

Review

A Review of Research on the Mustard Hill Coral, *Porites astreoides*

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Abstract: Coral reefs are the most diverse habitat per unit area in the world's oceans, supporting an estimated 1–3 million species in only 0.2% of its area. These ecosystems have suffered severe declines since the 1970s, largely as a result of climate change, ocean acidification, pollution, disease, and overfishing. *Porites astreoides* is a shallow species that is able to thrive in a variety of environmental conditions and has been a clear 'winner' on Atlantic reefs in the last decades. This, coupled with its ease of identification and wide distribution, has caused *P. astreoides* to become a focal species in many scientific studies. Given the current and increasing significance of *P. astreoides*, this review sought to (i) identify the key life history traits that allowed this species to thrive under stressful conditions; (ii) compile aspects of its biology and ecology to understand its future contribution to Atlantic reefs, and (iii) identify knowledge gaps. To date, no comprehensive overview of the literature exists for *P. astreoides*. All articles available on Google Scholar up to the time of submission containing the terms 'Mustard Hill Coral', '*Porites astreoides*', or '*P. astreoides*' were examined for potential inclusion in this review. Papers were assessed based on whether they captured the most influential or widespread theories, represented an important trend in the research, or contained novel findings relevant to the understanding of this species. This review provides a scholarly resource and wide-ranging synthesis of *P. astreoides* on Atlantic reefs of today and the future.



Citation: Eagleson, R.G.; Álvarez-Filip, L.; Lumsden, J.S. A Review of Research on the Mustard Hill Coral, *Porites astreoides*. *Diversity* **2023**, *15*, 462. <https://doi.org/10.3390/d15030462>

Academic Editors: Stuart Kininmonth and Bert W. Hoeksema

Received: 4 January 2023
Revised: 17 March 2023
Accepted: 17 March 2023
Published: 21 March 2023



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Keywords: scleractinian; weedy coral; reef biodiversity; Caribbean; coral diversity

1. Introduction

Coral reefs are an essential part of the global marine ecosystem and provide an array of ecological services as well as support complex and diverse species assemblages [1]. They are nurseries for more than a quarter of the oceans' fish, and nearly one billion people worldwide rely on these fisheries as a food source [1,2]. Healthy reefs also contribute to tourism-based economies in many developing states and are a significant source of pharmaceutical compounds [2].

Scleractinians (stony corals) produce calcareous skeletons from calcium carbonate that form corallites around the coral polyp [3]. This process is largely responsible for the construction of the physical structure of the reef itself [2,4]. Due to differences in life history strategy, habitat preference, symbiont types, competitive interactions, or yet to be determined processes, some species of scleractinian coral are more resilient to local community collapse following physical disturbances and long-term environmental stressors [4,5]. Scleractinian corals have adopted different life history strategies for survival that have had varying degrees of success in our changing oceans. These have been categorized as: weedy, stress tolerant, generalist, and competitive [6]. *Porites astreoides* is a 'weedy' scleractinian coral with a widespread distribution and is easily identifiable in the field, making it an ideal study organism [4] and a focal species in many Caribbean reef studies. As with

other weedy corals, *P. astreoides* is typically defined as a species with a brooding mode of reproduction; it is comparatively small and can rapidly colonize disturbed areas of reef [7,8]. *Porites astreoides* is considered a resilient shallow-water species as it has become one of the most abundant coral species in the Caribbean and is now responsible for a majority of carbonate production on many reefs [4,9,10]. Though widely regarded as a ‘winner’ on Atlantic reefs, some studies report recent declines in the abundance of this species, potentially indicating that *P. astreoides* may not be as resilient as previously assumed in a context of rapidly changing environmental conditions [11–13]. To date, no comprehensive overview of the literature exists for *P. astreoides*, with only a review of its ecophysiology being published [11]. For such a widespread and ecologically important species, we sought to (i) identify the key life history traits that have allowed the *P. astreoides* species to thrive under stressful conditions; (ii) compile aspects of its biology and ecology to understand its future contribution to Atlantic reefs, and (iii) identify knowledge gaps.

