Reef-Building Corals Do Not Develop Adaptive Mechanisms to Better Cope With Microplastics

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Microplastics are omnipresent in the oceans and threaten marine animals through physical contact or ingestion. Short-term studies have already shown that reef-building stony corals respond differently to microplastics than natural food. However, it remains unknown whether corals exhibit acclimation mechanisms to combat the effects of microplastic exposure. Specifically, the long-term effects of microplastics on the feeding and defense behavior of reef-building corals remain unexplored. Therefore, the goal of this study was to infer potential acclimation mechanisms in the behavior of the corals. For this, four reef-building species (*Acropora muricata*, *Porites lutea*, *Pocillopora verrucosa*, and *Heliopora coerulea*) were exposed in a long-term experiment to microplastics for 15 months. Subsequently, coral feeding rates on microplastics and natural food (*Artemia* sp. cysts), feeding discrimination, and reactions to both were assessed in a 24 h pulse exposure experiment. The results showed that corals' feeding rates did not decrease after long-term exposure to microplastics. Similarly, the feeding discrimination (i.e., ratio of feeding on microplastics and natural food) did not differ after long-term exposure to microplastics. Moreover, corals showed no changes in defense behavior (i.e., mucus production or extrusion of mesenterial filaments) against microplastics. These findings suggest that symbiotic, reef-building corals do not develop mechanisms to adapt to long-term microplastic exposure. Thus, microplastic pollution might constitute a constant stressor for coral organisms, likely leading to sustained energy expenditures and impaired health.

Keywords: coral reefs, feeding rate, ingestion, long-term exposure, acclimation

INTRODUCTION

Microplastic pollution poses an increasing threat to marine ecosystems (Law and Thompson, 2014; Auta et al., 2017; Galloway et al., 2017), including coral reefs (Lamb et al., 2018; de Oliveira Soares et al., 2020; Huang et al., 2021). Microplastics are defined as polymer particles between 1 μm and 1 mm in size and can occur in different shapes, structures, and densities (Hartmann et al., 2019). They may cause harm to marine organisms as they often harbor toxins that can be transferred to the organisms (Saliu et al., 2019; Patterson et al., 2020). In addition, microplastics also develop a distinct biofilm on the surface, called the "plastisphere" (Zettler et al., 2013; Amaral-Zettler et al., 2020), which may contain potential coral pathogens (e.g., *Vibrio* spp. strains; Franco et al., 2020; Kesy et al.,

2020) or foster confusion with prey (Hall et al., 2015). Ultimately, microplastics may also lead to compromised health through increased feeding efforts, reduced food uptake, and subsequent energy losses (Wright et al., 2013; Yin et al., 2018). In reef-building corals, exposure to microplastics is associated with reduced growth (Chapron et al., 2018; Hankins et al., 2021), lower feeding rates (Savinelli et al., 2020; Corinaldesi et al., 2021), changes in photosynthetic efficiency (Lanctôt et al., 2020), a compromised immune system (Tang et al., 2018), and an overall deterioration in health (Reichert et al., 2019). These adverse effects are often attributed to direct contact with microplastic particles, regularly followed by ingestions. Feeding on microplastics is suspected of causing increased energy demand through energetically costly microplastic handling (i.e., repeated particle captures, ingestion, and egestion) (Chapron et al., 2018; Mouchi et al., 2019; Reichert et al., 2019). Although microplastic particles are typically covered with a biofilm, ingestion does not likely result in a considerable nutritional return (Murphy and Quinn, 2018; Reichert et al., 2018; Reichert et al., 2019). Even though previous studies showed that corals typically egest indigestible material within 24 h (Mills and Sebens, 2004; Allen et al., 2017; Reichert et al., 2018), the gastric space is occupied by the indigestible and nutrient-deficient material, which prevents the digestion of food (Murphy and Quinn, 2018; Rotjan et al., 2019). Furthermore, recurrent ingestions and blockages of the digestive tract (Hankins et al., 2018) might cause incorporation into the coral skeleton (Hierl et al., 2021; Krishnakumar et al., 2021; Reichert et al., 2021a). Yet not all coral species ingest microplastics in the same amounts and might thus be unequally threatened. Some coral species, such as *Dipsastraea pallida*, ingest as much microplastics as natural food (Hall et al., 2015). Other species even appear to prefer plastic particles over their natural food, such as *Astrangia poculata* (Rotjan et al., 2019). Still other coral species appear to recognize plastic particles as indigestible or ingest them to a lesser extent compared to natural food, e.g., *Danafungia scruposa* (Corona et al., 2020), *Goniastrea retiformis* (Martin et al., 2019), and *Astroides calycularis* (Savinelli et al., 2020). However, methods vary between studies, limiting comparisons.

