (e.g., Sabellaria cementarium and Spionidae sp.) [41], Echinodermata (e.g., Holopneustes purpurascens, Lytechinus variegates, and Strongylocentrotus intermedius) [31,33,35,36], and Arthropoda species (Cancer oregonensis, Metacarcinus magister, and Pachygrapsus transversus) [35,46]. Furthermore, several researchers have reported the negative effects of macroalgae on Mollusca species e.g., [38,47,48]; they suggested that green macroalgae species (especially from the Ulvophyceae class) can inhibit the growth and development of co-occurring organisms from the genus Crassostrea. Moreover, oyster larvae (e.g., Crassostrea gigas) are susceptible to extracts from Ulvaria lactuca thallus at relatively low concentrations [48]. Although several researchers have reported both negative and positive effects of green algae species on invertebrates [41,46,49,50], few studies have reported the potential effects of Ulva sp. on the economically relevant Mollusca, Crassostrea virginica [38]. Many aquaculture farms cultivate C. virginica in areas where Ulva is present. Research has also shown that macroalgae can adversely affect species belonging to the Chordata phylum [8,30–32]. Moreover, certain investigated fishes that belong to Carassius sp. and Tilapia sp. are consumed by humans. As contribution of aquatic animals to global food is crucial, such results are alarming and warrant special attention [2].

The interactions of green algae on 13 different genera of aquatic animals (both competitors and predators) have also been reported (Figure 4). The allelopathic activity of Chlorophyta species was tested against six taxa belonging to Cnidaria, two to Mollusca, two to Annelida, two to Arthropoda, and one to Chordata phylum. Conversely, the influence of red algae was investigated on ten aquatic animals (five belonging to Cnidaria, two to Annelidida, two to Echinodermata, and one to Chordata). Overall, the greatest number of animal species have been tested for their sensitivity to brown algae. The allelopathic activity of these macroalgae was tested against 19 genera of different aquatic animals. Allelopathic activity of brown algae was tested on animals belonging to the Cnidaria, Mollusca, Annelida, Echinodermata, Arthropoda, and Chordata phyla. As in the case of other macroalgae, the allelopathic activity of brown algae has been most frequently studied for taxa belonging to the Cnidaria. Animals belonging to the genus Crassostrea and Haliotis (Mollusca), Strongylocentrotus (Echinodermata), Cancer and Metacarcinus (Arthropoda) as well as Carassius and Tilapia (Chordata), are commonly used in aquaculture. Therefore, it is important to further investigate and compare information on the interactions between macroalgal species and economically important animals.
activity of these macroalgae was tested against 19 genera of different aquatic animals. Allelopathic activity of brown algae was tested on animals belonging to the Cnidaria, Mollusca, Annelida, Echinodermata, Arthropoda, and Chordata phyla. As in the case of other macroalgae, the allelopathic activity of brown algae has been most frequently studied for taxa belonging to the Cnidaria. Animals belonging to the genus *Crassostrea* and *Haliotis* (Mollusca), *Strongylocentrotus* (Echinodermata), *Cancer* and *Metacarcinus* (Arthropoda) as well as *Carassius* and *Tilapia* (Chordata), are commonly used in aquaculture. Therefore, it is important to further investigate and compare information on the interactions between macroalgal species and economically important animals.

Figure 4. Number of target competitors and herbivores affected by green algae (A), red algae (B), and brown algae (C), based on taxa found in the literature.

4.1. The Allelopathic Activity of Green Algae

The allelopathic activity of green algae (Ulvophyceae, Chlorophyta) was confirmed by several authors (Table 1). Studies have shown that the presence of green algae has a generally negative effect on Cnidaria [21–26,28,39,51,52]. Tanner [21] was the first author who showed that *Chlorodesmis fastigiata* and *Halimeda* sp. had a negative impact on *Acropora* (*Isopora*) *cuneata*, *Acropora hrueggemanni*, *Acropora palifera*, and *Pocillopora damicornis*. Similar research was conducted by Rasher et al. [22]. Andras et al. [51] proved that the green alga *Rhiphilia pencilloides* caused coral bleaching when placed in contact with *Porites rus*. Morrow et al. [52] showed the impact of macroalgal extracts obtained from *Halimeda tuna* on the sublethal stress response of corals. In turn, Bonaldo and Hay [23] investigated macroalgae-coral interactions considering both non-allelopathic and allelopathic species. Furthermore, Lee et al. [28] examined the effects of macroalgal species on the settlement success of *P. damicornis* larvae under aquarium conditions. Ritson-Williams et al. [24] examined that *C. fastigiata* negatively affects *A. millepora*, *M. digitata*, and *P. damicornis*. Fong et al. [39] showed that the mortality of *Pocillopora acuta* larvae increased significantly with an increase in the concentration of the crude extract obtained from *Bryopsis* sp. Longo and Hay [26] demonstrated that the lipid-soluble extracts obtained from the green alga *C. fastigiata* suppressed coral *Pocillopora verrucosa* photochemical efficiency. Conversely, Del Monaco et al. [25] showed that donor macroalgae *C. fastigiata* damages corals via allelopathy regardless of CO₂ concentration. Only Birrell et al. [40] described a positive and neutral effect of Chlorophyta on Cnidaria. These authors demonstrated that *C. fastigiata* caused a slight delay in the settlement of coral larvae; however, these results were not statistically significant. Green-Gavrielidis et al. [38], Nelson et al. [47], and Nelson and Greg [48] have
shown that macroalgae from the genus Ulva have had a negative impact on Mollusca. Green-Gavrielidis et al. [38] showed that bloom-forming Ulva compressa negatively affected the growth of Crassostrea virginica and the strongest effect was seen in larvae exposed to Ulva compressa exudates growing on nutrient-sufficient medium. Nelson et al. [47] and Nelson and Greg [48] showed that oyster larvae (Crassostrea gigas) are susceptible to extracts from dried Ulva lactuca and Ulvaria obscura at relatively low concentrations. Conversely, Muñoz et al. [50] showed that the presence of Ulva sp. improved the growth rate of the Haliotis rufescens larvae, while Huggett et al. [49] noted high colonization of Haliotis rubra in the presence of Ulva australis, Ulva compressa, and Ulvaria obscura. Warkus et al. [41] were the only authors who studied the influence of Ulvophyceae on Annelida (Table 1). This work demonstrated the negative effect of Chaetomorpha sp., Codium fragile, Ulva sp. (formerly Enteromorpha sp.), and Ulva lactuca on polychaeta Sabellaria cementarium and Spinoidae sp. In turn, the diverse effects of Ulvaria obscura on Arthropoda have been described by Van Alstyne et al. [46]. The authors demonstrated that tested green algae did not affect the survival of Cancer oregonensis and Metacarcinus magister juveniles. It was also shown that Ulva obscura had little effect on the time of first molting of these animals. Alvarez-Hernández et al. [8] showed that various species belonging to Chlorophyta were considered highly toxic to Chordata (the goldfish Carassius auratus auratus) when acetonic or ethanolic extract was made. The most toxic Chlorophyta were: Caulerpa cupressoides, Caulerpa racemosa, Chaetomorpha antennina, and Penicillus capitatus. However, aqueous extract obtained from these green algae had no effect on C. auratus auratus (Table 1).