2. Taxonomy

Kingdom: Animalia
 Phylum: Cnidaria
 Class: Anthozoa
 Subclass: Hexacorallia
 Order: Scleractinia
 Family: Poritidae
 Genus: *Porites*

Porites astreoides is a scleractinian coral that was first categorized by Jean-Baptiste Lamarck in 1816, along with several other Caribbean coral species [14]. It has been present in the fossil record for approximately 9.9 million years [15]. At present, no subspecies of *P. astreoides* have been identified with bar-coding analysis [16]. Based on the available genetic sequences of 234 species, Figure 1 shows a summary of the cladogenic position of *Porites* within Hexacorallia and the phylogenetic relationships between *P. astreoides* and closely related scleractinians [17]. The genome of *P. astreoides* has been fully sequenced and is publicly available [18].

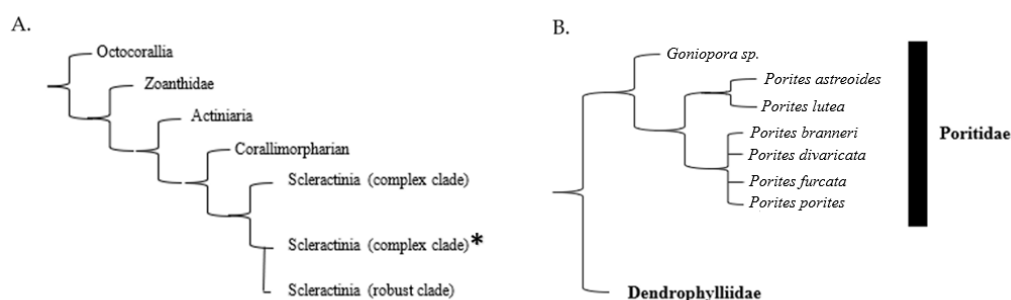


Figure 1. (A) Generalized taxonomic summary of the coral subclass Hexacorallia. Clade location of Poritidae is indicated with asterisks (B) A generalized phylogenetic tree, based on species with available mitochondrial sequence data. *Porites astreoides* is found within Poritidae (indicated with a black bar). Adapted from Kitahara et al., 2010 [17].

3. Distribution

Porites astreoides is found throughout the Caribbean, as well as along the coasts of Florida, Bermuda, Brazil, and West Africa (Figure 2). The geographic range of this species is approximately 6.1 million km², however it is unclear to what extent gene flow takes place between populations separated by great distances [15,19]. This zooxanthellate species can be found in a variety of reef and reef-associated habitats but is most abundant within shallow fore reef environments [20]. *Porites astreoides* commonly inhabits depths of 0.5–15 m but can be found as deep as 70 m [20]. The deepest recorded observation of this species was at a depth of 210 m, and it is unclear what conditions allowed these individuals to live in this low-light environment [15]. Colonies can typically be found on hard rocky substrate or

rubble and are largely absent from sandy bottom areas [8,21]. *Porites astreoides* is common throughout its range and is frequently noted as one of the most abundant species on today's reefs [20]. This species favors clear and calm water but can also tolerate a wide range of thermal and physical stressors [4,22].