Corals can also actively repel unwanted, indigestible particles. General defense mechanisms include active cleaning, i.e., polyp and ciliary movements, mucus production, mesenterial filaments extrusion, and tissue contraction and expansion to remove sediments from their surface (Stafford-Smith and Ormond, 1992; Stafford-Smith, 1993; Erftemeijer et al., 2012). Several coral species showed similar defensive reactions (i.e., mucus production in *Porites* spp. or extrusion of mesenterial filaments in *Pocillopora* spp.) when they encounter microplastics (Reichert et al., 2018; Martin et al., 2019; Mouchi et al., 2019; Lanctôt et al., 2020).

The numerous adverse effects following contact with microplastics suggest that microplastics are a stressor for reef-building corals (Reichert et al., 2019; Hankins et al., 2021). Corals possess various mechanisms to cope with environmental stressors (Dallmeyer et al., 1982; Brown, 1997; Gates and Edmunds, 1999). For example, corals respond with altered feeding behavior to better cope with elevated temperatures, sedimentation, and ocean acidification (Anthony and Fabricius, 2000; Grottoli et al., 2006; Towle et al., 2015). This phenomenon, known as heterotrophic plasticity, helps corals improve their energy budget and maintain their physiological status under extended periods of stress (Fox et al., 2018; Sturaro et al., 2021). However, it is still unclear whether reef-building corals can also adapt their behavior to microplastics and thus avoid microplastic ingestion in the future.

Therefore, the general goal of our study was to assess changes in coral behavior after long-term exposure to microplastic particles. Specifically, we determined whether corals adapt to long-term microplastic exposure through (I) heterotrophic plasticity (i.e., no. of ingested microplastic particles), (II) improved discrimination (i.e., no. of ingested microplastics per natural food particle), or (III) increased defense mechanisms (i.e., the occurrence of mucus production or extrusion of mesenterial filaments). To this end, we conducted a controlled long-term microcosm experiment in which the feeding and defense behavior of four common reef-building coral species exposed to polyethylene (PE) microplastics over 15 months was compared to a microplastic-free control group. The findings may help to better understand the adaptive response of vital reef-building organisms to microplastic pollution.

MATERIALS AND METHODS

Studied Coral Species

Four common Indo-Pacific coral species, *Acropora muricata* (Linnaeus, 1758), *Pocillopora verrucosa* (Ellis & Solander, 1786), *Porites lutea* Milne-Edwards & Haime, 1851, and *Heliopora coerulea* (Pallas, 1766), were used for the controlled microcosm experiment, representing similar polyp sizes (1–2 mm diameter) but different morphologies (i.e., branching, massive, and columnar). For *A. muricata*, *P. verrucosa*, and *P. lutea*, 18 fragments per species were included, derived from three origin colonies. For *H. coerulea*, six fragments were included, derived from one origin colony. Corals were sampled in the Red Sea and off Bali between 2013 and 2015 or derived from a zoological garden (for details on colony origin and CITES numbers see **Supplementary Table S1**), and kept under laboratory conditions in the Ocean2100 facility for at least six months before the start of the long-term experiment (temperature: 26 ± 0.5°C; light intensity: 200 μmol photons m^{-2} s^{-1} at a photoperiod of 10:14 dark:light).