Table 1. Examples of allelopathic activity of green algae against competitors and herbivores.

| Donor Chlorophyta | Target Organism—Cnidaria | Effect | References |
|-------------------|--------------------------|--------|------------|
| Bryopsis corymbose| Pocillopora damicornis    | −      | Lee et al. [28] |
| Bryopsis sp.      | Pocillopora acuta        | −      | Fong et al. [39] |
| Chlorodesmis fastigiata | Acropora millepora   | +/0    | Birrell et al. [40] |
|                   | Acropora aspera          | −      |            |
| Chlorodesmis fastigiata | Pocillopora damicornis | −      | Bonaldo and Hay [23] |
|                   | Porites cylindrica       | −      |            |
|                   | Porites lobata           | −      |            |
| Chlorodesmis fastigiata | Acropora intermedia    | −      | Del Monaco et al. [25] |
| Chlorodesmis fastigiata | Phialophora verrucosa  | −      | Longo and Hay [26] |
|                   | Acropora millepora       | −      |            |
| Chlorodesmis fastigiata | Montipora digitata      | −      | Rasher et al. [22] |
|                   | Pocillopora damicornis   | −      |            |
|                   | Acropora millepora       | −      |            |
| Chlorodesmis fastigiata | Pocillopora damicornis | −      | Ritson-Williams et al. [24] |
|                   | Acropora cuneata         | −      |            |
| Chlorodesmis fastigiata | Acropora hrueggemannii  | −      | Tanner [21] |
|                   | Acropora pnifera         | −      |            |
|                   | Pocillopora damicornis   | −      | Lee et al. [28] |
| Halimeda opuntia  | Pocillopora damicornis   | −      |            |
| Halimeda tuna     | Montastraea faveolata    | −      | Morrow et al. [52] |
|                   | Porites astreoides       | 0      |            |
|                   | Acropora cuneata         | −      |            |
| Halimeda sp.      | Acropora hrueggemannii   | −      | Tanner [21] |
|                   | Acropora pnifera         | −      |            |
|                   | Pocillopora damicornis   | −      |            |
| Rhithalia pencilloides | Porites rus             | −      | Andras et al. [51] |
Table 1. Cont.

| Donor Chlorophyta | Target Organism—Mollusca | Effect | References |
|-------------------|--------------------------|--------|------------|
| Ulva australis     | Haliotis rubra           | +      | Huggett et al. [49] |
| Ulva compressa    | Crassostrea virginica    | −      | Green-Gavrielidis et al. [38] |
| Ulva compressa    | Haliotis rubra           | +      | Huggett et al. [49] |
| Ulva fenestrata   | Crassostrea gigas        | −      | Nelson et al. [47] |
| Ulva lactuca      | Crassostrea virginica    | −      | Green-Gavrielidis et al. [38] |
| Ulva lens         | Crassostrea gigas        | −      | Nelson et al. [47] |
| Ulvaria obscura   | Haliotis rubra           | +      | Huggett et al. [49] |
| Ulvaria obscura   | Crassostrea virginica    | −      | Green-Gavrielidis et al. [38] |
| Ulva sp.          | Haliotis rufescens       | +      | Muñoz et al. [50] |

| Donor Chlorophyta | Target Organism—Annelida | Effect | References |
|-------------------|--------------------------|--------|------------|
| Chaetomorpha sp.  | Sabellaria cementarium   | −      | Warkus et al. [41] |
| Sabellaria cementarium | Spinoideae sp.         | −      | Warkus et al. [41] |
| Codium fragile    | Sabellaria cementarium   | −      | Warkus et al. [41] |
| Sabellaria cementarium | Spinoideae sp.         | −      | Warkus et al. [41] |
| Ulva (Enteromorpha) sp. | Sabellaria cementarium | −      | Warkus et al. [41] |
| Sabellaria cementarium | Spinoideae sp.         | −      | Warkus et al. [41] |

| Donor Chlorophyta | Target Organism—Arthropoda | Effect | References |
|-------------------|-----------------------------|--------|------------|
| Ulvaria obscura   | Cancer oreognensis           | 0/−    | Van Alstyne et al. [46] |
| Metacarcinus magister | 0/−                        |        |            |

| Donor Chlorophyta | Target Organism—Chordata | Effect | References |
|-------------------|--------------------------|--------|------------|
| Anadyomene stellata | Carassius auratus auratus | 0/−    | Alvarez-Hernández et al. [8] |
| Caulerpa cupressoides | Carassius auratus auratus | 0/−    | Alvarez-Hernández et al. [8] |
| Caulerpa paspaloides | Carassius auratus auratus | 0/−    | Alvarez-Hernández et al. [8] |
| Caulerpa racemosa  | Carassius auratus auratus | 0/−    | Alvarez-Hernández et al. [8] |
| Chaetomorpha antennina | Carassius auratus auratus | 0/−    | Alvarez-Hernández et al. [8] |
| Penicillus capitatus | Carassius auratus auratus | 0/−    | Alvarez-Hernández et al. [8] |

Note: − means inhibiting effects, + means stimulating effect, 0—means lack of effect.

Many macroalgae, such as Ulva sp., are cosmopolitan organisms, and in nutrient-rich coastal waters, they are often dominant and bloom-forming species [15,53,54]. These studies confirm that Chlorophyta may have a negative impact on co-occurring animal organisms. Therefore, allelopathy phenomenon of species belonging to Chlorophyta on coexisting animal organisms should be widely studied in the future.

4.2. The Allelopathic Activity of Red Algae

The allelopathic activity of red algae (Florideophyceae, Rhodophyta) on coexisting animals has also been confirmed by a few experimental studies (Table 2). The negative effect of red algae on Cnidaria was described by Tanner [21], Rasher et al. [22], Bonaldo and Hay [23], Ritson-Williams et al. [24], Del Monaco et al. [25], Longo and Hay [26], Fong et al. [39], and Andras et al. [51]. In addition, a few authors [22,24,39,42] observed that certain red algae species had no allelopathic effect on target Cnidaria (Table 2). Tanner [21] described that Acropora species growing faster in areas from which red macroalgae Peyssonnelia sp. had been removed compared to control areas where Rhodophyta species were present. Similarly, Andras et al. [51] used field experiments to show that contact with the red algae Callithamnion densus, Phaeoceros neurypnenthios, and Plocamium pacificum induces bleaching on natural colonies of Porites rus. Moreover, the corals in the control experiments, in which they encountered plastic imitation algae, showed no bleaching,
which may suggest the effect of the red macroalgae allelochemicals rather than the effect of shading or physical contact. Bonaldo and Hay, [23] demonstrated that the presence of allelopathic red macroalgae Galaxaura filamentosa caused faster and more extensive damage to Acropora aspera and P. damicornis than to Porites cylindrica, Porites lobata, and Montipora digitata. Furthermore, Longo and Hay [26] showed that the red algae Amansia rhodantha and Asparagopsis taxiformis extracts negatively affected the photochemical efficiency of the coral Phialophora verrucosa. Fong et al. [39] examined the effects of crude extracts from macroalgal species Endosiphonia hordida and Hypnea pannosa on Pocillopora acuta larvae. In turn, Del Monaco et al. [25] showed that common Rhodophyta Amansa glomerata damage corals Acropora intermedia via allelopathy, however, the effect of the macroalgal extracts was not stronger when the tested Rhodophyta species were grown under elevated CO2 conditions. Rasher et al. [22] and Ritson-Williams et al. [24] showed that red algae G. filamentosa had negative effects on Acropora millepora, M. digitata, and P. damicornis. Similarly, Kuffner et al. [42] demonstrated no allelopathic effects of Chondrophycus poiteaui (formerly Laurencia poiteaui) on the recruitment success of Porites astroideae larvae. Moreover, Warkus et al. [41] described the negative influence of Rhodophyta Grateloupia turu turu and Polyisiphonia denudata on Annelida Sabellaria cementarium and Spinoidae sp. Ishii et al. [36] also demonstrated that compounds obtained from red algae (Tichocarpus crinitus) exhibited feeding-deterrent properties against the Echinodermata Strongylometrus intermedius. Conversely, Williamson et al. [33] showed that allelochemicals produced by Delisea pulchra caused a positive effect on metamorphosis and triggered settlement in other Echinodermata Holopneustes purpurascens. The studies by Alvarez-Hernández et al. [8] showed that, in general, the aqueous extract did not affect the behavior of the Carassius auratus belonging to Chordata phylum. The only exception was Chondriopsis dasyphylla f. pyrifera, which showed strong toxicity to the tested animal after exposure to aqueous, acetonic, and ethanolic extracts. The studies by Alvarez-Hernández et al. [8] showed that the activity of macroalgae also depends on the place of occurrence of individual species.

