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Reef-building corals act as long-term sink for microplastic

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Abstract

The pollution of the marine environment with microplastics is pervasive. However, microplastic concentrations in the seawater are lower than the number of particles entering the oceans, suggesting that plastic particles accumulate in environmental sinks. Yet, the exact long-term sinks related to the "missing plastic" phenomenon are barely explored. Sediments in nearshore biogenic habitats are known to trap large amounts of microplastics, but also the three-dimensional structures of coral reefs might serve as unique, living long-term sinks. The main framework builders, reef-building corals, have been shown to ingest and overgrow microplastics, potentially leading to a deposition of particles in reef structures. However, little is known about the number of deposited particles and the underlying processes determining the permanent deposition in the coral skeletons. To test whether corals may act as living long-term sink for microplastic, we exposed four reef-building coral species to polyethylene microplastics (200 particles L^{-1}) in an 18-month laboratory experiment. We found microplastics in all treatment specimens, with low numbers of particles trapped in the coral tissue (up to 2 particles per cm^2) and much higher numbers in the skeleton (up to 84 particles per cm^3). The numbers of particles accumulated in the coral skeletons were mainly related to coral growth (i.e., skeletal growth in volume), suggesting that deposition is a regularly occurring stochastic process. We estimate that reef-building corals may remove 0.09%–2.82% of the bioavailable microplastics from tropical shallow-reef waters per year. Our study shows for the first time that microplastic particles accumulate permanently in a biological sink, helping to explain the "missing plastic" phenomenon. This highlights the importance of coral reefs for the ecological balance of the oceans and reinforces the need to protect them, not only to mitigate the effects of climate change but also to preserve their ecosystem services as long-term sink for microplastic.

KEYWORDS
coral skeleton, long-term experiment, marine microplastic, missing plastic phenomenon, particle uptake, plastic sink in the ocean, reef-building corals

1 | INTRODUCTION

The pollution of the marine environment with plastic debris has increased exponentially over the last decades (Brandon et al., 2019; Lavers & Bond, 2017) and is suspected to have adverse effects on marine life (Bucci et al., 2020; Wright et al., 2013). Not only are plastic concentrations in seawater highly variable depending on time, location, and type (Coyle et al., 2020 and references within), but they are also lower than the number of particles entering the oceans would suggest (Cózar et al., 2014; Eriksen et al., 2014; Law & Thompson, 2014). Recent assessments indicate rapid removal of ocean surface plastics and estimate that only 1% remains floating in surface waters (Law, 2017; van Sebille et al., 2015). Particles <1 mm (i.e., microplastics) have been found to be particularly depleted (Cózar et al., 2014; Martí et al., 2017), although especially smaller particles (<300 μm) are often underestimated due to sampling biases (Koelmans et al., 2020; Song et al., 2014). This suggests that "missing plastic" accumulates in environmental sinks. The Arctic sea ice (Obbard et al., 2014; Peeken et al., 2018), deep-sea sediments (Barrett et al., 2020; Kane et al., 2020; Woodall et al., 2014), and coastal sediments (de Smit et al., 2021; Martin et al., 2020; Van Cauwenberghe et al., 2015) have been identified as important permanent and temporary sinks for microplastics. In addition, aggregation of microplastics into marine snow or organisms may serve as temporary sinks (Kvale et al., 2020). Examples include the accumulation of particles in the food web through ingestion by fishes (Davison & Asch, 2011; Garnier et al., 2019; Savoca et al., 2021), marine mollusks (Arossa et al., 2019; Piarulli & Airoldi, 2020), and seabirds (Kühn et al., 2015). Recently, adhesion to coral structures has also been proposed as a temporary sink for marine plastics (Corona et al., 2020; Martin et al., 2020).

Worldwide coral reefs cover ~250,000 km^2, comprising biologically accreted calcium carbonate structures that could potentially seal large quantities of microplastics (Burke et al., 2011). Reef-building corals are the main framework builders of the complex three-dimensional reef structures, providing crucial ecosystem services such as shoreline protection, livelihoods for more than 500 million people, and habitat for a large diversity of organisms (Fisher et al., 2015). Microplastic pollution has been detected in reef environments across the tropics (Huang et al., 2021 and references within) and is suspected to constitute an insidious stressor for corals (Chapron et al., 2018; Lanctôt et al., 2020; Reichert et al., 2019).

Reef-building corals have been shown to ingest microplastics (Allen et al., 2017; Hall et al., 2015; Reichert et al., 2018), which occasionally remain in the digestive tract (Allen et al., 2017; Rotjan et al., 2019). Furthermore, corals may overgrow plastic particles attached to solid substrate or in areas of the colony where cleaning mechanisms are ineffective (Reichert et al., 2018). The extent to which microplastics adhere to coral structures presumably depends on morphology and feeding mode of the species (Corona et al., 2020; Lim et al., 2020; Martin et al., 2019; Reichert et al., 2018). First observations of microplastic particles in the skeleton of tropical coral species (Ding et al., 2019; Hierl et al., 2021; Krishnakumar et al., 2021) and the tissue of the temperate coral *Astrangia poculata* (Rotjan et al., 2019) suggest that reef-building corals may act as long-term sink for microplastic (Soares et al., 2020). However, it remains unclear what quantity of particles is deposited, and which processes determine the permanent deposition in coral colonies.

In this study, we tested whether tropical shallow-water reef-building corals may act as long-term sink for marine microplastic. We (I) quantified particle deposition rates in corals exposed to microplastics. For this, we subjected four common reef-building coral species to a defined concentration of polyethylene microplastics (PE, 200 particles L^{-1}) for 18 months. We (II) tested the permanent translocation of particles into the coral skeleton after temporary uptake in the coral tissue. For this, we compared the numbers of particles deposited in corals treated with microplastics in a pulse exposure to those from the long-term exposure. We (III) identified the morphological and physiological properties of the coral colonies (i.e., size, shape, and growth parameters) affecting the deposition process. Furthermore, we (IV) used these data to estimate the total annual deposition rate of microplastic particles in tropical shallow-water reef-building corals on a global scale to assess the relevance of coral reefs as a permanent living sink, which may explain part of the "missing plastic" phenomenon.