Experimental Design

Coral fragments were exposed to polyethylene (PE) microplastics (~200 particles L^{-1}) or microplastic-free control conditions for 15 months, and feeding and defense behavior was studied (**Figure 1**). Feeding rates and defensive reactions were quantified in individual incubations *via* the number of particles left after 24 h of pulse exposure. Coral feeding rates were assessed by exposure to control and microplastic particles: First, a control quantification of feeding activity was conducted with *Artemia* sp.
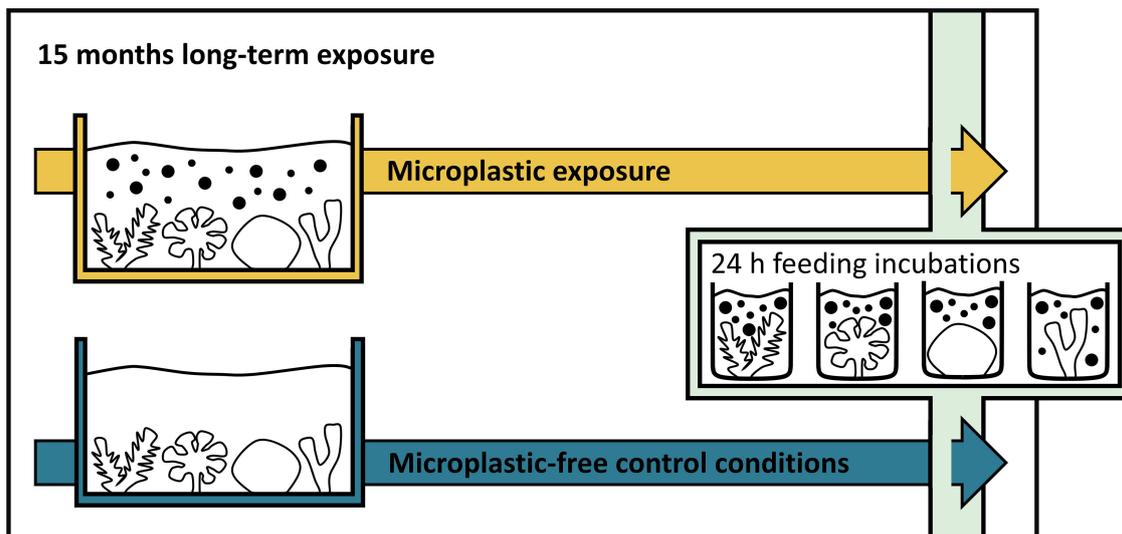
FIGURE 1 | The timeline of the experiment displays coral fragments from 15-month long-term microplastic exposure (in yellow; top) and from long-term control conditions (in blue; bottom). Corals' feeding and defense behavior on *Artemia* sp. cysts and microplastics were assessed in separate, consecutive 24 h pulse exposures at the end of the experiment.

cysts (Kellogg, 1906) to avoid potential effects of microplastic feeding on the control feed. Then the coral feeding rates on microplastics were assessed. Defense behavior was observed at the end of the 24 h exposure.

Long-Term Microplastic Exposure

The long-term exposure was conducted in six 80 L tanks ($n = 3$ per treatment). The tanks were connected to a reef mesocosm system (~4,000 L artificial seawater) to create near-natural conditions with an exchange rate of 120 L per day (≙ 150% of the tank volume). Three weeks prior to the start, coral fragments were distributed to the tanks (one fragment per colony per species per tank) and randomly allocated within the tanks with a min. distance of 5 cm to avoid interferences. Tank outflows were equipped with filters (65 μm mesh size) to retain particles inside the experimental tanks allowing a biofilm to form on the submerged particles. Water parameters were maintained under controlled conditions during the long-term experiment (temperature: 26 ± 0.2°C; light intensity: 135 μmol photons m^{-2} s^{-1} at a photoperiod of 10:14 dark:light), and corals were fed indirectly through the connected mesocosm system, which was supplied with frozen food (i.e., copepods and *Mysis* spp.) daily. For additional information on the technical setup see **Supplementary Methods S1.1**.

Microplastic Characteristics and Treatment

Irregular black PE microplastic particles (density: 0.95 g cm^{-3}; for FTIR chart see **Figure S1**; Novoplastik, Germany) were used, as it is one of the most common polymer types in reef waters (Saliu et al., 2018; Patterson et al., 2020). The size of the PE particles (diameter:

184 ± 95 μm (mean ± *SD*), for details, see **Figure S2** and **Supplementary Methods S1.2**) corresponds to the size of the plankton diet of corals (Houlbrèque and Ferrier-Pagès, 2009). Pristine particles were sterilized in ethanol (70% abv; 24 h) and then rinsed with deionized (DI) water. 2.5 mg L^{-1} sterilized microplastics were added to the tanks resulting in a concentration of ~ 200 particles L^{-1} or 0.25 mg L^{-1} after 48 h in the long-term experimental tank setup. The biofilm growth on the microplastics reduced the buoyancy to about the same density as seawater, making them available to the corals. Microplastic concentration in the water surrounding the corals was monitored every two months, with higher number of measurements at the beginning of the experiment until concentrations stabilized. For this, 50 mL tank water was filtered onto a 65 μm gauze filter (3–5 replicate measurements per tank) and the number of particles were counted under a stereo microscope to extrapolate the concentration per L. Concentrations were maintained at ~200 particles L^{-1} (201 ± 67 particles L^{-1}, $n = 518$ measurements at 125 timepoints) over the course of the experiment by the addition of fresh particles when necessary.