Table 2. Examples of allelopathic activity of red algae against competitors and herbivores.

| Donor Rhodophyta         | Target Organism—Cnidaria | Effect | References                              |
|--------------------------|--------------------------|--------|-----------------------------------------|
| Amphiroa crassa          | Acropora millepora       | −      | Rasher et al. [22], Ritson-Williams et al. [24] |
| Amansia glomerata        | Montipora digitata       | 0      | Del Monaco et al. [25]                  |
| Amansia rhodantha        | Acropora intermedia      | −      | Longo and Hay [26]                     |
| Asparagopsis taxiformis  | Phialophora verrucosa    | −      | Longo and Hay [26]                     |
| Callophycus densus       | Porites rus              | 0      | Andras et al. [51]                     |
| Chondrophycus poiteaui   | Pocillopora acuta        | −      | Fong et al. [39]                       |
| Endosiphonia hordida     | Acropora millepora       | −      | Rasher et al. [22], Ritson-Williams et al. [24] |
| Galaxaura filamentosa    | Montipora digitata       | −      |                                        |
|                          | Pocillopora damicornis   | −      |                                        |
|                          | Acropora aspera          | −      |                                        |
| Galaxaura filamentosa    | Pocillopora damicornis   | −      | Bonaldo and Hay [23]                   |
|                          | Porites cylindrica       | −      |                                        |
|                          | Porites lobata           | −      |                                        |
| Hypnea pannosa           | Pocillopora acuta        | 0      | Fong et al. [39]                       |
| Liagora sp.              | Acropora millepora       | −      | Rasher et al. [22], Ritson-Williams et al. [24] |
|                          | Montipora digitata       | 0      |                                        |
| Phacelocarpus neurymenhiodes | 0 Pocillopora damicornis | − | Andras et al. [51]                     |
| Plocamium pacificum      | Porites rus              | −      | Andras et al. [51]                     |
|                          | Acropora cuneata         | −      |                                        |
| Peyssonielia sp.         | Acropora hrueggemannii   | −      | Tanner [21]                            |
|                          | Acropora pritifera       | −      |                                        |
|                          | Pocillopora damicornis   | 0/−   |                                        |
Table 2. Cont.

| Donor Rhodophyta | Target Organism—Annelida | Effect | References |
|------------------|--------------------------|--------|------------|
| Grateloupia turu turu | Sabellaria cementarium | –      | Warkus et al. [41] |
| Polysiphonia denudata | Sabellaria cementarium | –      | Warkus et al. [41] |

| Donor Rhodophyta | Target Organism—Echinodermata | Effect | References |
|------------------|--------------------------------|--------|------------|
| Delisea pulchra | Holopneustes purpurascens | +      | Williamson et al. [33] |
| Tichocarpus crinitus | Strongylocentrotus intermedius | –      | Ishii et al. [36] |

| Donor Rhodophyta | Target Organism—Chordata | Effect | References |
|------------------|--------------------------|--------|------------|
| Acanthophora spicifera | Carassius auratus auratus | 0/–    | Alvarez-Hernández et al. [8] |
| Amphiroa beauvoisi | Carassius auratus auratus | 0/–    | Alvarez-Hernández et al. [8] |
| Ceramium nitens | Carassius auratus auratus | 0/–    | Alvarez-Hernández et al. [8] |
| Chondria littoralis | Carassius auratus auratus | 0      | Alvarez-Hernández et al. [8] |
| Chondriopsis dasyphylfa f. pyrifera | Carassius auratus auratus | –      | Alvarez-Hernández et al. [8] |
| Crassiphyceca caudatus (Gracilaria caudata) | Carassius auratus auratus | 0      | Alvarez-Hernández et al. [8] |
| Dermopema virens | Carassius auratus auratus | 0      | Alvarez-Hernández et al. [8] |
| Digenea simplex | Carassius auratus auratus | 0      | Alvarez-Hernández et al. [8] |
| Gracilaria cervicornis | Carassius auratus auratus | 0/–    | Alvarez-Hernández et al. [8] |
| Gracilaria tikebahae | Carassius auratus auratus | 0/–    | Alvarez-Hernández et al. [8] |
| Grateloupia filicina | Carassius auratus auratus | 0      | Alvarez-Hernández et al. [8] |
| Hypnea musciformis | Carassius auratus auratus | 0/–    | Alvarez-Hernández et al. [8] |
| Hypnea spinella | Carassius auratus auratus | 0/–    | Alvarez-Hernández et al. [8] |
| Laurencia obtusa | Carassius auratus auratus | 0/–    | Alvarez-Hernández et al. [8] |
| Liagora ceranoides | Carassius auratus auratus | 0/–    | Alvarez-Hernández et al. [8] |
| Tayloriella dictyurus | Carassius auratus auratus | 0      | Alvarez-Hernández et al. [8] |
| Yuzurua poiteaui var. gemmifera | Carassius auratus auratus | 0      | Alvarez-Hernández et al. [8] |

Note: – means inhibiting effects, + means stimulating effect, 0—means lack of effect.