2 | MATERIALS AND METHODS

2.1 | Microplastic particle properties and preparation

We used black PE microplastic particles (density: 0.95 g cm^{-3}; Novoplastik) to study microplastic deposition patterns in reef-building corals. PE is one of the most common polymers in the marine environment in general (Efimova et al., 2018) and coral reefs in particular (Nie et al., 2019; Patterson et al., 2020; Saliu et al., 2018). PE with black color was chosen to ease the visual identification of the particles in the coral tissues and skeletons. The particles were irregularly shaped and exhibited a rough surface structure, resembling natural secondary microplastics. Microplastic particles had a diameter of 175.5 ± 73.5 μm (mean ± SD; for detailed particle properties, see Reichert et al., 2019), comparable to the size of particulate food commonly ingested by reef-building corals (Houlbrèque & Ferrier-Pagès, 2009). Particles were cleaned with ethanol (70%, 24 h) and rinsed with deionized water before being used in the experiments.

2.2 | Microplastic exposure treatments

We investigated the deposition of microplastics in the coral tissue and skeleton of four common and widespread shallow-water reef-building coral species: *Acropora muricata* (Linnaeus, 1758), *Pocillopora verrucosa* (Ellis and Solander, 1786), *Porites lutea* Milne Edwards and Haime, 1851, and *Heliopora coerulea* (Pallas, 1766). The species share similar corallite sizes (*A. muricata*: 800–1200 μm, *P. verrucosa*: 300–700 μm, *P. lutea*: 100–1300 μm; [Madin et al., 2016

and references within] and *H. coerulea*: 500–1200 μm [here measured]), which allow for an ingestion of the chosen particles. The species cover a broad range of morphologies and growth rates (*A. muricata*: arborescent, 7.53 ± 3.08 cm year^{-1}; *P. verrucosa*: branching, 2.77 ± 0.85 cm year^{-1}; *P. lutea*: massive, 1.22 ± 0.43 cm year^{-1}; *H. coerulea*: columnar, 1.5 ± 0.64 cm year^{-1}; Madin et al., 2016 and references within; Courtney et al., 2021). The analyses were conducted in the "Ocean2100" long-term coral experimental facility of Justus Liebig University, Giessen, Germany (Schubert & Wilke, 2018).

To test the time frame of the temporary deposition of particles into the coral tissue and their permanent translocation into the coral skeleton, we compared particle accumulation in coral nubbins continuously exposed to microplastics over 18 months to nubbins exposed in a pulse exposure treatment over 24 h. This approach is further used to evaluate whether short-term experiments can mirror the results of long-term studies.

For the continuous treatment, nubbins were exposed to microplastics over 18 months (75 weeks) at a concentration of ~200 particles L^{-1} (201 ± 67 particles L^{-1}, n = 518 measurements at 125 timepoints), while the pulse treatment nubbins were kept under microplastic-free control conditions. After 17 months (68 weeks), nubbins from both treatments were exposed to microplastics over 24 h at a concentration of 1850 particles L^{-1} (1850 ± 230 particles L^{-1}, n = 24 measurements at 8 timepoints). Afterwards, nubbins were re-exposed to 200 particles L^{-1} (continuous treatment) or left for recovery under microplastic-free conditions (pulse treatment) for another month. As baseline reference, we analyzed coral nubbins kept under control conditions, with no microplastics added.

The concentration of 200 particles L^{-1} for the continuous treatment was chosen to represent a high-pollution scenario based on values found in polluted coastal ecosystems (e.g., up to 125 particles L^{-1}, Patterson et al., 2020, 360 particles L^{-1}, Chae et al., 2015, and 76,000 particles L^{-1}, Badylak et al., 2021). Values were chosen so that the corals had regular contact with the particles during the time of the experiment while still representing a realistic scenario. Moreover, microplastic concentrations in the oceans are projected to increase 3–50 times by 2100 (Everaert et al., 2018; Koelmans et al., 2017). Therefore, the concentrations applied in this study lie both within measured environmental particle concentrations in polluted waters and within the broad range of future predictions for microplastic pollution. The concentration of ~1850 particles L^{-1} for the pulse treatment was chosen to provide at least one particle per coral polyp in the 24 h incubation, based on a count of the number of polyps in a subset of corals (n = 1 per species), while not causing stress reactions or feeding saturation (>10,000 particles L^{-1}; Clayton & Lasker, 1982; Hii et al., 2009). This concentration still lies within measured environmental particle concentrations in highly polluted waters (Badylak et al., 2021). For the long-term experiment, coral nubbins were kept in six 80 L tanks (three continuous treatment tanks and three pulse treatment tanks, i.e., microplastic-free control tanks).

The experimental tanks were supplied with water from a closed recirculation system (4000 L artificial seawater) at an exchange rate of 120 L day^{-1}. The outflows of the tanks were fitted with 65 μm filters to keep the microplastic particles within the experimental tanks and allow for a biofilm to form on the particles. For the short-term experiment, coral nubbins were incubated individually in 800 ml beakers. Microplastic particles for the short-term experiment were incubated under reef-aquaria conditions (26°C, salinity: 34 ± 2) for at least 16 days to allow for biofilm formation on the particle surfaces before being used. After the short-term incubation, corals were placed back in the respective 80 L tanks of the long-term experiment. Further details on the exposure setups are shown in Supplementary Material and Methods S1.1 and S1.2.

2.3 | Coral preparation and experimental replication

Coral colonies were maintained under laboratory conditions (10:14 light:dark photoperiod, light intensity (PAR) 200 μmol photons m^{-2} s^{-1}, and temperature 26 ± 0.5°C) for at least 6 months prior to the experiment (for details on coral colonies, see Table S1). Coral nubbins were generated from larger colonies using a small angle grinder (Dremel Multitool 3000-15; Robert Bosch Tool Corporation). *Acropora*, *Pocillopora*, and *Heliopora* nubbins consisted of 2–4 cm long terminal branches; *Porites* nubbins consisted of small cubes with an edge length of approximately 2 cm. All nubbins were attached to self-made concrete bases with a two-component glue (CoraFix SuperFast; Grotech). For *Acropora*, *Pocillopora*, and *Porites*, nubbins were generated from three original colonies. For *Heliopora*, nubbins were generated from a single colony due to the lack of further colonies. Three nubbins per colony (each from a different tank) were analyzed for microplastic deposition in the tissue and skeleton in each, the continuous and the pulse exposure treatment (n = 9 for *Acropora*, *Pocillopora*, and *Porites*, n = 3 for *Heliopora*). One additional nubbin per species was analyzed as a blank control that was not exposed to microplastics at any time to assess potential background contamination in coral colonies (n = 1 for *Acropora*, *Pocillopora*, *Porites*, and *Heliopora*). As one colony of *P. verrucosa* experienced high mortality over the course of the experiment, it was excluded from subsequent analyses. This resulted in a total of n = 27 nubbins, analyzed from each, the continuous and the pulse exposure treatment, with each nubbin treated as replicate.