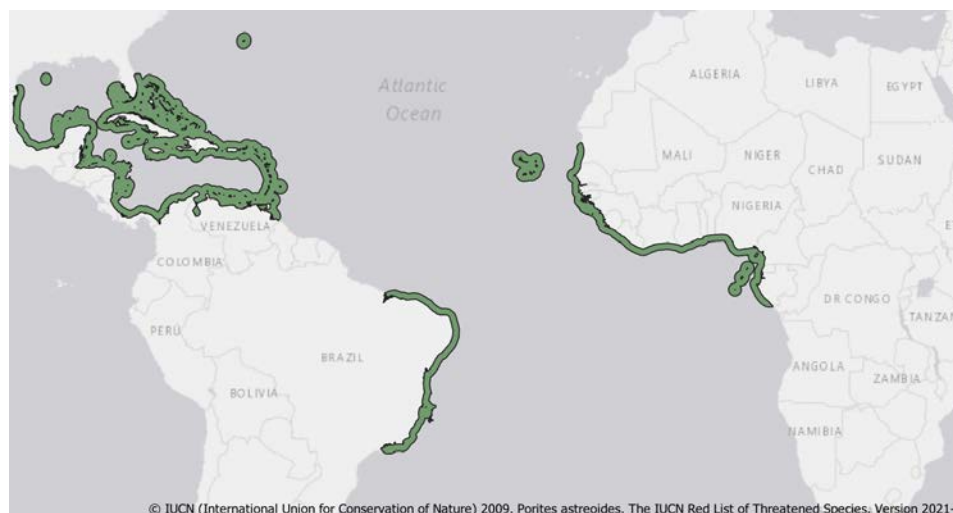


Figure 2. Geographic distribution of the mustard hill coral (*Porites astreoides*) in the Atlantic Ocean, indicated in green [20].

4. Physiology & Life-History

Porites astreoides colonies reach maturity at approximately 8–10 years of age, as reported by the ‘Coral Trait Database’ [15]. Field monitoring of individual colonies of *P. astreoides* has shown that the production of gametes can begin at a colony size of 2–4 cm² [23]. As a member of the family Poritidae, *P. astreoides* contains many small corallites filled with septa [15]. Polyp density is ~18 polyps/cm², with each corallite 1.2–1.6 mm in diameter [15].

Estimates for *P. astreoides* skeleton extension are 4.5 mm/year; increases in skeletal density occur at 1.5 g/cm³/year, and the rate of calcification is 0.55 ± 0.12 g/cm/year [9,24]. Growth is largely focused on the extension of the colony edges and is limited at the apex, similar to what has been observed in *Porites* sp. inhabiting the Pacific Ocean [24]. Colonial growth rates vary based on the environmental conditions that occur across its large range. For instance, colonies in the Gulf of Mexico have reduced growth rates with varied seasonal timing compared to the rest of the Caribbean [24]. Skeletons of *P. astreoides* have been shown to be useful as a paleoclimate archive in the tropical South Atlantic [25].

Porites astreoides colony form is typically either plate or massive [15] and ranges in size from 4 cm² to 400 cm², with the most frequent size of adults being 250 cm² and under (Figure 3) [8,15,26].

Porites astreoides populations are dominated by medium (41–80 cm in diameter) and large-sized colonies (≥80 cm in diameter), and colony success is typically high, making it very unlikely for large colonies to reduce in size once they have reached this growth stage [27]. A recent study that compared the size–frequency distribution of colonies of this species over three years (2014 vs. 2017) revealed substantial increases in colony size of *P. astreoides* with a shift towards fewer, larger colonies [8].

Two distinct color morphs of *P. astreoides* have been identified: green and brown [28]. The green morph is typically found in shallow environments, and the brown morph is found in deeper water [29]. Distinct phenotypical differences between colonies living on mangrove roots and those living on patch reefs have also been observed [30]. Mangrove colonies have lower ecological volume, lower color intensity, and greater corallite density when compared to lagoonal colonies [30].



Figure 3. A colony of *Porites astreoides*, found at a depth of 2 m on the island of Bonaire, Dutch Caribbean.

Corals provide habitat to an array of zooxanthellae and other diverse microbiota communities on their surface, including in mucus [31], and within their intracellular holobiont [32]. The composition and diversity of these microorganisms in the Caribbean is understudied, but initial observations of *P. astreoides* have revealed a diverse microbial surface community with a high proportion of gammaproteobacteria [32]. The bacterial family *Oceanospirillaceae* has been observed in the mucus of all examined *P. astreoides* colonies and may also play some sort of symbiotic role [33]. A number of environmental and ecological factors alter the taxonomic composition and health in the surface microbiota of *P. astreoides*, including bleaching, physical creation of lesions, and macroalgal exposure [34,35]. Macroalgae presence has been shown to cause shifts in the surface holobiont of *P. astreoides*, with varying impacts depending on the algal species [35,36]. Algal-colony interactions have been shown to have a less pronounced impact on the holobiont of *P. astreoides* when compared against *Montastraea faveolata* [36].

Like all shallow-water corals, *P. astreoides* has symbiotic photosynthetic zooxanthellae that provide much of the coral's energy needs [37]. Zooxanthellae clade composition can vary within *P. astreoides* colonies and populations due to seasonal changes in gradients of environmental stress and different habitats (i.e., offshore vs. coastal) [37,38].