Pulse Exposure to Natural Feed and Microplastic

Artemia sp. Cysts Fed as Natural Feed Control

Decapsulated brine shrimp eggs (*Artemia* cf. *franciscana* (Kellogg, 1906); INVE Technologies, Belgium) were used as control feed in the 24 h pulse exposure because they are a standard feed for corals in aquaculture (Helmuth and Sebens, 1993; Sebens et al., 1998). The size of the *Artemia* sp. cysts (diameter: 175 ± 16 (mean ± *SD*) was comparable to the size of the microplastic particles used (**Figure S2**).

Biofouled Microplastics

The same PE particles were used in the long-term and the 24 h pulse exposure. To mimic near-natural conditions in the pulse exposure, biofouled particles were generated. For this, pristine microplastics were sterilized as described above. Then microplastics were incubated for 16 days in 50 L of 35 μm filtrated artificial seawater from the reef mesocosm system to allow for a biofilm to form [26°C, salinity: 34 ± 2 ‰, two 80 W fluorescent lamps (Aquablue Special and Blue Plus, ATI, Germany), two pumps (SW-4, Jebao, China)].

Incubations

Feeding and defense behavior were assessed in incubations where corals were provided with *Artemia* sp. cysts (control feed) or microplastics for 24 h of pulse exposure. The number of particles added to the incubation was chosen to match the number of polyps per coral fragment to ensure the availability of particles. For the *Artemia* sp. cyst feeding, 5 ± 0.008 mg cysts, equivalent to ~1,760 ± 66 particles L^{-1} (weighed with analytical balance (accuracy: 0.001 mg, CPA2P, Sartorius, Germany)) were suspended in 0.8 L of 0.22 μm filtrated seawater (Express Plus Membrane, Millipore, USA). For the microplastic feeding, 270 ml of a microplastic-seawater suspension (see section biofouled microplastics) was added to 530 ml of 0.22 μm filtrated seawater, equivalent to 1,850 ± 230 particles L^{-1}. The coral fragments were hung upside down in the beakers and secured with fishing line ($d = 0.12$ mm, Spiderwire stealth code red braid, Pure Fishing, USA). This positioning was chosen to avoid particle accumulation at the base of the concrete socket. Particles were uniformly distributed within the water column by air supply (two 228 mm glass pipettes) and a stir bar (20 mm × 8 mm ($l \times d$) rotating at ~500 rpm). Ten pulse exposure incubations were performed simultaneously in one run on a multipoint stirring incubator (Rades et al. 2022). For each run, coral fragments were randomly chosen from the microcosm setup ($n = 7$), and their feeding behavior was assessed simultaneously with coral-free control incubations ($n = 3$, equipped with pipettes, stir bars, and bare fishing lines only). A total of eight runs per treatment (each lasting for 24 h, for both microplastics and natural food) were conducted, with a mean time interval of 2–3 days between each run. Temperatures were kept at 26 ± 0.3°C through a water bath.

Assessment of Feeding Rates
Particle Recovery, Documentation, and Quantification

After the 24 h pulse exposure, particles were retrieved from each incubation and quantified. For this purpose, all equipment was removed from the incubation chambers. Fragments were gently shaken in the water to free adhering particles and placed back in the microcosm setup. All equipment and fragments were carefully rinsed with 0.22 μm filtered seawater between all steps to retain all adherent particles and avoid contamination. The seawater particle suspension was vacuum filtrated onto a cellulose nitrate filter (8 μm pore size, Sartorius, Germany). The filter was documented under a digital microscope (VHX-2000, Keyence, Japan) using the automatic 2D image stitching mode

with the VH-Z20W lens at 50x magnification and a mounted polarizing filter. Pictures were saved as TIFF. Microplastic particle numbers were automatically determined using ImageJ (v1.51s; Rueden et al., 2017). For a detailed description of image processing and counting, see **Table S2**.