2.4 | Sample preparation and microplastic extraction

Coral samples (continuous treatment, pulse treatment, and control) were snap-frozen with liquid nitrogen and stored at −80°C until processing. All further processing was performed under a fume hood to minimize potential contamination. Utilized tools were rinsed carefully between all steps to minimize particle loss and cross-contamination between samples. We quantified

microplastics separately in the tissue and skeleton of the coral nubbins. Particles were counted and not weighed as preliminary tests revealed high standard errors when assessing the weight of small numbers of particles (1 particle ≅ 0.005 mg). For this, nubbins were defrosted at room temperature for at least 30 min, rinsed thoroughly with distilled water to remove adhering particles and transferred to glass beakers. The coral tissue was dissolved in 7% sodium hypochlorite (NaClO) for 24 h. The remaining skeleton was rinsed with distilled water and transferred to a clean beaker. The NaClO solution, containing microplastics and organic residues, was filtered through a 50 μm stainless steel sieve (ISO 3310-1; Edinger Industrievertretung) to remove the NaClO. The cleaned residues in the sieve were transferred with filtered seawater to a 50 ml Falcon tube. Coral skeletons were dissolved in 5.5% hydrochloric acid (HCl) for 18 h and particles were retrieved through sieving as described for the tissue sample. To further separate the microplastic particles from other residues, samples were centrifuged (479 *g* for 10 min) so that the positive buoyant microplastic particles were floating at the surface. The organic residues, remaining at the bottom of the tube, were removed using a glass pipet. The seawater containing the microplastics was vacuum-filtered onto cellulose nitrate filters (diameter: 47 mm, pore size: 8 μm; Sartorius) and documented as stitched image using a digital microscope (VHX-2000 together with VH-Z20W lens; Keyence; magnification: 100×).

2.5 | Image processing

We visually identified and counted plastic particles on the cellulose nitrate filters using the software package Fiji (Schindelin et al., 2012) for the image processing software ImageJ (Rueden et al., 2017). Briefly, all images were adjusted (set to equal dimensions, corrected for white balance and brightness), smoothened (tool: "Non-Local Means Denoise" and "Thresholded Blur"), and preselected through a color threshold (tool: "Color Threshold"). Contrasts in clusters were enhanced (tool: "Enhance Local Contrast"), noise was reduced ("Thresholded Blur" and "Bi-Exponential Edge-Preserving Smoother"), and particle aggregates were separated ("Greylevel Watershed" and "Watershed Irregular Features"). Then, we counted all particles in a size range of 65–200 μm ("Extended Particle Analyzer"). Further details are given in Table S2.

2.6 | Documentation of corals using 3D scanning and modeling

We documented the coral nubbins using 3D scanning at the beginning (t_{start}) and the end of the experiment (t_{end}, after 75 weeks). We used a handheld 3D scanner (Artec Spider 3D together with the software Artec Studio 10; Artec 3D), following established procedures (Reichert et al., 2016). Briefly, corals were placed on a rotating plate and scans were captured in air within 60–90 s. Models were calculated with a final mesh size of 0.2 mm; for detailed settings, see Table S3.

2.7 | Model processing for size, growth, and shape determinations

We determined size parameters (i.e., coral tissue surface area, coral volume, surface area of the base, and number of branches) for all nubbins at both timepoints (t_{start} and t_{end}). Branches larger than 1 cm in length were counted. Absolute and relative growth rates (i.e., growth in tissue surface area, growth in volume, linear extension, and overgrown area) were calculated for each nubbin over the time of the experiment (t_{start} to t_{end}). Growth in tissue surface area and volume was calculated as absolute increase (total) and in percent of the original size (relative). Linear extension (absolute in mm) was determined as mean from 3 to 6 randomly selected points over a colony's surface in the aligned models (t_{start} and t_{end}). The surface area overgrown by the coral was determined as difference between the surface area of the base at the beginning (t_{start}) and at the end (t_{end}) of the experiment. The occurrence of bleaching or tissue necrosis (i.e., paling or necrotic tissue surface area) was monitored over the course of the experiment. As bleaching and necrosis often occurred together, they were summarized as occurrence of signs of compromised health. Shape parameters (compactness, surface complexity, convexity, and overhang) were quantified for each coral nubbin as mean values from the start (t_{start}) and the end of the experiment (t_{end}). Shape parameters were calculated from models of the coral nubbin, excluding the base. Compactness was quantified as surface-to-volume ratios, based on values of total surface area and volume. Surface complexity was estimated as fractal dimension, using the Bouligand–Minkowski method previously applied to coral nubbins (Reichert et al., 2017). Convexity was quantified via the calculation of alpha shapes, modified after Gardiner et al. (2018). The overhang of the coral was calculated as sum of all downward-pointing faces. Details on model processing and derived parameters are found in Supplementary Material and Methods S1.3 and Table S4).

2.8 | Effects of dissolution procedures on particle integrity

To control for the effect of the dissolution procedures of the coral tissue and skeletons, individual PE particles (n = 20) were incubated in NaClO, HCl, and DI water (as control) for 24 h. Afterwards, particle integrity was assessed to observe possible fragmentation processes during dissolution. As fragmentation rates were equal in all three solutions (DI water: 2/20, HCl: 1/20, NaClO: 2/20), we concluded that the procedure had no substantial impact on particle integrity. The observed fragmentation is probably due to the irregular shape and the electrostatic charge of the plastic particles, leading to an entanglement of two particles, which dispersed in the solution.