4.3. The Allelopathic Activity of Brown Algae

Ochrophyta (Phaeophyceae) were the most frequently studied organisms among all macroalgal phyla in which allelopathic activity on target organisms was confirmed (Table 3). The strong negative impact of brown algae on Cnidaria has been described in detail by Tanner [21], Del Monaco et al. [25], Webster et al. [29], Fong et al. [39], Kuffner et al. [42], Paul et al. [55], and Olsen et al. [56]. Tanner [21] demonstrated that changes in Acropora sp. cover were significantly affected by the presence of this brown algae. Later, Kuffner et al. [42] showed that tested brown algae (Dictyota menstrualis and Lobophora variegata) inhibited recruitment and avoidance behavior in Porites astreoides larvae. Olsen et al. [56] also provided evidence that the presence of the brown alga D. menstrualis has direct negative effects on the survival and recruitment of Caribbean coral P. astreoides. Moreover, Webster et al. [29] showed the negative effect of brown algae Sphacelaria sp. on larval settlement and the growth as well as the survival of coral recruits Acropora millepora. Fong et al. [39] demonstrated that mortality of Pocillopora acuta larvae increased considerably with increasing concentrations of Lobophora sp. extracts. Furthermore, Del Monaco et al. [25] shown that elevated CO₂ concentrations increased the deleterious effect of Canistrocarpus (=Dictyota) cervicornis on Acropora intermedia. In turn, Paul et al. [55] provided evidence that Dictyota pulchella and Dictyota pinnatifida may adversely affect larval settlements and recruitment.
| Donor Ochrophyta | Target Organism—Cnidaria | Effect | References |
|-----------------|--------------------------|--------|------------|
| Dictyota bartayresiana | Phialophora verrucosa | — | Longo and Hay [26] |
| Dictyota bartayresiana | Acropora millepora | — | Rasher et al. [22], Ritson-Williams et al. [24] |
| Dictyota bartayresiana | Montipora digitata | — | Ritson-Williams et al. [27] |
| Dictyota bartayresiana | Pocillopora damicornis | 0 | — |
| Dictyota cervicornis | Acropora millepora | — | Del Monaco et al. [25] |
| Dictyota menstrualis | Porites astreoides | — | Olsen et al. [56] |
| Dictyota pinnatifida | Porites astreoides | — | Paul et al. [55] |
| Dictyota pulchella | Porites astreoides | — | Paul et al. [55] |
| Dictyota pulchella | Acropora cervicornis | 0 | — |
| Dictyota pulchella | Acropora palmata | — | Ritson-Williams et al. [27] |
| Dictyota sp. | Montastraea faveolata | 0/— | Morrow et al. [52] |
| Dictyota sp. | Briareum asbestinum | — | Kuffner et al. [42] |
| Lobophora abscondita | Montipora hirsute | 0 | Vieira et al. [57] |
| Lobophora abscondita | Stylophora pistillata | — | — |
| Lobophora crassa | Montipora hirsute | 0 | Vieira et al. [57] |
| Lobophora dimorpha | Montipora hirsute | 0 | Vieira et al. [57] |
| Lobophora hederacea | Montipora hirsute | 0 | Vieira et al. [57] |
| Lobophora monticola | Montipora hirsute | 0 | Vieira et al. [57] |
| Lobophora nigrescens | Montipora hirsute | 0 | Vieira et al. [57] |
| Lobophora rosacea | Montipora hirsute | 0 | Vieira et al. [57] |
| Lobophora undulata | Montipora hirsute | 0 | Vieira et al. [57] |
| Lobophora variegata | Acropora millepora | + | Birrell et al. [40] |
| Lobophora variegata | Briareum asbestinum | — | Kuffner et al. [42] |
| Lobophora variegata | Montastraea faveolata | — | Morrow et al. [52] |
| Lobophora sp. | Pocillopora acuta | — | Fong et al. [39] |
| Lobophora sp. | Acropora cervicornis | — | — |
| Lobophora sp. | Acropora palmata | — | Ritson-Williams et al. [27] |
| Lobophora sp. | Pseudodiploria strigosa | 0 | — |
Several studies have shown that brown algae can have different effects on animals depending on the donor and target species [22,24,26–28,52,57]. Lee et al. [28] examined the effects of macroalgal species on the settlement success of Pocillopora damicornis larvae under aquarium conditions. Longo and Hay [26] also conducted field experiments assessing the effects of extracts obtained from Dicystota bartayresiana and Turbinaria ornata on the coral Pocillopora verrucosa. Ritson-Williams et al. [24] showed that the brown algae

$$\text{Note: } - \text{ means inhibiting effects, + means stimulating effect, 0—means lack of effect.}$$

### Table 3. Cont.

| Donor Ochrophyta | Target Organism—Cnidaria | Effect | References |
|------------------|---------------------------|--------|------------|
| Padina boryana   | Acropora millepora        | 0      | Rasher et al. [22], Ritson-Williams et al. [24] |
| Padina minor     | Montipora digitata        | 0      | Lee et al. [28] |
| Padina sp.       | Acropora millepora        | 0      | Birrell et al. [40] |
| Sargassum polycystum | Montipora digitata       | 0      | Ritson-Williams et al. [24] |
| Sphacelaria sp.  | Acropora millepora        | 0      | Webster et al. [29] |
| Turbinaria conoides | Montipora digitata      | 0      | Rasher et al. [22] |
| Turbinaria conoides | Pocillopora damicornis   | -      | Lee et al. [28] |
| Turbinaria ornata | Acropora cuneata          | -      | Tanner [21] |
| Turbinaria ornata | Acropora haeurgemanni    | -      | - |
| Turbinaria ornata | Acropora palifera         | -      | - |
| Turbinaria ornata | Pocillopora damicornis    | -      | - |

| Donor Ochrophyta | Target Organism—Mollusca | Effect | References |
|------------------|---------------------------|--------|------------|
| Dilophus okamurae | Haliotis discus hannai    | -      | Suzuki et al. [34] |

| Donor Ochrophyta | Target Organism—Annelida | Effect | References |
|------------------|---------------------------|--------|------------|
| Desmarestia viridis | Sabellaria cementarium  | -      | Warkus et al. [41] |
| Laminaria sp.    | Sabellaria cementarium    | -      | Warkus et al. [41] |

| Donor Ochrophyta | Target Organism—Echinodermata | Effect | References |
|------------------|-----------------------------|--------|------------|
| Dictyota pfaffii | Lytechinus variegates       | -      | Barbosa et al. [35] |
| Ecklonia radiata | Holopneustes purpurascens   | 0      | Williamson et al. [33] |
| Stypopodium zonale | Strongylocentrotus purpuratus | -      | Gerwick and Fenical [31] |

| Donor Ochrophyta | Target Organism—Arthropoda | Effect | References |
|------------------|-----------------------------|--------|------------|
| Dictyota pfaffii | Pachygrapsus transversus    | 0      | Barbosa et al. [35] |