Mucus is produced for protection from ultraviolet radiation, physical damage, and to facilitate the capture of prey [33]. The microbial community of older mucus (mucus present at the outer layer) includes more pathogenic microbes [33]. After the sloughing and replacement of older mucus, the microbial community returns to its original state [33]. The communities living within the mucus seem to be essential to the health of the colony; one study found that removal of these microbial communities through the administration of antibiotics resulted in colony bleaching and death [33]. Innate immune-system related gene expression in *P. astreoides* colonies has been observed to increase up to fourfold in response to thermal and bacterial stressors [39]. The mucus of *P. astreoides* has also been found to have toxic and vasoconstricting qualities, particularly against aortic tissue, that may facilitate its capture of prey organisms [40].

Porites astreoides has a brooding reproductive strategy as opposed to broadcast spawning and is capable of sexual or asexual reproduction [41]. Parthenogenesis has also been recently documented in *P. astreoides*, aiding in successful reproduction in a variety of conditions. However, this also acts to limit genetic diversity and can lead to the isolation of

populations [42]. Approximately 47% of scleractinian coral species in the Caribbean share this mode of reproduction, with the remaining 53% being broadcast spawners [43]. Many brooding species populations have increased in the Caribbean while coral communities continue to collapse, perhaps mirroring the coral extinction event of the early Miocene, where brooding coral species experienced far higher survival rates [4,6,44]. Not all areas of the Caribbean have experienced these rapid shifts in community reproductive strategy. Spawning corals were slightly more abundant than brooding corals in the Eastern Caribbean (12% vs. 10%) in 2016 [45]. In one study, half of *P. astreoides* populations were hermaphroditic, the other half were female only, and no exclusively male colonies were found [46]. Inbreeding in *P. astreoides* through self-fertilization can occur in hermaphroditic colonies. Histological studies have shown that the very close proximity of eggs and spermaries in the mesenteries of *P. astreoides* facilitates this mode of reproduction [46]. Reproductive status of colonies in a population can vary with season, lunar day, polyp location/age, and colony size/age [46]. Individual colonies that are hermaphroditic contain a roughly equal mix of male and female polyps and, as mentioned, are capable of self-fertilization [46].

Like many scleractinian species, sexual reproduction of *P. astreoides* is a carefully timed event synchronized with the temperature of the water and the lunar phase. Typically, the closer a population of this species is to the equator, the longer their period of reproduction will last due to the relative stability of water temperatures year-round [47]. For instance, the reproductive period for *P. astreoides* in Bermuda is only 2–3 months, Florida 4–6 months, while in Bonaire or Panama it is continuous year-round [23,41]. Release of larvae still peaks around the new moon across its range and occurs at sea temperatures of 25.6–27.5 °C [48]. The higher the latitude, e.g., Bermuda, the more pronounced climatic seasonality becomes, narrowing the time in which conditions are available for *P. astreoides* to reproduce [47]. As temperature increases, the colony shifts how its energy budget is managed, and reproductive effort and the number of planulae has been found to decrease [47]. *Porites astreoides* colonies are equally successful in the production of larvae at depth compared with shallow waters, with any differences in the total being a result of abundance of reproductive colonies [49]. Long distance dispersal of larvae is typical of similar Caribbean species and is largely dependent on prevailing ocean currents. For instance, gene flow is strong between *P. astreoides* colonies in Florida and USVI but more limited between Florida and Bermuda [19]. Within-site genetic diversity of populations has been found to be high and dependent on factors such as local environmental conditions and depth [50]. Upon release to the environment, larvae from *P. astreoides* can metamorphose into polyps within 10 h [41]. Although brooding corals such as *P. astreoides* have larger larvae than broadcast spawning species, size can vary across different habitats in their range [51]. A positive correlation exists between the size of *P. astreoides* colony and the number of planulae larvae that are released [48].