2.9 | Polymer identification using ATR-FTIR and method validation

To control for false particle identification during image processing, pre-contamination of the used coral nubbins, and to confirm polymer identity, we applied ATR-FTIR (Attenuated total reflection Fourier-transform infrared) spectrometry (Nicolet iS10 FT-IR coupled with SMART iTR; Thermo Electron Corporation) to a subset of samples (one tissue and one skeleton filter per species for each treatment: $n = 8$ from each, pulse exposure, continuous exposure, and control). Up to 10 particles present on the filters were selected and identified (Figure S1). In all, 32 scans at a resolution of 4 cm^{-1} and wave numbers between 4000 and 525 cm^{-1} were performed per particle. Particles were classified as (1) source PE or (2) other polymer type/not identifiable.

To control for potential transfer of particles from the coral tissue samples to the skeleton sample during the dissolution process, particles were added to coral nubbins ($n = 4$, one per species) during the tissue dissolution step and number of particles found in the skeleton were analyzed. Additionally, coral nubbins ($n = 4$, one per species) were exposed to PE microplastics in a concentration of 200 particles L^{-1} without regeneration time and numbers of particles found in the skeletons were analyzed.

2.10 | Statistical analyses

We performed all data processing and analyses in the R statistical environment (v.3.6.1; R Core Team, 2019). Particle data were analyzed as (a) total numbers per colony and (b) densities. Particle numbers in the tissue were standardized to the tissue surface area (cm^2) at the end of the experiment (t_{end}). Particle numbers in the skeleton were standardized to the volume (cm^3) gained over time (t_{start} to t_{end}).

Differences in particle numbers were assessed using linear mixed-effect models followed by Tukey posthoc comparison in the R packages lme4 v.1.1-26 (Bates et al., 2015) and multcomp v1.4-16 (Hothorn et al., 2008). Individual models were constructed for the response variables (total particle numbers and particle densities) with treatment (continuous and pulse exposure), compartment (tissue and skeleton), and species (*A. muricata*, *P. verrucosa*, *P. lutea*, and *H. coerulea*) included as fixed factors, respectively. Origin colony and experimental tank were included as random factors. Data were log-transformed prior to analysis to meet test assumptions. Residual structures were checked visually. Detailed model specifications are provided in Tables S5 and S6. All values are stated as mean ± standard deviation and displayed as box-and-whisker plots with lines indicating medians, boxes indicating the first and third quartiles, and whiskers indicating ±1.5 IQR.

We used regression tree (RT) analyses (De'ath, 2002) to identify morphological and physiological parameters determining microplastic deposition in the coral tissue and skeleton. The method implements hierarchical dichotomous clustering of the data by selecting the morphological parameters that maximize homogeneity of particle data. The analyses were performed in the R package "mvpart" 1.6-2 (Therneau & Atkinson, 2014) and run with 1000 cross-validations on absolute particle numbers and particle densities in the tissue and skeleton of continuously exposed corals. The morphological parameters included in the analyses and their calculations are given in Table S4. While size and shape parameters were used for both, total particle numbers and particle densities, growth rates were chosen to match the deduction of the analyzed parameters (i.e., absolute growth rates [growth in cm^2 or cm^3] for total particle numbers and relative growth rates [growth in %] for particle densities). Additionally, coral species identity was included in the analysis to study whether the observed patterns are species-specific or consistent across the tested species as well as the occurrence of signs of compromised health.

2.11 | Extrapolation of particle deposition rates to coral reefs worldwide

We estimated total global microplastic particle clearance rates of tropical shallow-water reef-building corals to assess their role in the "missing plastic" phenomenon. Since coral skeletal growth (i.e., growth in volume) was identified as main parameter determining deposition of particles, skeletal incorporation rates found herein were extrapolated to the area covered by tropical shallow-water coral reefs worldwide (Supplementary Material and Methods S1.4). For this, skeletal incorporation was calculated as particles g^{-1}, derived from particles in coral tissue and skeleton deposited per cm^3 during the experiment and species-specific skeletal densities (Supplementary Material and Methods S1.5). Reef carbonate budgets (G, where G = kg $CaCO_3$ m^{-2} $year^{-1}$) from Perry et al. (2018) were used as measures of reef growth incorporating coral growth and bioerosion, derived from the Indian Ocean ($n = 601$ sites) and the Tropical Western Atlantic ($n = 441$ sites), and including post-bleaching records ($n = 169$). We calculated the amount of microplastic removed from the water column by coral growth (gross deposition), the amount of microplastic released by bioerosion (gross release), and the amount of microplastic permanently deposited in tropical shallow-water reef-building corals (net deposition) per year. Values were calculated separately for the Indo-Pacific and the Atlantic realm and the area-weighted mean was derived (Indo-Pacific: 223,864 km^2, Atlantic realm: 25,849 km^2; Burke et al., 2011). We constructed our model based on five assumptions (i.e., simplifications): (1) The area covered by tropical shallow-water coral reefs (<30 m depth) constitutes 249,713 km^2 (Burke et al., 2011) and, for simplification, is covered by a 15 m deep water column. (2) Coral production, gross erosion, and net production (Perry et al., 2018) are representative of coral reefs worldwide. (3) Particle deposition rates found herein are representative of other reef-building coral families. (4) The uptake of PE particles used here is representative of other polymer types. (5) Environmental microplastic concentration and particle deposition rate stand in a linear relationship following the here tested 200 particles L^{-1}.

To calculate the total numbers of particles removed, released, and deposited, high (152,688 particles per m^3 [Chae et al., 2015]) and low (0.12 particles per m^3 [Jensen et al., 2019]) particle concentrations in shallow coastal waters (see Huang et al., 2021 for review) were used to approximate upper and lower ranges. We then calculated the percentage of permanently deposited microplastic particles relative to the particles present in tropical shallow coral reef waters using mean, minimum, and maximum numbers of particles found in the tissue and skeleton of corals in this study. We provide details to our assumptions in the Supplementary Material and Methods S1.4, together with their justifications and derived formulas of the calculation. Therefore, this extrapolation should be viewed as a conservative estimation that, while well founded in detail, also contains areas of uncertainty.