| Donor Ochrophyta | Target Organism—Chordata | Effect | References |
|------------------|---------------------------|--------|------------|
| Dictyopteris delicatula | Carassius auratus auratus | 0/-    | Alvarez-Hernández et al. [8] |
| Dictyota bartayresiana | Carassius auratus auratus | 0/-    | Alvarez-Hernández et al. [8] |
| Dictyota implexa    | Carassius auratus auratus | -/-    | Alvarez-Hernández et al. [8] |
| Dictyota spinulosa  | Tilapia mossambica        | -      | Tanaka and Higa [32] |
| Lobophora variegata | Carassius auratus auratus | 0/-    | Alvarez-Hernández et al. [8] |
| Padina gymnospora  | Carassius auratus auratus | 0/-    | Alvarez-Hernández et al. [8] |
| Sargassum liebmannii | Carassius auratus auratus | 0/-    | Alvarez-Hernández et al. [8] |
| Stypopodium zonale | Carassius auratus auratus | 0/-    | Alvarez-Hernández et al. [8] |
| Stypopodium zonale | Eupomacentrus leucostictus | -      | Gerwick and Fenical [31] |
| Stypopodium zonale | Eupomacentrus leucostictus | -      | Gerwick et al. [30] |
D. bartayresiana negatively affected Acropora millepora, Montipora digitata, and P. damicornis. Four years later, Ritson-Williams et al. [27] tested settlements in the presence of different algae of three coral species: Acropora pulmapa, Acropora cervicornis, and Pseudodiploria strigosa. Vieira et al. [57] showed that extracts obtained from Lobophora sp. can bleach certain coral species during direct contact. Furthermore, the authors demonstrated that the studied corals differed in their sensitivity to the presence of an extract obtained from brown algae. In turn, Morrow et al. [52] found that both the crude extracts and the presence of live brown algae induced significant changes in the bacterial complex associated with corals and sub-lethal stress responses in Montastraea faveolata. Furthermore, Rasher et al. [22] demonstrated that macroalgae can directly cause bleaching and death of corals by the transfer of hydrophobic allelochemicals present on their surfaces. It was found that damage to corals has generally been confined to places where it encounters the macroalgae. However, contact with the corals had no effect on these brown algae species. These findings suggest that the deleterious effects on corals are caused by allelopathic compounds rather than by physical contact. Conversely, Birrell et al. [40] have shown that Ochrophyta (Lobophora variegata) can also have a positive effect on Cnidaria Acropora millepora. To study allelopathic compounds that control seaweed-herbivore interactions, Suzuki et al. [34] investigated the effects of Dilophus okamurae on Mollusca (Halotitis discus hannai). Only Warkus et al. [41] described the negative allelopathic effect of brown algae Desmarestia viridis and Laminaria sp. on polychaeta Sabellaria cementarium and Spinidae sp. (Annelida). Barbosa et al. [35] showed that compounds obtained from Dictyota pfaffii were effective in inhibiting feeding by the sea urchin Lytechinus variegatus (Echinodermata). Research conducted by Gerwick and Fenical [31] also confirmed the negative effect of Ochrophyta on Echinoderma. Conversely, Williamson et al. [33] showed that Ecklonia radiata had no effect on the development and metamorphosis of Holopneustes purpurascens (Echinoderma) larvae. Barbosa et al. [35] were the only authors who documented that the compound obtained from Dictyota pfaffii did not inhibit feeding by the crab Pachygrapsus transversus (Arthropoda). Research conducted by Alvarez-Hernández et al. [8] showed that brown algae may adversely affect animals belonging to Chordata phylum. Gerwick et al. [30] performed an experiment showing that when Stypopodium zonale was placed in the aquarium, the water became a rust colored and toxic to the herbivorous fish Eupomacentrus leucostictus. Later, Gerwick and Fenical [31] described that nearly all the compounds isolated from S. zonale showed negative effects on the same species of reef-dwelling fish. It has been suggested that the production of noxious and allelopathic substances contributes significantly to the survival of S. zonale in predator-rich areas in which it abounds.

All these results indicate that brown algae may affect the marine ecosystem by limiting the development of associated animals. Moreover, recent field assays have suggested the potential role of chemical mediators in this interaction. It has also been suggested that certain brown algae species may produce allelopathic compounds that may play an important ecological function as a defense strategy against herbivores worldwide [35].

5. Allelopathic Compounds Produced by Macroalgae

Since there is very little information about the compounds produced by macroalgae, this section provides examples of characterized macroalgae compounds that interact with other heterotrophic organisms (not only competing and herbivorous).

Many studies have reported novel secondary metabolites produced by marine Chlorophyta species, which have significant biological activity on target organisms (Table 4). Capisterones, caulerpals, cycloeudensol, cymobarbatol, halitunal, isorawsonol, lyengaroside, and sphingosin are compounds that have been isolated from Penicillus capitatus, Caulerpa taxifolia, Chondria oppositiflada, Cymopolia barbat, Halimeda tuna, Arrainvillia rawsonii, Codium lyengarii, and Ulva fasciata green algae, respectively [58]. Dopamine is an allelopathic compound produced by the green algae Ulvaria obscura that negatively affects the development of coexisting aquatic animals [46,59]. The U. obscura is a common Chlorophyta that often forms the green tides in the northeastern Pacific [47], where it can
coexist with other green macroalgal species such as *Ulva lactuca*, *U. prolifera*, and *U. linza*. Nelson et al. [47] hypothesized that dopamine is responsible for some harmful effects observed in coexisting aquatic animals. Paul and Fenical [60] showed that halimedatrial can completely inhibit the motility of sea urchin (*Lytechinus pictus*) sperm. Halimedatrial is a diterpene trialdehyde isolated from various species of the genus *Halimeda* ( Chlorophyta) such as *H. tuna*, *H. opuntia*, *H. incrassata*, *H. simulans*, *H. scabra*, and *H. copiosa*. This compound is also toxic toward reef damselfishes (*Eupomacentrus planifrons* and *Dascyllus aruanus*) and significantly reduces feeding in these herbivorous fishes [60].

Marine red algae are the most important source of many biologically active compounds (Table 4). For instance, the Rhodophyta *Callurophybus serratus*, *Plocumium cartilagineum*, *Portieria hornemanii*, *Laurencia okamurai*, and *Laurencia viridis* are sources of bromophycolides C-I, furoplocamioid C, halmon, laurinterol, and thyresenol A-B compounds, respectively [58]. Moreover, tichocarpols A and B are compounds isolated from the red alga *Tichocarpus crispus*, and they exhibit antifeedant activity against the sea urchin *Strongylocentrotus intermedius* [36]. Williamson et al. [33] described that the floridoside-isethionic acid complex produced and released by *Delisea pulchra* induced metamorphosis in the *Holopneustes purpurascens* sea urchin.

Many bioactive metabolites with different biological activities have also been isolated from Ochrophyta (Table 4). Brown algae species such as *Bifurcaria bifurcata*, *Dictyota dichotoma*, *Cystoseira tamariiscifolia*, *Lobopha variegata*, *Sargassum siliquastrum*, and *Turburaria ornata* can produce compounds such as bifurcadiol, dictyotins, meroditerpenoid, lobophorolide, sargachromanols, and turbinaric acid, respectively [58]. Tanaka and Higa [32] noted that *Dictyota spinulosa* are not commonly eaten by the herbivorous fish *Tilapia mossambica* because it produces allelopathic diterpene. Similarly, two diterpenoids (dictyterepenoids A and B), which were isolated from the *Dilophus okamurae* brown algae, display antifeedant activity against the *Haliotis discus hannai* abalone [34]. Furthermore, *Dictyota pfaffi* brown algae also produce antifeedant compounds (diterpenoid 10,18-diacetoxy-8-hydroxy-2,6-dolabelladiene) against herbivores (sea urchins and fishes) [35]. Gerwick et al. [30] showed that stypoldione isolated from *Stypopodium zonale* brown algae exhibits ichthyotoxic activity on herbivorous reef-dwelling fish *Eupomcentrus leucostictus*. Two years later, Gerwick and Fenical [31] described other compounds obtained from this brown alga, including stypotriol, stypodiol, epistypodiol, epitaondiol, 2-(geranyl-geranyl)-5-methyl-1,4-benzohydroquinone, 2-(geranyl-geranyl)-5-methyl-1,4-benzoquinone, taondiol, and acidic aromatic, which showed toxic effects toward *E. leucostictus*. These authors also reported that stypoldione from *S. zonale* is a potent inhibitor of cell division in the fertilized eggs of the sea urchin *Strongylocentrotus purpuratus*.

