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Habitat-forming species trap microplastics into coastal sediment sinks

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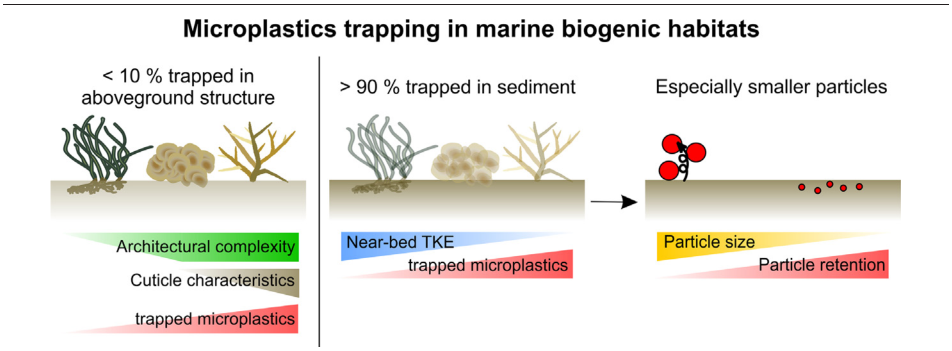
HIGHLIGHTS

- Biogenic habitats facilitate microplastic sequestration in coastal sediments.
- Plastic trapping mechanisms were studied in situ using a field flume.
- >90% of particles was trapped in bottom sediments.
- Microplastics sedimentation is exponentially related to near-bed TKE.
- Microplastics smaller than sediment particles are most likely to be retained.

GRAPHICAL ABSTRACT



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ABSTRACT

Nearshore biogenic habitats are known to trap sediments, and may therefore also accumulate biofouled, non-buoyant microplastics. Using a current-generating field flume (TiDyFLOW), we experimentally assessed the mechanisms of microplastic trapping of two size classes, 0.5 mm and 2.5 mm particle size, by three contrasting types of biogenic habitats: 1) seagrasses, 2) macroalgae, and 3) scleractinian corals. Results showed that benthic organisms with a complex architecture and rough surface – such as hard corals – trap the highest number of microplastics in their aboveground structure. Sediment was however the major microplastic sink, accumulating 1 to 2 orders of magnitude more microplastics than the benthic structure. Microplastic accumulation in the sediment could be explained by near-bed turbulent kinetic energy (TKE), indicating that this is governed by the same hydrodynamic processes leading to sediment trapping. Thus, the most valuable biogenic habitats in terms of nursery and coastal protection services also have the highest capacity of accumulating microplastics in their sediments. A significantly larger fraction of 0.5 mm particles was trapped in the sediment compared to 2.5 mm particles, because especially the smaller microplastics are entrained into the sediment. Present observations contribute to explaining why especially microplastics smaller than 1 mm are missing in surface waters.

1. Introduction

Plastic pollution is threatening marine ecosystems worldwide. Increasing plastic concentrations are found in open-ocean surface waters due increasing plastic production and input into the environment, and their longevity (Gewert et al., 2015; Jambeck et al., 2015;

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Lebreton et al., 2018). However, the estimated total amount of floating plastic debris only accounts for less than 1% of the total estimated plastic input (Van Sebille et al., 2015). Moreover, the size distribution of floating debris is skewed to larger particle sizes, while it would be expected that small particles are by far the most abundant, as without mass loss fewer large particles break down a larger number of smaller particles (Cózar et al., 2014). Especially plastics smaller than 1 mm, i.e. microplastics (Browne et al., 2007), are missing in ocean surface waters. This indicates the presence of extensive microplastics sinks (Law, 2017; Martí et al., 2017). Increasing microplastic concentrations, corresponding to the increase of plastic production and consumption, have indeed been found in coastal sediment deposits (Brandon et al., 2019; Martin et al., 2020). Quantities of microplastics in coastal sediments are often closely related to human population density and the presence of sources such as wastewater treatment plants, indicating that the nearshore zone is an important sink for microplastics from local sources (Browne et al., 2011).