3 | RESULTS

3.1 | Quantification of particle deposition in the coral tissue and skeleton

We quantified microplastic deposition in the coral tissue (Figure 1a) and skeleton (Figure 1b) of the four reef-building coral species (i.e., *A. muricata*, *P. verrucosa*, *P. lutea*, and *H. coerulea*). Microplastics were present in all studied nubbins, both in the continuous and the pulse treatment (numbers summarized from tissues and skeletons). Particle numbers were significantly higher in continuously exposed nubbins than in the nubbins from the pulse exposure, both in the tissue and skeleton, summarized from all species (Figure 1, Linear mixed-effects model followed by Tukey posthoc comparison, $p < .0001$, Table S5). Furthermore, particle numbers found in the skeleton were higher than in the tissue, both in the continuous and the pulse treatment (linear mixed-effects model followed by Tukey posthoc comparison, $p < .0001$, Table S5). In particular, particle numbers were 15 times higher in the skeleton (194.70 ± 161.60 particles, max. 592 particles) than in the tissue (12.78 ± 14.77 particles, max. 68 particles) after 18 months of continuous microplastic exposure. Similarly, pulse exposure led to a higher deposition of microplastic particles into the skeleton compared to the tissue (19.63 ± 18.33 particles, max. 18 particles in the skeleton and 2.93 ± 2.88 particles, max. 10 particles in the tissue), although the difference was less pronounced.

Densities of particles in the coral tissue, standardized to tissue surface area (cm^2) at the end of the experiment, ranged from 0.06 ± 0.06 particles per cm^2 in pulse exposed nubbins to 0.27 ± 0.35 particles per cm^2 in continuously exposed nubbins (linear mixed-effects model followed by Tukey posthoc comparison, $p < .0001$, Table S5; Figure S2). Densities of particles in the skeleton, standardized to volume (cm^3) gained over the time of the experiment, ranged from 3.96 ± 4.34 to 37.51 ± 25.68 particles per cm^3 in

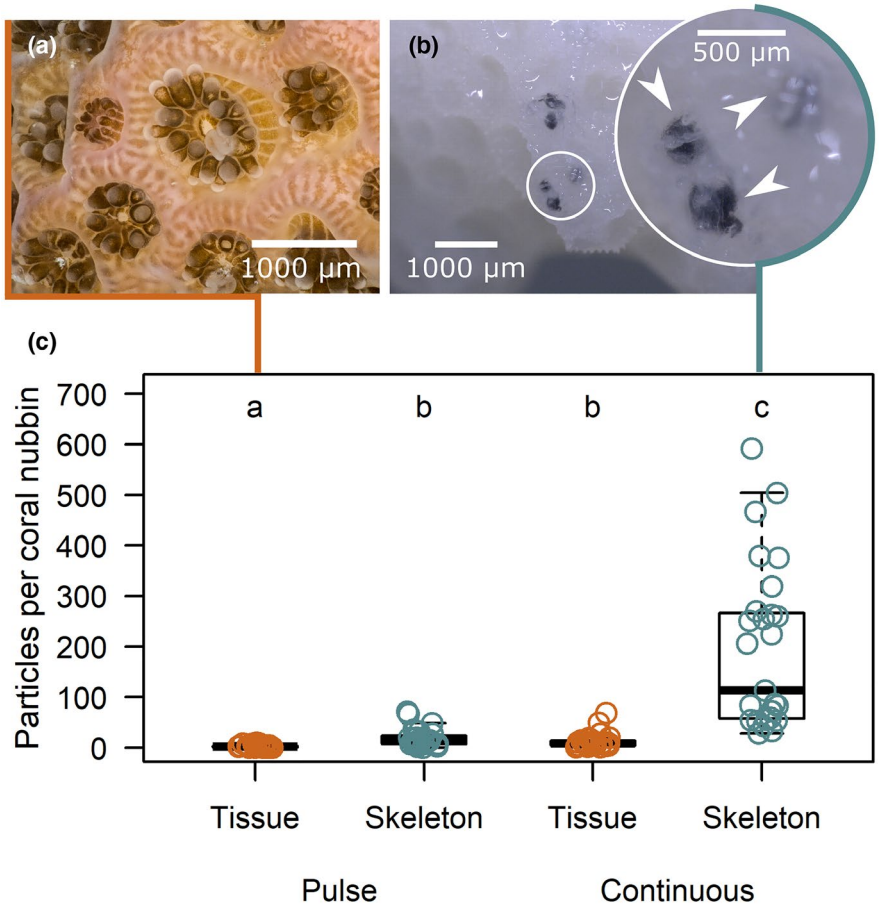

FIGURE 1 Microplastic particles in the coral tissue and skeleton. (a) Living tissue of *Pocillopora verrucosa*. No embedded microplastic particles are detectable in the coral tissue. (b) Overview and closeup of the coral skeleton of *P. verrucosa* after tissue removal with sodium hypochlorite. Microplastic particles (black) are embedded in and between corallites, partly covered by skeletal material. Arrows indicate the position of three particles in the closeup. (c) Total number of microplastic particles found in the coral tissue and skeleton of all four studied reef-building coral species after pulse and continuous exposure. Data are displayed as box-and-whisker plots with raw data points; lines indicate medians, boxes indicate the first and third quartiles, and whiskers indicate ±1.5 IQR. Letters indicate significantly different groups, derived from linear mixed-effects model followed by Tukey posthoc comparison ($n = 27$)

pulse and continuously exposed nubbins, respectively (linear mixed-effects model followed by Tukey posthoc comparison, $p < .0001$, Table S5). Maximum density in the tissue was found in a *P. lutea* nubbin (1.76 particles per cm^2) and in the skeleton in an *A. muricata* nubbin (83.65 particles per cm^3).

As nubbins in the pulse exposure treatment accumulated only a low number of particles, species-specific, morphological, and physiological factors affecting particle accumulation were further analyzed based on the results from the continuous exposure treatment. Particle numbers did not differ significantly between coral species (linear mixed-effects models followed by Tukey posthoc comparison, $p > .1$, Table S6). Particle densities differed between some coral species in the skeleton but not in the tissue (Figure 2). Pairwise comparisons showed that *H. coerulea* accumulated particles in significantly lower densities than the three other tested species (linear mixed-effects models, followed by Tukey posthoc comparison, $p < .01$, Table S6).