Although freshwater and brackish macroscopic green algae (Chlorophyta and Charophyta) can produce allelochemicals with interesting properties [61–64], they have not been widely investigated (Table 4). Wium-Andersen et al. [61,62] showed that freshwater *Chara globularis* (Chlorophyta, Charophyceae) negatively affects natural phytoplankton assemblages via two sulfuric compounds: dithiolane and trithiane. Anthoni et al. [63] isolated charamin, which has strong antibiotic activity, from *C. globularis*. More recently, Korzeniowska et al. [64] identified nine phenolic compounds obtained from freshwater *Cladophora glomerata* (Chlorophyta, Ulvophyceae) however, the activity of these compounds on aquatic animals has not been tested (Table 4).
Table 4. Macroalgae capable of producing bioactive compounds against other heterotrophic organisms (not only competing and herbivorous), location of their environmental occurrence, name of compounds, and their effect on target organisms.

| Phylum/Species | Habitat        | Compound                                      | Activity                                      | References                                   |
|----------------|----------------|-----------------------------------------------|-----------------------------------------------|----------------------------------------------|
| **Green Algae (Chlorophyta)** |               |                                               |                                               |                                              |
| Avrainvillea nigricans | marine     | Nigricanosides A–B                           | Antimitotic agent                             | Williams et al. [65]                         |
| Avrainvillea nigricans | marine     | Hydroxyisoavrainvilleol                      | Protein tyrosine phosphate 1B inhibitors (PTP1B)            | Colon et al. [66]                           |
| Avrainvillea rawsonii  | marine     | Isorawsonol                                   | Cytotoxic and immunosuppressive activities     | Chen et al. [67]                            |
| Bryopsis sp.         | marine     | Kahalalide F                                  | Cytotoxic and immunosuppressive activities     | Hamann and Scheuer [68]                      |
| Bryopsis sp.         | marine     | Kahalalide P                                  | Cytotoxic and immunosuppressive activities     | Dmitrenok et al. [69]                       |
| Caulerpa racemosa    | marine     | Sulfonovosyldiacylglycerol                   | Antiviral activity                            | Wang et al. [70]                            |
| Caulerpa taxifolia   | marine     | Caulerpals A–B                               | Anti-fungal activity                          | Aguilar-Santos [71]                         |
| Chara globularis     | freshwater  | Charamin                                       | Antibiotic activity                           | Anthoni et al. [63]                         |
| Chara globularis     | freshwater  | Dithiolane, Trithiane                         | Antialgal activity                            | Wium-Andersen et al. [61]                   |
| Cladophora glomerata | freshwater  | Gallic acid, Chlorogenic acid, Syringic acid,  p-coumaric acid, Myricetin, 3,4-dihydroxybenzoic acid, Vanillic acid, 4-hydroxybenzoic acid, Rutin | Unknown                                      | Korzeniowska et al. [64]                    |
| Codium iypengarii    | marine     | Lyngaroside                                   | Antibacterial activity                        | Ali et al. [72]                             |
| Cymopolia barbata    | marine     | Cymobarbatol, 4-isocymobarbatol               | Antimutagenic activity                        | Wall et al. [73]                            |
| Halimeda tuna, Halimeda incrassata, Halimeda simulans, Halimeda scabra, Halimeda copiosa | marine | Halimedatrial                                 | Cytotoxic and antimicrobial activities         | Paul and Fenical [60]                        |
| Halimeda tuna        | marine     | Halitunal                                      | Antibacterial activity                        | Koehn et al. [74]                           |
| Halimeda sp.         | marine     | Halimedatrial                                 | Antimicrobial and cytotoxic properties         | Paul and Fenical [75]                       |
| Penicillus capitatus | marine     | Capisterones A–B                             | Anti-fungal activity                          | Puglisi et al. [76]                         |
| Tydemania expeditionis | marine    | Cycloartenol disulfates                       | Cytotoxic and immunosuppressive activities     | Govindan et al. [77]                        |
| Ulva (Enteromorpha) intestinals | marine | Penostatins A–H                              | Cytotoxic and immunosuppressive activities     | Takahashi et al. [78], Iwamoto et al. [79,80] |
| Ulva (Enteromorpha) intestinals | marine | Cytochalasans, penochalasins A–H              | Cytotoxic activity                            | Numata et al. [81]                          |
| Ulva (Enteromorpha) intestinals | marine | Chaetoglobosin                                | Cytotoxic activity                            | Iwamoto et al. [82]                         |
| Ulva (Enteromorpha) intestinals | marine | Communesins A–B                               | Cytotoxic and immunosuppressive activities     | Numata et al. [83]                          |
| Ulva lactuca         | marine     | 3-0-β-D-glucopyranosyl-5,25-diene             | Anti-inflammatory substances                  | Awad et al. [84]                            |
| Ulvaria obscura      | marine     | Dopamine                                      | Feeding-deterrent substances                  | Tocher and Craigie [59], Van Abltynge et al. [46] |
| **Red Algae (Rhodophyta)** |              |                                               |                                               |                                              |
| Beckerella (Gelidiolum) subcostatum | marine | Bromo- beckerelide, epimer, chlorobeckerelide | Antimicrobial activity                        | Ohta [85]                                   |
| Callophycus serratus | marine      | Bromophycyllides A-B                          | Cytotoxic activity                            | Kubanek et al. [86]                         |
| Callophycus serratus | marine      | Bromophycyllides C–I                          | Cytotoxic activity                            | Kubanek et al. [87]                         |
| Callophycus serratus | marine      | Callophycic acids A–H, diterpene-phenols, callophycals A–B | Antibacterial, antimalarial, anti-tumor and antifungal activity | Lane et al. [88]                            |
| Chondria armata      | marine     | Isidomic acid A–C                            | Insecticidal activity                         | Maeda et al. [89]                           |
| Chondria atropurpurea | marine    | Chondriamide C, 3-indolacrylamide             | Anthelmintic activity                         | Davyt et al. [90]                           |
| Chondria oppositoclda | marine     | Cycloeduesmol                                 | Antibacterial activity                        | Fenical and Sims [91]                       |
| Delisea pulchra      | marine     | Floridoside-ethionionic acid complex          | Induction of animal metamorphosis             | Williamson et al. [33]                      |
| Phylum/Species         | Habitat   | Compound                                      | Activity                                      | References                          |
|------------------------|-----------|-----------------------------------------------|-----------------------------------------------|--------------------------------------|
| **Red Algae (Rhodophyta)** |           |                                               |                                               |                                      |
| *Digenea simplex*      | marine    | α-alko-kainic acid                            | Neurophysiological activity                   | Biscoe et al. [92], Ferkany and Coyle [93] |
| *Gracilaria asiatica*  | marine    | Cerebroside gracilarioside, ceramides gracilamides A–B | Cytotoxic activity                            | Sun et al. [94]                      |
| *Gigartina tenella*    | marine    | Sulquinovosyldiacylglycerol: KM043             | Antiviral activity                            | Ohata et al. [95]                    |
| *Jania rubens*         | marine    | Deoxyparguerol-7-acetate                      | Anthelmintic activity                         | Awad [96]                           |
| *Laurencia broncniartii* | marine    | Polyb romoindoles                            | Antimicrobial activity, cytotoxic activity     | Carter et al. [97], El Gamal et al. [98] |
| *Laurencia broncniartii* | marine    | Brominated indoles                           | Antibacterial activities                       | Carter et al. [97]                  |
| *Laurencia elata*      | marine    | Elatol                                        | Cytotoxic activity                            | Suzuki et al. [100]                 |
| *Laurencia obtusa*     | marine    | Teurilene, thyrsiferyl 23-acetate, 3,7-dihydroxydihydrolaurene, perforeno B | Cytotoxic activity                            | Kladi et al. [101]                  |
| *Laurencia obtusa*     | marine    | Neorogiodiol B, prevezol B–D                 | Cytotoxic activity                            | Ilopooulou et al. [102]             |
| *Laurencia obtusa*     | marine    | Iso-obtusiol Sesquiquaterpene                 | Antibacterial activities, antimalarial activity | Gonzalez et al. [103,104], Topeu et al. [105] |
| *Laurencia obtusa*     | marine    | Dehydrothysinol, thysrenol A and B            | Cytotoxic activity                            | Norte et al. [106], Pec et al. [107] |
| *Laurecia pinnatífida* | marine    | Laurepinnacin, isolaurepinnacin Brominated diterpene, 10-hydroxydihydrolaurene B | Insecticidal activity                         | Fukuzawara and Masamune [108]       |
| *Laurencia pinnata*    | marine    | 9-deoxylanostanol, isolauretnoide A, C15-acetogenin, laurenmariallone, sesquiterpenes | Antibacterial activities                       | Gonzalez et al. [109]               |
| *Laurencia mariannensis* | marine    | Laurint erol, isolaurent erol, alypin, α-bromocoumarine (Z)-Laureatin, (Z)-isolaureatin, deoxyprecapenol, sesquiterpenes | Insecticidal and repellent activities         | Ishii et al. [110]                  |
| *Laurencia nipponica*  | marine    | Laurinterol, laurint erol, alypin, α-bromocoumarine (Z)-Laureatin, (Z)-isolaureatin, deoxyprecapenol, sesquiterpenes | Insecticidal activity                         | Watanabe et al. [111], El Sayed et al. [112] |
| *Laurencia scoparia*   | marine    | Cholest-5-en-3β,7α-diol Debromoepiaplysinol | Cytotoxic activity                            | Sun et al. [115]                    |
| *Laurencia venusta*    | marine    | Venustatriol                                  | Antiviral activity                            | Sakemi et al. [116]                 |
| *Laurencia yongangnensis* | marine    | Neorogiodiol B, prevezol B–D                 | Cytotoxic activity                            | Takahashi et al. [117]              |
| *Lophocladia sp.*      | marine    | Lophocladine B                                | Cytotoxic activity                            | Gross et al. [118]                  |
| *Murrayella periclados* | marine    | 12S-hydroxyeicosapentaenoic acid Lipoxygenase inhibitor Inhibition of isocitrinate lyase enzyme | Lipoxygenase inhibitor                        | Bernari and Gerwick [119]           |
| *Okolithia coromnibera* | marine    | Bromophenol                                    | Antiviral activity                            | Talip et al. [121]                  |
| *Pepsonnella sp.*      | marine    | Avarol                                        | Antiviral activity                            | Knott et al. [122]                  |
| *Plocamium alternifolius* | marine    | Plocaralides B–C                              | Cytotoxic activity                            | Watanabe et al. [123]               |
| *Plocamium telfairae*  | marine    | Telfarine                                      | Insecticidal activity                         | Lopez and Gerwick [124]             |
| *Ptilota filicina*     | marine    | Ptiloloidene                                   | Aldose reductase inhibitors activity          | Wang et al. [125]                   |
| *Symphyocladia latiuscula* | marine    | Ta sipeptins A–B                              | Anti-inflammatory activity                     | Wiemer et al. [126]                 |
| *Vidalia obtusiloba*   | marine    | Vidalols A–B                                  | Anti-inflammatory activity                     |                                      |
| **Brown Algae (Ochrophyta)** |           |                                               |                                               |                                      |
| *Chondria oppositilida* | marine    | Cycloeudesmol                                  | Antibacterial activity Free radical scavenger and antioxidant activities | Fenical and Sims [91]               |
| *Cystoseira crinita*   | marine    | Meroterpenoids                                 | Cytotoxic activity                            | Fisch et al. [127]                  |
| *Cystoseira myrica*    | marine    | Hydroazulene diterpenes                        | Cytotoxic activity                            | Ayyad et al. [128]                  |
| *Cystophora tamariscifolia* | marine    | Methoxybifurcarenone                           | Cytotoxic activity Antifungal and pheromone   | Bennamara et al. [129]              |
| *Cystophora siliculosus* | marine    | Cystopheore                                    | Antimicrobial activity                        | Muller et al. [130]                 |
| *Dictyopteris undulata* | marine    | Yahazunol                                      | Antifungal activity                           | Ochi et al. [131]                   |
| *Dictyopteris undulata* | marine    | Cyclozanarone                                  | Antifungal activity                           | Kurata et al. [132]                 |
| *Dictyopteris zonaroides* | marine    | Zonarol, isozonarol                            | Antifungal activity                           | Fenical et al. [133]                |
| *Dictyota pectinata*   | marine    | 10,18-diacetoxy—8-hydroxy-2,6-diolbadiene (dolabellane I) | Antiviral activity                            | Barbosa et al. [35,134]             |
| *Dictyota spinulosa*   | marine    | Hydroxydictyodial                              | Feeding-deterent substances                   | Tanaka and Higa [32]                |
| *Dictyota sp.*         | marine    | Dolabellane diterpenes                         | Cytotoxic activity                            | Tringali et al. [135]               |
| *Dilophus okamurae*    | marine    | Diictyterpenoids A–B                           | Antifeedent activity                          | Suzuki et al. [34]                  |
| *Ecklonia cava*        | marine    | Fucodiphloethol G                              | Antioxidant activity                          | Ham et al. [136]                    |
Table 4. Cont.