Most previous research has focused on monitoring microplastic accumulation and deposition, but the fundamental questions about how the plastics are transported, accumulated and removed remain largely unanswered (Zhang, 2017). Plastics with a higher density than seawater (e.g. due to biofouling) can sink and be deposited in sediments. This can cause them to accumulate in the nearshore zone due to wind and wave dynamics (Forsberg et al., 2020). These areas often support habitat-forming benthic organisms, which may accumulate and retain plastic particles by either ingestion or adhesion to their surface (see e.g. Martin et al., 2019c; Seng et al., 2020). Biogenic canopies are known to trap particles into the sediment as they reduce the bottom shear stress, hampering sediment resuspension under stormy conditions (Gacia and Duarte, 2001). Given that high-density plastic particles behave similar to natural suspended particles, it can be deduced that, besides ingestion and surface adhesion, marine benthic organisms may also exacerbate the accumulation of plastic particles in the sediment by increasing particle deposition and retention. In a pioneer experiment, Agawin and Duarte (2002) calculated, using fluorescently-labelled 1 μm diameter plastic beads, that a tropical seagrass meadow to trap as much as 70% of the suspended particles present within the canopy in less than an hour, with the bulk (95%) of the particles deposited in the sediments. Higher concentration of microplastics have indeed been found in seagrass meadows (Huang et al., 2020), and long-term microplastic sequestration has been observed (Dahl et al., 2021), but equal concentrations have also been found in seagrasses and macroalgae compared to adjacent bare sediment (Cozzolino et al., 2020).

As of yet, to our knowledge, there are no studies investigating in situ the mechanisms of microplastics trapping in benthic structures and sediment under controlled flow conditions. This is necessary to be able to relate observations of microplastic accumulation to observed mechanisms on plastic particle and sediment transport in nearshore ecosystems. Experimental studies on plastic trapping mechanisms by benthic organisms are often conducted in laboratory mesocosms, which helped understand the mechanisms at play, as shown by flume experiments explaining high particles sedimentation rates in seagrass and macroalgal canopies (de los Santos et al., 2021; Hendriks et al., 2010, 2008; Lim et al., 2020). However, laboratory flume studies require transplantation of organisms which typically involves simplifications of the studied ecosystem, of which the consequences cannot always be quantified (de Smit et al., 2020). In this study we therefore used a current-generating field flume (the TiDyFLOW, James et al., 2019) to measure the accumulation of two types of microplastics (2.5 mm particle size and 0.5 mm particle size) onto the canopies and sediment of three contrasting tropical biogenic coastal habitats (corals, seagrasses, and macroalgae) under a unidirectional flow regime.

2. Methods

Plastic trapping experiments were conducted on common species from three typical tropical nearshore biogenic habitats: 1) *Enhalus acoroides*, a seagrass species characterizing a benthic structure with a smooth surface, i.e., a coriaceous cuticle, and low architectural complexity (Fig. S1A, Table S1, 3 replicates), 2) *Padina pavonica*, a brown macroalgae species with a rose-like shape creating benthic structures with a smooth surface, i.e., a membranous cuticle, and a more complex architecture (Fig. S1B, Table S1, 4 replicates) and 3) *Stylophora pistillata*, a hard coral species forming benthic structures with a rough surface, i.e., consisting of corallites, and complex architecture (Fig. S1C, Table 1, 4 replicates for trapping in the benthic structure and 3 for trapping in the sediment). In addition, control measurements were conducted on bare sediment (4 replicates). The measurements were conducted in February 2020 at two locations along the Red Sea coastline of the kingdom of Saudi Arabia: (22°19′36″; 39°04′14″) for *Padina pavonica*, and (22°22′52″; 39°07′54″) for *E. acoroides* and *S. pistillata*. For *E. acoroides* the experiments were conducted in a natural, undisturbed meadow. *Padina pavonica* and *S. pistillata* specimens were surrounded by other species at the field sites. Therefore these specimens were reallocated to an adjacent patch of bare sediment in order to obtain isolated individuals in the field flume experiments. Individuals were selected for size to maintain a similar total aboveground structure volume or surface area between the replicates and species (Table S1).