3.2 | Coral properties affecting particle deposition

We used size, growth, and shape parameters of the coral nubbins, documented over the course of the experiment with 3D scanning, to identify parameters that may affect plastic deposition in corals. Size and growth parameters were strongly correlated, while shape parameters were mostly independent of size and growth (Figure S3). Regression tree analyses revealed that the studied parameters explained 48%–72% of the variation in deposition patterns in the coral skeleton ($error_{total} = 0.279$, $error_{density} = 0.521$). The total number of particles accumulated in the coral skeleton was mainly determined by growth parameters (i.e., growth in volume and linear extension, Figure 3), with higher growth promoting particle deposition. In contrast, particle density was mainly determined by coral shape parameters (i.e., surface complexity, Figure S4), and less complex shapes were associated with higher particle densities.

Deposition patterns in the coral tissue were less well explained (20%–39%) by the studied parameters ($error_{total} = 0.608$, $error_{density} = 0.799$). The total number of particles accumulated in the coral tissue was mainly determined by shape (i.e., surface complexity). Although not identified as determining parameter in the RT analyses, the two highest numbers of particles in skeletons (592 and 504 particles) occurred in nubbins of *A. muricata*, which showed signs of compromised health (bleaching or necrosis) during the course of the experiment (Figure S5).

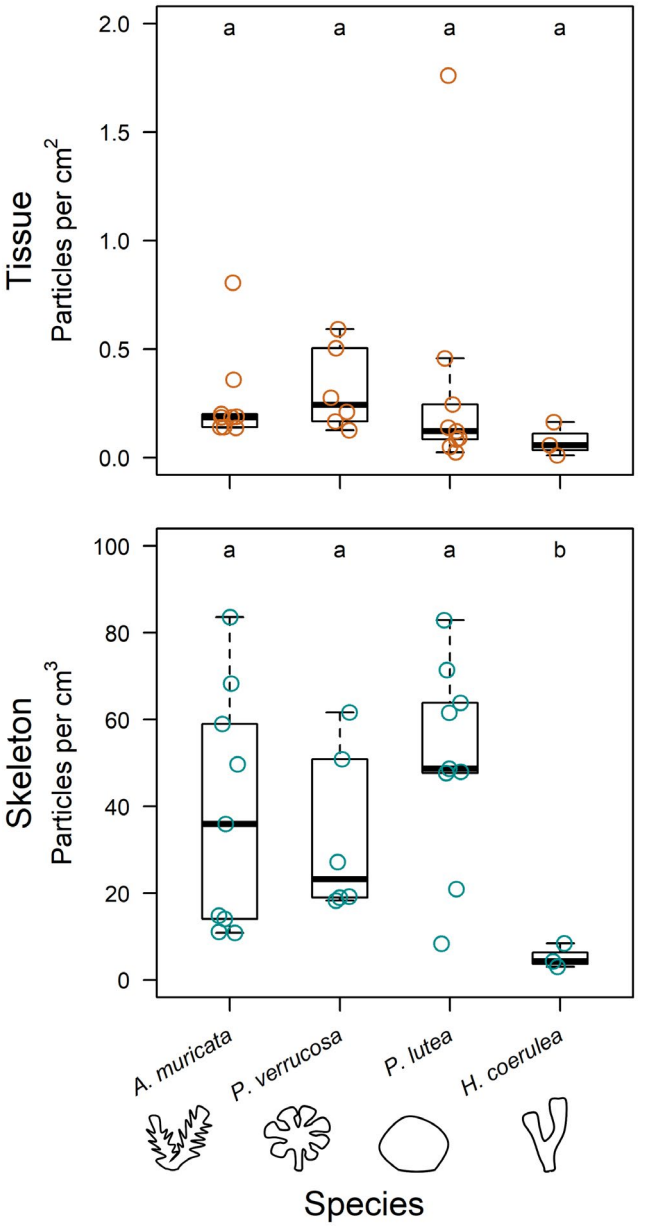

FIGURE 2 Species-wise microplastic particle densities in the coral tissue and skeleton of continuously exposed coral nubbins. Densities of microplastic particles found in the coral tissue (number of particles per cm^2) and skeleton (number of particles per cm^3) of four continuously exposed reef-building coral species *Acropora muricata* ($n = 9$), *Pocillopora verrucosa* ($n = 6$), *Porites lutea* ($n = 9$), and *Heliopora coerulea* ($n = 3$). Species growth forms are indicated on the *x*-axis. Data are displayed as box-and-whisker plots with raw data points; lines indicate medians, boxes indicate the first and third quartiles, and whiskers indicate ±1.5 IQR. Letters indicate significantly different groups, derived from linear mixed-effects model followed by Tukey posthoc comparison

3.3 | Characterization of polymer particles and method validation

To control for false particle identification during image processing, we identified the polymer type of a subset of particles in the coral tissue and skeleton by ATR-FTIR spectrometry. The analyses determined 98% (54 of 55) of the studied particles as "source PE."

Additionally, to control for pre-contamination of the used coral nubbins, we analyzed a set of control corals that were not exposed to microplastics but kept in the same aquarium system. In the control corals, a total of eight particles were detected visually in the tissue and skeleton samples of the four control corals but were all classified

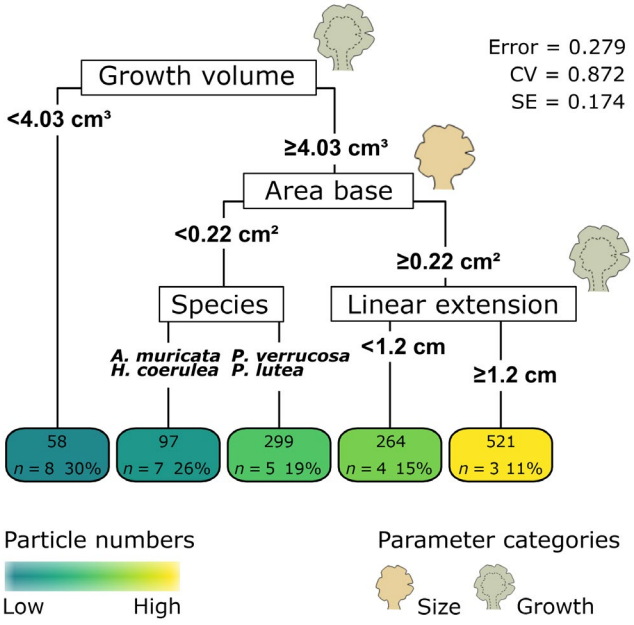

FIGURE 3 Parameters determining microplastic deposition (total numbers) in the coral skeleton. Regression tree analysis were used to identify parameters (categorized as size, growth, and shape parameters) that determine microplastic deposition in the coral skeleton. Error, cross-validation error (CV), and standard error (SE) are given (top right). The bold numbers on each branch indicate the splitting of the data. Colored boxes on each branch tip indicate the mean number of particles per coral nubbin (top), the number of coral nubbins (bottom left, *n*), and the percentage of total sample size (bottom right)

as "other polymer or not identifiable". No "source PE" was detected in the control corals. No particles were transferred during the dissolution process. We found no evidence for a methodological particle transfer to the skeleton after a 24 h microplastic exposure. A total of five particles were detected in the skeletons, which is within the range of the background particles found in the control corals.