| Phylum/Species | Habitat | Compound | Activity | References |
|----------------|---------|----------|----------|------------|
| **Brown Algae (Ochrophyta)** |         |          |          |            |
| *Ecklonia stolonifera* | marine  | Phloroglucinol, eckstolonol, eckol, phlorotucofuroeckol A, dieckol | Hepatoprotective activity | Kang et al. [137] |
| *Giffordia mitchelliae* | marine  | Giffordene | Game-attracting pheromone | Boland et al. [138] |
| *Hizikia fusiformis* | marine  | Arsenic-containing ribofuranosides | Cytotoxic activity | Edmonds et al. [139] |
| *Hormosira banksii* | marine  | Hormosirene | Sperm-attractants pheromone | Muller et al. [130] |
| *Leptosiphon sp.* | marine  | Leptosins M, ML, N, N1 | Cytotoxic activity | Yamada et al. [140] |
| *Lobophora variegata* | marine  | Lobophorolide | Antifungal activity | Kubanek et al. [141] |
| *Notheia anomala* | marine  | *cis* dihydroxyte-trahydrofuran | Nematocidal activity | Capon et al. [142] |
| *Osmundaria serrata* | marine  | Lanosol enol ether | Antifungal and antibacterial activity | Barreto and Meyer [143] |
| *Perithalia caudata* | marine  | Caudoxirene | Game-attracting pheromone | Muller et al. [144] |
| *Pelvetia siliquosa* | marine  | Fucosterol | Anti-diabetic activity | Lee et al. [145] |
| *Sargassum siliculosum* | marine  | Sargachromanols A–P | Antioxidant activity | Jang et al. [146] |
| *Sargassum tortile* | marine  | Dihydroxy-sargaquinone | Cytotoxic activity | Numata et al. [147] |
| *Sargassum thunbergii* | marine  | Hydroxy-sargaquinone, sargasal-I-II | Cytotoxic activity | Numata et al. [148] |
| *Sargassum thunbergii* | marine  | Thunbergs A–B | Scavenging activities, antioxidant activity | Seo et al. [149] |
| *Sargassum thunbergii* | marine  | Sargothunbergol A | Antioxidant activity | Seo et al. [150] |
| *Stypopodium flabelliforme* | marine  | Dicyglycerols | Antifungal activity | Kim et al. [151] |
| *Stypopodium zonale* | marine  | Isoeptioandiol | Insecticidal activity | Rovirosa et al. [152] |
| *Stypopodium zonale* | marine  | Strypobil, stypodilone | Cytotoxic activity | Dorta et al. [153] |
| *Stypopodium zonale* | marine  | Stryquinning acid, taondiol, atomeric acid | Ichthyotoxic activity | Gerwick et al. [30] |
| *Stypopodium zonale* | marine  | Strypolidone, stypolotil, stypodil, epistypodil, epitaondiol | Ichthyotoxic activity, cytotoxic activity | Gerwick and Fenical [31] |
| *Taonia atomaria* | marine  | Taondiol | Antimicrobial activity, cytotoxic activity | Othmani et al. [155] |
| *Taonia atomaria* | marine  | Tetraprenyl benzoquinone | Anti-inflammatory activity | Tziveleka et al. [156] |
| *Taonia atomaria* | marine  | Sargachromanols | Cytotoxic activity | Abatis et al. [157] |
| *Turbinaria ornata* | marine  | Turbinaric acid | Cytotoxic activity | Asari et al. [158] |