2.1. Experimental set-up

An in situ unidirectional flow channel (the TiDyFLOW, James et al., 2019) was used to generate constant hydrodynamic conditions under which microplastics transport and trapping was quantified. Two electrical boat propellers were used to generate turbulent flow (Fig. 1A). A mixture of 2.5 mm and 0.5 mm microplastics was seeded into the flume at a constant rate for 10 min and dispersed through the channel area through a 1-m closed section (Fig. 1B). A 0.5 m section with an open flume bottom contained the benthic structure and seafloor (Fig. 1C). A 2 m long plankton net with a 0.25 mm mesh was used to catch the plastic microspheres that were not retained to

Table 1
Canopy volume, surface area and surface area to volume (A/V) ratio of the benthic organisms used in the field flume experiments. The surface area of the *Enhalus acoroides* specimens in the sediment cores is given between brackets, and canopy height is reported including blade bending by flow, while other measurements are based on total blade length.

	Replicate #	Canopy / organism height (cm)	Canopy / organism volume (cm^3)	Surface area (cm^2)	A/V (-)
Enhalus acoroides	1	10.3	5769	276 (118)	0.048
	2	9.9	9063	557 (214)	0.061
	3	10.8	7706	557 (372)	0.072
	Mean ±SE	**10.33 ±0.45**	**7712 ±1655**	**463 ±162 (235 ±128)**	**0.061 ±0.012**
Padina pavonica	1	11.0	2777	1074	0.387
	2	12.1	2619	1029	0.393
	3	11.1	5834	1940	0.333
	4	16.2	3497	1278	0.369
	Mean ±SE	**12.6 ±2.45**	**3682 ±1485**	**1160 ±458**	**0.369 ±0.027**
Stylophora pistillata	1	10.0	3024	1175	0.389
	2	12.7	5319	1286	0.242
	3	12.5	5437	1126	0.207
	4	9.7	2743	921	0.336
	Mean ±SE	**11.23 ±1.59**	**4130 ±1446**	**1127 ±153**	**0.293 ±0.084**

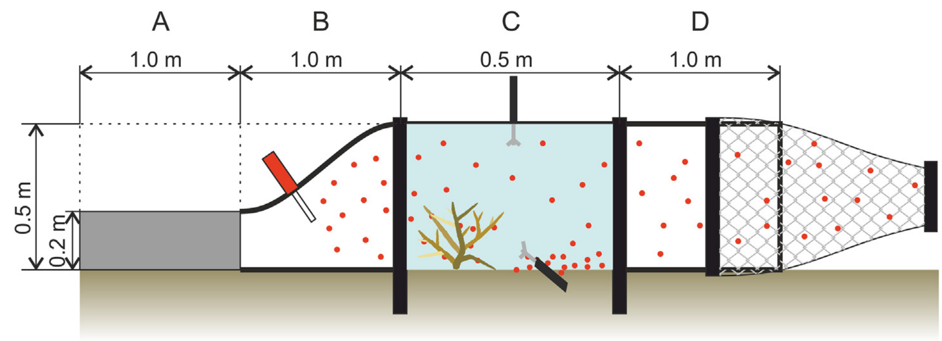

Fig. 1. The TiDyFLOW field flume set up used for the plastic trapping experiments. The flow chamber was slightly modified from James et al. (2019), to enable hosting a taller canopy and to be able to mount a plankton-net to the outflow side of the flume. A: Flume engine with 2 electrical boat propellers drive a 0.15 m s^{-1} flow. B: Plastics are seeded and dispersed in a 1-m closed section, here the channel height is increased to 0.5 m. C: Measurement section with open bottom contains the benthic structure and sediment. A downwards looking ADV probe measures average free-stream velocity, and a side-looking ADV measures near-bed flow and TKE. D: A plankton net attached to a 1-m closed section of the field flume catches plastic particles that were not retained by the benthic structure or trapped in the sediment.

prevent polluting the study area (Fig. 1D). The plankton net was attached to a second 1 m closed section behind the open flume section, which was added to avoid flow alteration inside the measurement section caused by deceleration and deflection of the flow as it enters the plankton net.