The proper settlement of coral colonies is essential for the continuation of viable populations. Without sufficient larval settling, coral recruits will not reach adulthood to replace adult colony mortality [52]. Like most coral species, *P. astreoides* larvae settle on coral rubble or hard rocky substrate in the shallow reef environment, and are impacted by algal coverage, competition, and sedimentation [8,52,53]. *Porites astreoides* larvae are also able to detect the intensity of ultraviolet radiation (UVR) and have settlement preferences for areas of reef with a lower level of UVR, such as partially sheltered overhangs [54]. Larvae of *P. astreoides* are also drawn to settle in areas with higher reef noise, which is the cumulative sound of the reef ecosystem and includes herbivore foraging and scavenger actions. Higher reef noise is often indicative of a healthy reef environment [55]. This larval preference for ‘louder’ reef areas takes place regardless of light conditions [55]. It has been found that, while branching species such as *Acropora palmata* do not settle on macroalgae, *P. astreoides* larvae can; however, the chances of those larvae surviving to adulthood are very limited [52,53]. Larval survival and settlement success in *P. astreoides* is dependent on site-specific conditions [56], with the larvae of colonies in upper mesophotic habitats having increased survival and settlement success [56]. *Porites astreoides* frequently

settles on biofilms as well as coralline algae, particularly on species such as *Titanoderma prototypum* and *Hydrolithon boergesenii*, and has a higher rate of post-settlement survival when compared to broadcast spawning corals (i.e., *A. cervicornis*) [57]. *Porites astreoides* colony numbers have been found to be negatively associated with fleshy macroalgae and positively associated with coralline algae [8]. This is particularly important as many coral communities in the Caribbean have been shifting from coral- or coralline-dominated states to a state dominated by macroalgae and biofilms. In the water column itself, increased water temperatures (31 °C) have been found to have no effect on the survival of released *P. astreoides* larvae, their ability to properly settle on the substrate, or the process of metamorphosis that leads to the adult stage [58]. However, long-term stress events, such as incidences of extreme rainfall and storm events, can impact the ability of larvae in the water column to settle on the substrate [26].

5. Resilience

Colony morphology of *P. astreoides* provides the ability to resist damage from physical storm and wave conditions [59]. In weedy scleractinian species, size and circularity (non-branching physiology) reduces the susceptibility of the colony to breakage from physical disturbance compared to large species with a complex physiology, such as *Acropora palmata* [59]. *Porites astreoides* has a 'massive' growth form, and its low-lying colonies can be found in a wide range of current and storm impacted environments (Figure 3) [6,15].

Energy budgets within individual coral colonies are believed to play a major role in tolerance to chronic environmental stressors and determining the rates of growth and recovery in colonies [60]. This has been shown to be hereditary among certain populations of *P. astreoides* distributed across habitats [61]. Shallow-water forms have been observed to be more tolerant to thermal stress compared to those found in deeper water on the reef face [62]. Smaller colonies are hardier and more resilient to bleaching stresses under laboratory conditions, and these colonies have been found to have more protein and a higher zooxanthellae density after bleaching [63]. *Porites astreoides* adapt to their respective local environments, with shallower brown corals faring better following transplantation to novel environmental conditions than offshore reef colonies or shallow-dwelling green color morphs [29,37,64]. Even within these habitats, the differences between individual colonies plays a role in thermal tolerance, with corals less than 10 km apart exhibiting significant differences in response to bleaching events.

Porites astreoides recruitment and reproductive success may reduce the impact of any thermal sensitivity on a population level [65]. *Porites astreoides* has high antioxidant capability during dark phases, which could aid in its survival when facing stressors such as bleaching events [66]. Following single bleaching events, *P. astreoides* is able to make up for the resultant reduced carbon budget (due to zooxanthellae loss) with polyp uptake of dissolved organic carbon (DOC) and zooplankton [67]. Uptake of DOC following a single bleaching event accounted for 11–36% of the carbon budget for sampled colonies [67]. However, following repeat bleaching events, this was insufficient to prevent carbon budget reductions in *P. astreoides*, showing that there are limits in the resilience of colonies to repeated stressors [12,67]. Populations of *P. astreoides* in Florida have been shown to experience 3.8% partial mortality, and 1.6% full mortality of colonies following a repeat bleaching event [68]. Reduced colony recruitment has also been observed in post-bleaching populations of *P. astreoides* [69].