Allelopathic activity is likely to involve more than one mechanism. Allelochemicals may indirectly influence multiple physiological processes, and phenotypic reactions to a particular compound may result from secondary effects [159]. Different mechanisms function depending on whether allelopathy occurs in open water (pelagic zone) or is associated with substrate (benthic habitats) [12], and many biotic and abiotic factors influence the severity of allelopathic interactions. Macroalgae secrete allelochemicals by direct contact or through masses of water; this is especially facilitated due to the small molecules that make up these compounds. In the case of direct contact, this happens through compounds contained in epidermal glands, secretory trichomes, or in other ways associated with the plant surface [20]. Allelopathic compounds can alter the permeability and fluidity of cell membranes and disturb the activity of membrane proteins and intracellular enzymes, particularly those that build antioxidant systems [160]. Moreover, allelochemicals can also cause oxidative damage and activation of antioxidant mechanisms [161]. In addition, allelopathic compounds have been observed to affect photosynthesis [162] and have been influenced by environmental factors (temperature, light intensity, water availability, CO₂ concentration, and microorganisms) [163]. A potential site of action for allelochemicals is the mitochondria because mitochondrial respiration is essential for the production of ATP, which is used in metabolic processes, for example, macromolecular synthesis [164].

Macroalgae are a rich source of highly bioactive secondary metabolites that may have potential applications. Macroalgae biomass are widely used in the chemical, food, agriculture, cosmetics, pharmacy, and medicine industries. Macroalgae are also rich in various biologically active substances valued for their, among others, antimicrobial,
anti-inflammatory, antioxidant, antifungal, cytotoxic, and insecticidal activity [58,165]. Additionally, allelochemicals from macroalgae on herbivores may have potential in limiting the negative expansion of invasive species worldwide (Table 4). This research highlights the possibility of exploiting the allelopathic potential of macroalgae in commercial aquaculture. The characterization of macroagal allelochemicals as well as their mode of action are still poorly understood. In addition, most studies have focused on the activity of allelopathic compounds derived from marine macroalgae. Therefore, future research should also include the isolation and identification of allelopathic compounds from freshwater and brackish macroalgae.

6. The Limitation of Macroalgae-Herbivores Interactions

Herbivores have a great influence on macroalgae in all water types [166]. A multidisciplinary ecophysiological approach is required to study macroalgae-herbivores interactions in combination with other mechanisms affecting plants. Most macroalgae show some form of anti-herbivore strategy. These relate to physical features that allow escape or chemical features that allow for defense, e.g., by release of secondary metabolites [167]. Thus, research can include both the ecological and molecular levels. The production of allelochemicals has been shown to increase under certain conditions. Del Monaco et al. [25] suggested that increasing ocean acidification can cause advantages to seaweeds over corals and that ocean acidification may enhance the allelopathy of certain macroalgae. Conversely, Ritson-Williams et al. [24] described that increased seawater temperatures made larvae more susceptible to a concurrent local stressor disrupting a key process of coral reef recovery and resilience. The process of synthesizing molecules of allelopathic compounds is controlled by a number of physiological, chemical, and spatial-temporal variables [8]. The toxicity gradient may be related to habitat complexity. More toxic macroalgae extracts are found in reef sites and in rocky intertidal environments. The presence or absence of toxicity was also observed depending on sample collection site and climate [8]. Additionally, allelopathy can only be effective when plants are under stress caused by other mechanisms, such as deprivation of water or intense competition for both nutrients or light. The target plant is also more susceptible to phytotoxins when under stress [168]. Furthermore, bacteria associated with the target or donor organism may metabolize the excreted allelochemicals [12]. It is important to pay attention and avoid misunderstandings, especially in distinguishing allelopathy from any other competitive or noncompetitive relationship [12]. A small number of authors model allelopathic interactions using field or experimental data e.g., [169–174]. Such studies usually must oversimplify processes, which may not always be satisfactory. Thus, the method for testing the effects of allelopathic macroalgae on target organisms should be chosen carefully. Macroalgae extracts and exudates provide an environment that is distant from the environmental conditions of the test organisms while experiments in mesocosms or arranged co-culturing experiments are closer to the conditions of natural occurrence of macroalgae and studied animals and are thus more reflective of naturally occurring processes.

7. Conclusions

Macroalgae are the sources of many harmful allelopathic compounds, which are synthesized as a defense strategy against competitors and predators. Macroalgae can produce inhibitory compounds affecting competitors for the Cnidaria phylum on tropical reefs. The strongest negative effect against Cnidaria occur from macroalgae of the genus Bryopsis, Chlorodesmis, Halimeda, and Rhhiphila (Chlorophyta, green algae); Amansia, Asparagopsis, Callophyccus, Endosiphonia, Galaxaura, Phacelocarpus, and Plocamium (Rhodophyta, red algae); as well as Sphacelaria (Ochrophyta, brown algae). Several studies have also demonstrated the negative effects of macroalgae on predators (Mollusca, Annelida, Echinodermata, Arthropoda, and Chordata species) upon ingestion. Chaetomorpha, Codium, and Ulva (green algae); Grateloupia and Polysiphonia (red algae); and Desmarestia and Laminaria (brown algae) strongly inhibit Annelida development. Furthermore, red (Tichocarpus sp.)
and brown (Dictyota sp. and Stypopodium sp.) algae negatively affect species belonging to Echinodermata. Some studies also examined negative effects of Ulvaria obscura (green algae) on Arthropoda species. The strong negative influence of the red algae Chondriopsis sp. on Chordata, and brown algae Dilophus sp. on Mollusca has been demonstrated. Although the term macroalgal allelopathy refers to the effects of substances produced by macroalgae that can be both harmful and beneficial to target organisms, positive effects of algae on aquatic animals are extremely rare. Only certain species of green (Chlorodesmis sp., Ulva sp., and Ulvaria sp.), red (Delisea sp.), and brown algae (Lobophora sp.) positively affect certain Cnidaria, Mollusca, and Echinodermata species. In addition, the allelopathic activity of macroalgae can change according to the taxonomic position of the donor and target organisms, as well as their habitat. However, most studies have focused on the allelopathic effects of macroalgae in marine environments. Therefore, future studies should consider the nature of released substances and their effect on target organisms of freshwater and brackish macroalgae. Furthermore, the allelopathy phenomenon of macroalgae in aquatic ecosystems should be further studied considering both scientific and commercial aspects.

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