Determination of Coral Surface Area

Coral tissue surface area was used to standardize feeding rates per cm². The surface area was quantified *via* 3D scanning, following established procedures (Reichert et al., 2016; Reichert et al., 2018; Reichert et al., 2019). Briefly, 3D models of coral fragments were created after the pulse exposure using a hand-held 3D scanner (Artec Spider with Artec Studio 10, Artec 3D, Luxembourg) and coral tissue surface area derived (for details, see **Table S3** and **Supplementary Methods S1.3**).

Calculation of Feeding Rates

Feeding rates (in number of particles per cm² per 24 h) were assessed as the difference between the residual particles of the incubations with corals and the control incubations, based on established procedures (Hii et al., 2009). For this, the count of remaining particles in the coral feeding chamber (number of particles$_{coral}$) was subtracted from the mean number of particles found in the control chambers (mean number of particles$_{control}$) of the respective run (Equation 1).

$$Feeding\ rate\ (number\ of\ particles\ cm^{-2}\ 24\ h^{-1})$$
$$= \frac{mean\ number\ of\ particles_{control} - number\ of\ particles_{coral}}{surface\ area}$$

$$\tag{1}$$

Calculated feeding rates were standardized to the surface area of the coral and expressed as the number of particles ingested per cm² coral surface area per 24 h.

Quantifying the Ability of Corals to Discriminate Between Microplastics and Natural Food

The number of fed microplastic particles per fed *Artemia* sp. cyst was determined to assess the ability of corals to discriminate microplastics from natural food. This discrimination ability value was calculated per coral fragment. These values were then compared between long-term exposure conditions (microplastic vs. microplastic-free).

Reactions of Corals to Microplastic Pulse Exposure

Visible physiological reactions of corals to the microplastic pulse exposure (i.e., mucus production, extruded mesenterial filaments) were documented at the end of the 24 h incubation for each fragment. Because of a possible simultaneous occurrence of both reactions, observations were broadly classified as (1) reaction or (2) no reaction. Reactions during the control feeding with *Artemia* sp. cysts were assessed similarly to distinguish between reactions to the feeding procedure itself and the microplastic exposure.

Statistics

Statistical analyzes were conducted with "R" (v4.1.2, R Core Team, 2021) using the "RStudio" interface (v2021.9.0.351, RStudio Team, 2021). Unless otherwise stated, tests from the "rstatix" package (v0.7.0, Kassambara, 2021) were used. Data were tested for normality using the histogram, Shapiro-Wilk test, and Q-Q and P-P plots (Almeida et al., 2019) and found to be non-normally distributed. Therefore, non-parametric tests were used further on. Kruskal-Wallis with Dunn's *post hoc* tests examined interspecific differences in microplastic and *Artemia* sp. cyst feeding rates. Wilcoxon tests were used to evaluate intraspecific differences in feeding rates between particle types (microplastics vs. *Artemia* sp. cysts). Wilcoxon tests were also used to compare the impacts of the two long-term exposure treatments on feeding rates. The effect of long-term exposure on the ability of corals to discriminate between microplastics and natural food (*Artemia* sp. cysts) was evaluated using Wilcoxon tests, with one extreme value ($> Q_3 + 3 \times IQR$) removed beforehand. Kruskal-Wallis with Dunn's *post hoc* tests examined interspecific differences in the ability of discrimination. The impact of long-term exposure to microplastics on coral reactions was assessed using Fisher's exact tests. Pearson's χ^2 tests were used to compare coral reactions between microplastics and *Artemia* sp. cysts. Effect sizes for Fisher's exact test and the χ^2 test were obtained using the "effectsize" package (v0.5, Ben-Shachar et al., 2020).

RESULTS

Coral Feeding Rates on Microplastics After Long-Term Exposure

Long-term microplastic exposure did not affect coral feeding rates on microplastic particles in any species (Wilcoxon tests, $p > 0.05$; **Figure 2A** and **Table S4**). Similarly, the exposure did not affect feeding rates on the control feed (*Artemia* sp. cysts), (Wilcoxon tests, $p > 0.05$; **Figure S4A** and **Table S5**). In general, corals showed lower feeding rates on microplastics (1.06 ± 2.08; mean $\pm$ *SD*) than on *Artemia* sp. cysts (7.02 ± 8.18; mean $\pm$ *SD*). Specifically, *A. muricata* (Wilcoxon test, $p < 0.001$) and *P. verrucosa* (Wilcoxon test, $p < 0.001$) fed significantly fewer microplastics (**Figure S5** and **Table S6**). However, there were no interspecific differences in feeding rates for either microplastics or *Artemia* sp. cysts (Kruskal-Wallis and Dunn's tests, $p > 0.05$; **Figure S6** and **Table S7 and S8**).