3.4 | Worldwide particle removal rates of reef-building corals

We estimate that shallow-water reef-building corals annually remove 1.88×10^{10}–2.40×10^{16} particles (gross deposition). Through bioerosion, 1.30×10^{10}–1.65×10^{16} of these particles are released (gross release). As a result, 5.84×10^{9}–7.44×10^{15} particles are permanently deposited in the corals every year (net deposition). This deposition corresponds to 1.30 ± 0.88% (range: 0.09%–2.82%) of the bioavailable particles in coral reef waters.

4 | DISCUSSION

Our study is the first that experimentally quantified the permanent deposition of microplastics in reef-building corals. We showed that after 18 months of exposure to microplastics, all coral colonies deposited particles in their skeletons. In contrast, we found much lower numbers of particles in coral tissues. Also, nubbins exposed in a pulse treatment over 24 h accumulated much fewer particles, both in the skeleton and tissue. We identified coral growth as the main parameter determining particle deposition rates. Based on these results, we estimate that worldwide tropical shallow-water reef-building corals annually take up ~0.09%–2.82% of the particles present in coral reef waters.

Our results confirm the deposition of microplastics in the coral skeletons and provide a quantitative assessment of the incorporation based on an ecologically relevant experimental scenario. The permanent deposition was previously suspected based on occasional field observations (Ding et al., 2019; Krishnakumar et al., 2021), but not further explored. Densities of microplastics in the skeleton of all species (37.51 ± 25.68 particles cm^{-3}, range: 3.02–83.65 particles cm^{-3}) are equivalent to 30.93 ± 20.85 particles g^{-1} (range: 2.15–67.18 particles g^{-1}), referring to species-specific skeletal densities (Supplementary Material and Methods S1.5). When considering our applied experimental microplastic concentrations and incorporation rates, these numbers correspond well with the ranges reported from wild-collected coral colonies. For instance, reef-building coral species studied in natural systems with average microplastic concentrations of 10^{-4}–10^{0} particles L^{-1} (Huang et al., 2019; Jensen et al., 2019; Nie et al., 2019; Saliu et al., 2018) incorporated 0.09 particles g^{-1} coral skeleton (Ding et al., 2019). Both, environmental concentrations and incorporated particles, are approximately two orders of magnitude lower than in our experiment (Table 1). Thus, the relationship between environmental concentrations and incorporated rates of particles into the skeleton is constant between natural systems with lower concentrations and our experimental setup with 10^{2} particles L^{-1}. This constancy supports the notion of a linear relationship between environmental particle concentrations and incorporation rates into the coral skeleton across several orders of magnitude. Thus, although generated under a higher exposure scenario, our results appear to represent natural processes that might occur in coral reefs.

In comparison to other major sinks, densities found in the here studied corals are similar to deep-sea sediments, but higher than in Arctic sea ice, reef, or mangrove sediments (Table 1). Considering the experimental exposure conditions, reef-building corals seem to remove microplastic particles at rates comparable to coastal sediments. In absolute comparison, total amounts deposited in tropical shallow-water reef-building corals are likely lower as coral reefs cover a smaller area than other environmental sinks (Barrett et al., 2020; Halsband & Herzke, 2019). Nonetheless, tropical shallow-water reef-building corals constitute a previously unknown long-term sink for marine microplastic, especially in coastal areas where most particles enter the oceans (Jambeck et al., 2015).

In our study, particles were found 15 times more frequently in coral skeletons than in tissues. This shows that the coral tissue is likely only a temporary sink before particles are egested (Allen et al., 2017) or permanently translocated to the skeleton (Hierl et al.,

TABLE 1 Particle densities reported for environmental microplastic sinks. Size ranges of studied particles are given with their densities in which they occur in the respective environmental sink in relation to environmental microplastic concentrations (mean ± standard deviation)

Environmental sink	Size range	Particle density	Environmental concentration	References
Reef-building corals	65–200 μm	37.51 ± 25.68 particles per cm^3 30.93 ± 20.85 particles g^{-1}	201 ± 67 particles L^{-1}	This study
Reef-building corals	20–1000 μm	0.09 ± 0.09 particles g^{-1}	6 ± 12 particles L^{-1}	Ding et al. (2019)
Reef sediments	50–1000 μm	0.43 ± 0.19 particles g^{-1}	0.32 ± 0.15 particles per m^3	Saliu et al. (2018)
Reef sediments	100–5000 μm	0.10 ± 0.09 particles g^{-1}	127 ± 97 particles L^{-1}	Patterson et al. (2020)
Mangrove sediments	50–1000 μm	0.08 ± 0.04 particles g^{-1}	3546 ± 8154 particles L^{-1}	Martin et al. (2020); Martí et al. (2017)
Deep-sea sediments	50–5000 μm	1.26 ± 0.68 particles g^{-1}	nd	Barrett et al. (2020)
Arctic sea ice	≤2000 μm	0.000038–0.000234 particles per cm^3	nd	Obbard et al. (2014)

Abbreviation: nd, environmental concentration not determined in the reference.