Porites astreoides' ability to rapidly colonize habitats made available by disturbance events is a major factor in its success. As a brooding coral, successful fertilization occurs at much higher rates for *P. astreoides* colonies compared to broadcasting species that release their gametes into the water column [41]. In more southern areas of its range, reproduction of *P. astreoides* takes place year-round, allowing the population of colonies to expand continually in damaged areas [46]. Brooding corals also typically produce fewer, and much larger, larvae than broadcasting species, and these have been found to have increased resistance to rising CO₂ conditions [55]. *Porites astreoides* is also able to successfully reproduce in

a wide range of abiotic and biotic conditions [46]. Increasing depth does not appear to impact the successful production of planula larvae by *P. astreoides*, and this occurs well into the mesophotic zone [49]. Planulae larvae of *P. astreoides* are also resistant to temperature stresses (such as those during bleaching events), but not when cyanobacteria levels are elevated [70]. *Porites astreoides* has been shown to be particularly effective at both vertical, and horizontal gene flow in reef environments despite its brooding form of reproduction [19,71]. This is significant as populations in the deeper, cooler mesophotic zone can act as a source of population rescue for shallower populations and are able to use this environment as a refugia [19]. *Porites astreoides* colonies in Florida have also been found to have higher calcification rates, reproductive potential, and zooxanthellae densities in cooler waters [72].

6. Ecology

The ecology of *P. astreoides* is strongly linked to its weedy life-history strategy [43]. Weedy corals are typically defined as species with a brooding mode of reproduction, a prolonged planulation period, high larval success, are small and short-lived, that rapidly colonize disturbed areas of reef, are resistant to wave action, and that recover rapidly from stressors [6,7,43]. Weedy corals also have limited long-distance dispersal ability at the larval stage and are vulnerable to shading by faster growing branching corals [6,7,43].

Perhaps the best example of the success of the life-history strategy of *P. astreoides* has been made evident over the last decades, during which several species of reef-building corals have drastically declined, with *P. astreoides* alone now responsible for 16–72% of live coral cover in the Caribbean [27]. Furthermore, even in sites that have experienced increases in coral cover, this has been driven mainly by the increase in cover or abundance of *P. astreoides* and other weedy coral species, not by key reef-framework builders [73].

Brooding corals such as *P. astreoides* and *Agaricia* sp. are often the most abundant following disturbance; they were found to compose 30–80% of juveniles in Tobago after a large-scale bleaching event in 2010 [74]. *Porites astreoides* is often able to persist in these environments, and therefore, its abundance is frequently used to differentiate high stress sites with those that have more optimal conditions [75]. Colonies already thriving in high stress environments may prove to be more resilient to the forecasted impacts of climate change [76]. The establishment of marine protected areas has been shown to increase the success and abundance of *P. astreoides* recruits, with this species (along with *Agaricia* sp., and *Montastrea* sp.) comprising much of the reef recovery observed following the implementation of protection [77]. Due to high levels of recruitment of *P. astreoides* following disturbances, a majority of colonies following protection were typically found to be small [77]. In addition, although the populations of *P. astreoides* regionally in the Caribbean can be fragmented, with the loss of adult colonies impacting regional success of the species and population connectivity [78], self-recruitment rather than larvae flow from other regions is the predominant method of growth for *P. astreoides* populations [78].

Despite the individual success of *P. astreoides* (and other non-framework building coral species such as *Agaricia* sp.), they will be unable to ensure continued ecosystem functionality without the preservation of key framework species such as *A. palmata* or *Orbicella* sp. [79]. *Porites astreoides* colonies can, however, play an important host role, providing habitat to accessory species such as Christmas tree worms, feather duster worms, barnacles, sponges, bivalves, and snails [80–84]. Some coral-associated species, such as barnacles, Christmas tree worms, and feather duster worms, can cause damage to colonies, particularly in higher numbers and/or in poor water quality conditions [82,84,85]. Parrotfish frequently predate on *P. astreoides* and have been found to prefer colonies inhabited by many of these associated species [80]. The relative or absolute increases in the abundance or cover of *P. astreoides* is unlikely to result in increases in habitat complexity, refuge availability, net community calcification, reef growth, or available habitat for fishes [79,86]. On the contrary, as the proportion of non-framework-building coral species increases in the Caribbean, total net carbon production and reef rugosity will continue to decline [4,79], locking the ecology of coral assemblages into diminished states of physical functionality [87]. *Porites astreoides* has