Coral Ability to Discriminate Between Microplastics and Natural Food After Long-Term Exposure

Discrimination ability (no. of microplastic particles ingested per *Artemia* sp. cyst ingested) did not differ between the two long-term conditions (microplastic exposure: 0.34 ± 0.76 microplastic particles per *Artemia* cyst; mean $\pm$ *SD* vs. microplastic free: -0.06 ± 1.24 microplastic particles per *Artemia* cyst; mean $\pm$ *SD*) in any species (Wilcoxon tests, $p > 0.05$, **Figure 2B** and **Table S8**). In addition, no interspecific differences were found (Kruskal-Wallis and Dunn's tests, $p > 0.05$, **Figure S7** and **Table S10 and S11**).

Coral Defense Reactions After Long-Term Exposure

A. muricata and *P. lutea* reacted with mucus release and extrusion of mesenterial filaments to the 24 h pulse exposures. *P. verrucosa* and *H. coerulea* did not show physiological reactions. Although the reactions occurred more frequently after long-term microplastic exposure, the effect was not statistically significant (Fisher's exact tests, $p > 0.05$; **Figure 2C** and **Table S12**). Similarly, the long-term microplastic exposure did not affect the frequency of reactions when corals were fed *Artemia* sp. cysts (Fisher's exact tests, $p > 0.05$; **Figure S4B** and **Table S12**). In general, reactions occurred more often when corals were fed with microplastics than with *Artemia* sp. cysts (significant for *A. muricata*; Chi-squared test, $p = 0.013$; **Figure S8** and **Table S13**). Specifically, corals fed less when they showed defense reactions (significant for *A. muricata*; Wilcoxon test, $p = 0.048$; **Figure S9** and **Table S14**).

DISCUSSION

Corals Do Not Adapt Feeding Mechanisms to Decrease Microplastic Uptake

Our results indicate that corals do not exhibit heterotrophic plasticity in response to long-term microplastic exposure as feeding rates remained unaltered after long-term microplastic exposure (research question I). To avoid stress potentially caused by long-term microplastic exposure, corals would need to either reduce their feeding rates in general or increase their feeding selectivity. However, unchanged feeding rates suggest that the corals studied do not possess or do not activate mechanisms of heterotrophic plasticity to reduce microplastic uptake in response to long-term exposure to microplastics.

Heterotrophic feeding activity has been found to shift (Hughes and Grottoli, 2013; Fox et al., 2019) under certain environmental stresses (e.g., heat stress, turbidity, or ocean acidification; Anthony and Fabricius, 2000; Bessell-Browne et al., 2014; Towle et al., 2015; Pupier et al., 2021). However, microplastics apparently do not trigger mechanisms of heterotrophic plasticity to reduce microplastic uptake. This suggestion is in line with Axworthy and Padilla-Gamiño (2019), who showed that microplastic feeding rates did not change in response to temperature stress. Furthermore, the findings of the short-term study by Chapron et al. (2018), in which *Artemia* capture rates remained unchanged after microplastic exposure conditions, are confirmed by our findings. A lack of adaptation to changing environmental conditions suggests that as concentrations increase, microplastic particle uptake might also increase linearly, possibly as seen for suspended particulate matter (Anthony, 1999; Anthony and Fabricius, 2000) or suspended sediments (Anthony, 2000).