2021). The assumption is also supported by the much lower number of incorporated particles in the pulse experiment over 24 h, suggesting that the deposition process is relatively slow, and most particles are egested before being translocated to the skeleton. This result also underlines the need for long-term experiments to study deposition and removal processes of microplastics in reef-building corals. Short-term high-exposure studies of reef-building corals showed that up to 30% of administered particles adhered to coral surfaces, while ingestion of particles, and therefore the chance to be translocated to the skeleton, occurred only occasionally (Corona et al., 2020; Martin et al., 2019). This suggests that not all particles attaching to reef surfaces are inevitably deposited permanently in corals. Reasons might be that corals clean themselves from adhering particles (Reichert et al., 2018), or have discrimination mechanisms that minimize the uptake of microplastics and cause particle egestion (Allen et al., 2017).

As the most obvious determinant of particle deposition rates, differences between coral species might be suspected. However, despite the different feeding modes of the tested coral species (e.g., active capture feeding in *A. muricata* and *P. verrucosa* or feeding on dissolved organic matter in *P. lutea* and *H. coerulea*, Houlbrèque & Ferrier-Pagès, 2009), particle densities were similar in the scleractinian coral species in our experiment. Only the octocoral *H. coerulea* accumulated significantly fewer particles, potentially due to its suspected low heterotrophic feeding, which may be attributed to a lower polyp density compared to the other coral species tested (polyps per cm^2: *A. muricata*: 21, *P. verrucosa*: 129, *P. lutea*: 70, *H. coerulea*: 19; for details, see Supplementary Material and Methods S1.5), while following a similar feeding strategy (Colgan, 1984). However, the comparably low number of replicates of *H. coerulea* ($n = 3$ for *H. coerulea* vs. $n = 9$ for the three other coral species) calls for confirmation of these findings in future studies. The absence of species-specific patterns suggests that, although different rates and forms of heterotrophy might influence deposition rates, they are rather determined by the physiological and morphological properties of the coral colonies. Our analyses revealed that growth parameters mainly determined particle deposition in the coral skeleton. In particular, high skeletal growth and linear extension facilitated the deposition of particles. This indicates that the deposition is mainly a stochastic process, regularly occurring during coral growth. Ingested particles occasionally get stuck in gastrovascular cavities (Allen et al., 2017) and can be translocated from tissue to the skeleton during growth. Translocation of microplastic to the skeleton has been recently proven through thin section analyses and likely occurs during the formation of a new basal plate, which is periodically built on top of the old one and leads to the formation of chambers within the skeleton (Hierl et al., 2021). Another mechanism of plastic uptake is the overgrowth and encrustation of particles stuck to a surface (Hierl et al., 2021; Reichert et al., 2018). Particle density, in contrast, was stronger determined by colony shape parameters. This is likely because different spatial complexities of biogenic structures confer specific boundary layer characteristics and affect the risk of microplastic accumulation (Lim et al., 2020).

Extrapolating our results to coral reefs worldwide shows that tropical shallow-water reef-building corals may remove every year ~1.3% of the particles present in coral reef waters. We consider these rates to represent conservative estimates of how much microplastic might be deposited in reef-building corals at present. Particle ingestion and following deposition rates might be even higher in other species, as previous studies indicate that some species ingest microplastics in similar amounts as natural food (e.g., *Dipsastraea pallida*; Hall et al., 2015) or even prefer microplastics over natural food (e.g., *A. poculata*; Allen et al., 2017)—contrary to the here tested species, which differentiate between microplastics and natural food (Martin et al., 2019). Given that the coral families studied on average represent ~70% of worldwide coral communities (Aeby et al., 2021; Jouval et al., 2020; Pandolfi & Minchin, 1996; Pratchett et al., 2011; Rodríguez-Zaragoza & Arias-González, 2015; Schmidt et al., 2012), we suspect that the remaining ~30% of the coral communities might have even higher particle deposition rates, rendering the presented estimates conservative. However, with progressing global change, ocean acidification and elevated temperatures will compromise coral calcification and increase bioerosion (Perry et al., 2018). This might lead to reduced microplastic deposition rates in the future.

Moreover, our extrapolation is based on a linear relationship between environmental microplastic concentrations and particle deposition rates. This is conceivable as we did not detect strong signs of altered physiology caused by the exposure (Reichert et al., 2019), yet needs to be addressed in future studies. Additionally, we only included particles that can be potentially ingested (based on the size range of the corallites), which likely differ for smaller or larger particles as well as for other shapes (e.g., fibers). We therefore emphasize that our results constitute the first step for assessing the quantity of microplastics deposited in tropical shallow-water reef-building corals. Future estimations require concentration- and polymer-dependent deposition rates using different particle sizes and shapes for an extensive range of coral species. Extrapolations might incorporate species-specific spatial distributions and deposition rates, as well as complementary findings from field evidence.

Previously, non-living sinks such as the deep-sea floor (Barrett et al., 2020), beach or mangrove sediments (Cózar et al., 2014; Martin et al., 2020; Van Cauwenberghe et al., 2015), or the Arctic sea ice (Obbard et al., 2014; Peeken et al., 2018) have been identified as long-term repositories for marine microplastic. We identify tropical shallow-water reef-building corals as the first living long-term sink for marine microplastic, which constitutes an important piece in the puzzle of the "missing plastic". Although fractions of the particles are released through bioerosion, microplastics are likely to become permanent parts of reef structures, with unknown consequences for the sensitive coral organisms and their skeletal integrity. This underlines the importance of coral reefs for the ecological balance of the world's oceans and demonstrates their role in removing microplastics from coral reef waters (both through direct deposition in the skeleton and indirect transfer to the sediments; de Smit et al., 2021). Their function as such is, however, threatened by the impacts of global change. Marine heatwaves decimate coral reefs worldwide (Hughes et al., 2018) and ocean acidification gradually compromises the accretion potential of new reef structures (Kvitt et al., 2015). Therefore, conservation strategies to protect coral reefs are necessary not only to mitigate the effects of climate change, but also to sustain the ecosystem service of corals as long-term sink for microplastic.

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AUTHORS' CONTRIBUTIONS

JR, AA, PS, and TW conceived the ideas and designed the methodology; JR, AA, NH, IM, and MR performed the experiment and collected the data; JR and MZ analyzed and interpreted the data; JR, MZ, and TW led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication. The authors declare to have no conflict of interest.

DATA AVAILABILITY STATEMENT

The analyzed data and 3D models of the studied corals are openly available at figshare.com at https://doi.org/10.6084/m9.figshare.14602311.

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