low reef building potential, but currently accounts for 68% of total carbonate production in the Caribbean [4], which explains the low or even net-negative rates of reef-growth estimated for most contemporary Caribbean reefs [79,88]. Although *P. astreoides* does not contribute to reef-physical functionality, the presence of this species is still beneficial, as it could still protect the reef from erosive processes, such as scraping herbivores or other physical disturbances, and thus maintain a balance at the tipping point between reef growth and erosion [71,73].

Pressures to Caribbean coral reefs are not static; on the contrary, it is estimated that pressures originating from rapidly changing environmental conditions will further affect reef-building corals. Calcification rates in *P. astreoides* and other common species, such as *Orbicella annularis* and *Montastrea* sp., are expected to decline in response to increasing ocean temperatures and ocean acidification [3]. *P. astreoides* has been shown to respond to warming conditions more effectively than other scleractinian species, though it does demonstrate negative responses to rising acidification [89]. Negative responses to multiple life-history factors for *P. astreoides* have been demonstrated under laboratory conditions for forecasted ocean conditions in 2050 and 2100 (Table 1) [90].

Table 1. Impacts of ocean acidification on *P. astreoides* under laboratory conditions based on forecasted levels for mid- and late century [90].

<i>Porites astreoides</i>	2050	2100
Larval metabolism	−27%	−63%
Settlement success	−43.50%	−57.50%
Post-settlement growth	−16%	−35%

P. astreoides is commonly found alongside other currently abundant species in the Caribbean such as: *Sidastrea radians*, *Orbicella annularis*, *Madracis* sp., and *Agaricia agaricites* [45,91]. *Porites astreoides* has been shown to be positively associated with massive corals and negatively associated with branching coral species [8]. *Porites astreoides* colonies compete with other coral species found in the same habitats, but the current competitive dynamics between *P. astreoides* and other scleractinian species are not likely to continue in warmer, more acidic seas [92–94].

7. Conclusions

This study has presented a review and synthesis of the key literature for *P. astreoides*. Though not a formal systematic review, our research team is confident we have reviewed and presented the key research relevant to understanding *P. astreoides* on both current and future reefs; we have also identified some research gaps and areas for future work.

Though *P. astreoides* has become a ubiquitous species, one of the most prolific in the Atlantic, it is certainly not immune to the anthropogenic changes occurring in the world's oceans. *Porites astreoides* faces similar settlement, competitive, physiological, and environmental challenges as other tropical scleractinian coral species in the Atlantic. Indeed, some demographic declines have been observed in populations that have long experienced success, raising concerns about their long-term viability [13]. Further studies on the resiliency of this species will be essential. Continued research on the physiology, ecology, and life-history of *P. astreoides* coupled with routine monitoring will be critical to understanding the potential role of this species on future reefs and to fill in any knowledge gaps identified throughout this review.

Author Contributions: Conceptualization, R.G.E. and J.S.L.; methodology, R.G.E. and J.S.L.; validation, R.G.E. and L.Á.-F.; resources, J.S.L.; writing—original draft preparation, R.G.E.; writing—review and editing, R.G.E., L.Á.-F. and J.S.L.; supervision, L.Á.-F. and J.S.L.; project administration, J.S.L.; funding acquisition, J.S.L. All authors have read and agreed to the published version of the manuscript.

Funding: Funding for this research was provided by a NSERC Discovery Grant (Lumsden), the Ontario Veterinary College, and the University of Guelph. Eagleson was the recipient of an Ontario Veterinary College Scholarship.

Institutional Review Board Statement: Not applicable.

Data Availability Statement: Data is available from the corresponding author upon request.

Acknowledgments: The efforts of peer reviewers and fellow authors are gratefully acknowledged for their useful comments which helped to improve the final version of the manuscript.

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

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