After offering both types of particles independently, we found that the corals ingested the natural food at a higher rate than
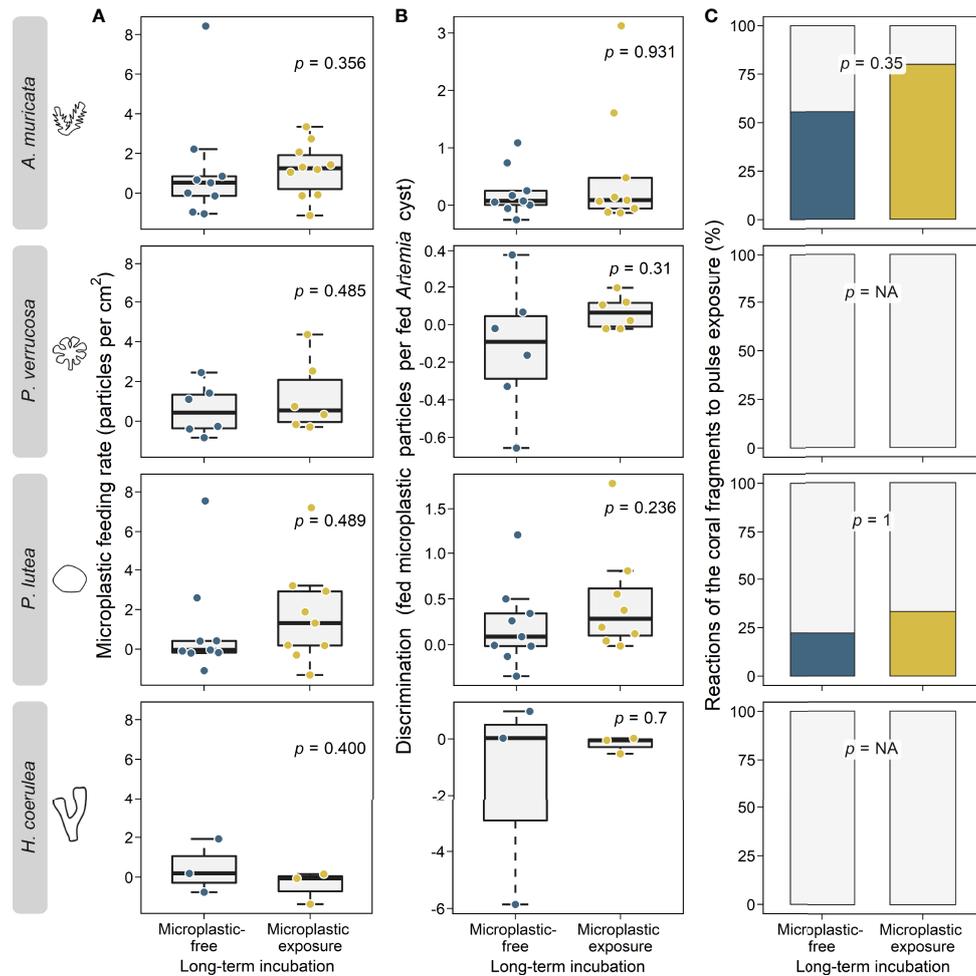
FIGURE 2 | Impacts of long-term exposure to microplastics (in yellow) and microplastic-free control conditions (in blue) on coral microplastic feeding and defense behavior of the four coral species *A muricata*, *P. verrucosa*, *P. lutea*, and *H coerulea*. **(A)**: Coral feeding rates on microplastics (particles per cm^2 coral tissue per 24 h) after long-term exposure to microplastics and microplastic-free control conditions. Data is displayed as box-and-whisker plots with raw data points. *P*-values are derived from Wilcoxon tests. **(B)**: Corals' discrimination ability (no. of fed microplastic particles per fed particle of natural food (*Artemia* sp. cysts)) after long-term exposure to microplastics and microplastic-free control conditions. Data is displayed as box-and-whisker plots with raw data points. *P*-values are derived from Wilcoxon tests. **(C)**: Corals' defense reactions to microplastic (% of fragments that show reactions) after long-term exposure to microplastic and microplastic-free control conditions Data is displayed as percent stacked bar charts and p-values are derived from Fisher's exact tests. NA, not available.

microplastics. In general, these findings are consistent with previous studies (Axworthy and Padilla-Gamiño, 2019; Savinelli et al., 2020), although there is also a counterexample (Rotjan et al., 2019). Yet, particle numbers deviated (*SD*) in average by 38 microplastic particles and 141 *Artemia* sp. cysts in the pulse exposures. Thus, the sometimes even negative feeding rates are a result of the mathematical approach used to quantify the feeding rates, and indicate low or no the feeding during the pulse exposure.

Long-Term Exposure Does Not Lead to Better Discrimination Between Microplastics and Natural Food

Our results also suggest that corals do not better discriminate between microplastics and natural food (research question II).

The number of microplastics fed per *Artemia* cyst fed remained unchanged for all species. This result indicates that corals were not more effective in avoiding microplastic ingestion after long-term exposure. Although corals generally fed fewer microplastics than natural food, discriminatory ability did not improve further. The basic discriminatory ability of corals leading to higher feeding rates on natural food has been previously shown for reef-building corals (Hall et al., 2015; Martin et al., 2019) but seems to be species-specific as indicated by other studies (Allen et al., 2017; Rotjan et al., 2019). Chemical stimuli might mediate the discrimination process (Houlbrèque and Ferrier-Pagès, 2009). Microplastic feeding may be triggered by both biofilm- or plastic-related stimulants (Allen et al., 2017; Diana et al., 2020). It can be assumed that the biofilm on the particle mainly drives microplastic uptake, as most studies indicate that particles

covered with a biofilm are more likely to be ingested than pristine particles (Corona et al., 2020; Weideman et al., 2020). A comparison with sediments supports this concept: particles that are perceived as a source of nutrients due to microbiota colonization are more likely to be taken up by corals than sediments that are poor in nutrients (Mills et al., 2004).

Corals Do Not Increase Defense Mechanisms to Reduce Microplastic Uptake

Our results indicate that corals do not change the frequency of defense reactions to adapt to long-term microplastic exposure (research question 3) and do not appear to develop adaptive defense mechanisms to reduce the impacts of microplastic exposure. On the one hand, an increase in defense reactions could reduce the number of ingested particles. However, such defense behavior may also hinder feeding on natural food (Hughes, 1980; Anthony, 2000) and would thus be unfavorable in the long term. On the other hand, it could also have been assumed that defense reactions would be reduced in response to long-term microplastic exposure to avoid continuous energy expenditures. However, none were detected here, suggesting that microplastic exposure does not alter these reactions.

As an aside, our results confirm that defensive reactions like mucus production and extrusion of mesenterial filaments are typical reactions of *A. muricata* and *P. lutea* to microplastics (Reichert et al., 2018; Martin et al., 2019; Mouchi et al., 2019; Jiang et al., 2021). Reactions were observed when corals were exposed to microplastics and less frequently when corals were exposed to natural food. The observed reactions can be interpreted as either defense or feeding reactions, which explains their designation as so-called "multitools" (Brown and Howard, 1985; Brown and Bythell, 2005). However, the observed reactions seem to be defensive, as corals ingested fewer microplastics when reactions were shown.

Our results further indicate that corals apparently ingest microplastics even in the absence of natural food (*sensu* Corona et al., 2020). Yet, coral microplastic feeding rates might be even higher in the presence of natural food, which triggers feeding through inherent chemical stimulants (Helland et al., 2000; Houlbrèque and Ferrier-Pagès, 2009). Additionally, different polymer types might cause different reactions because of their physical and chemical properties (e.g., shape, size, additives). Further, the influence of microplastics may vary over time as the particles' properties can be altered through environmental conditions and absorb locally present pollutants. Therefore, further studies should also consider using other microplastics and combinations (i.e., different shapes, polymer types, concentrations, and mix with natural feed) to better resemble *in situ* conditions.

CONCLUSIONS

In summary, our findings suggest that reef-building corals lack acclimation mechanisms (i.e., feeding, avoidance, and defense mechanisms) to reduce the effects of microplastic exposure over longer periods of time. A lack of acclimation implies that microplastics will constitute a permanent stressor in coral reefs. However, it is still unclear to what degree corals will be cumulatively affected by repeated microplastic contacts during their lifetime. Given the projected increase in microplastic concentrations (Everaert et al., 2018; Isobe et al., 2019) and the lack of adaptive mechanisms (i.e., foraging and defensive), microplastic pollution might be of increasing concern. In combination with other stressors (e.g., global warming and ocean acidification; Hoegh-Guldberg et al., 2007; Conti-Jerpe et al., 2020; Reichert et al., 2021b), microplastics are likely to contribute to shifts in coral reef communities worldwide. Therefore, immediate action is needed to curb microplastic and plastic pollution, in close coordination with protective measures against global warming and ocean acidification, to preserve the remaining coral reefs.

DATA AVAILABILITY STATEMENT

The datasets presented in this study are publicly available at figshare: https://doi.org/10.6084/m9.figshare.19073312.

AUTHOR CONTRIBUTIONS

MR: Methodology, Software, Formal Analysis, Investigation, Writing – Original Draft, Visualization. JR: Conceptualization, Methodology, Formal Analysis, Resources, Data Curation, Writing – Review and Editing, Project Administration, Supervision. PS: Resources, Writing – Review and Editing. TW: Conceptualization, Writing – Review and Editing.

SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fmars.2022.863187/full#supplementary-material

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