The flow velocity was set at 0.15 m s^{-1}, corresponding to the peak tidal flow velocity in the study area (Gharbi et al., 2018), which is typical for a microtidal system. The free-stream flow velocity above the benthic structure was measured at 25 Hz with an Acoustic Doppler Velocimeter (ADV, Nortek®) to verify the 0.15 m s^{-1} flow velocity setting. A peak tidal flow velocity was used as 1) microplastics are mobile under these conditions, 2) more water flows through the benthic structure, increasing the likelihood of plastic trapping, and 3) this determines to which extent microplastics are potentially washed out of the benthic structure or retained during peak flow conditions. In this study only unidirectional flow is considered, as the studied biogenic habitats are sheltered from waves.

A plastic mixture containing two size classes of polyethylene spheres (particle density 1070 kg m^{-3}) was used to investigate particle size dependency on plastic trapping both directly by the benthic structure and indirectly by sedimentation. The plastic was biofouled prior to the experiments for a period of at least 4 weeks to obtain surface properties similar to that of microplastics in the marine environment (Lobelle and Cunliffe, 2011). The microplastics mixture consisted of 50 ml of 2.5 mm spherical polyethylene particles, amounting to approximately 540 particles, and 14 ml of 0.5 mm polyethylene particles, amounting to approximately 20,000 particles. These specific particle sizes were selected in order to include larger and smaller particles than the 1 mm size threshold for microplastics missing from surface waters, and polyethylene was chosen as material because this is the most commonly found plastic in the Red Sea (Martí et al., 2017). In order to easily distinguish the microplastics from each other and from environmental plastics, white 2.5 mm and bright red 0.5 mm particles were used. A much smaller number of 2.5 mm particles was used in order to keep the total volume of each size class within the same order of magnitude. Given the 0.15 m s^{-1} velocity inside the flume, which corresponds to a discharge of 15 l s^{-1}, the concentration of 2.5 mm particles is 0.06 particles l^{-1} and for the 0.5 mm particles this is 2.22 particles l^{-1}. These concentrations are three orders of magnitude higher than typical concentrations found in the central Red Sea surface waters (Martin et al., 2019a). Floating plastics are however only a small fraction of plastics present in the marine environment, of which the majority is expected to sink. Therefore, the used concentrations are environmentally relevant. A side-viewing and top-viewing camera was used to observe the trapping mechanisms of the 2.5 mm plastic spheres and to count the number of particles that were retained on the sediment. The 0.5 mm particles were too small for detailed visual observation, and were therefore collected after the experiments with sediment corers.

A second ADV was placed 2 cm above the seabed, inside the *E. acoroides* canopy and behind the *P. pavonica* and *S. pistillata* specimens, to measure the near-bed flow velocity and turbulent kinetic energy (TKE) at 25 Hz. Near-bed TKE drives the retention and entrainment of sediment particles under benthic structures (Tinoco and Coco, 2018; Yang et al., 2016) and may thus drive the settlement and retention of plastic particles on the sediment. The TKE per unit volume (J m^{-3}) was calculated from the turbulence-generated fluctuations in the flow velocity signal as (Soulsby, 1983):

$$TKE = \frac{1}{2}\rho\left(\overline{u_{x'}}^2 + \overline{u_{y'}}^2 + \overline{u_{z'}}^2\right)$$

where $\overline{u_{x'}}$, $\overline{u_{y'}}$ and $\overline{u_{z'}}$ (m s^{-1}) are the root-mean-squares of the flow velocity fluctuations in x, y and z direction respectively, and ρ is the seawater density (1025 kg m^{-3}). The velocity fluctuations were extracted from the flow velocity signal by applying a 0.1 Hz high-pass 5th order Butterworth filter to remove minor changes in the mean velocity during the measurement period, and a 10 Hz low-pass 5th order Butterworth filter to remove frequencies where the signal was dominated by noise.

2.2. Sample collection & processing

After running the experiment, the *P. pavonica* and *S. pistillata* specimens with attached plastic particles were carefully removed from the flume and placed in sealed bags. The microplastics that were trapped inside the sediment were collected with three 10 cm diameter cores which were placed in the beginning, middle, and end of the measurement section. These cores also contained the *E. acoroides* specimens. After the specimens were removed from the flume and the cores were collected, the flume was set at maximum velocity (>0.5 m s^{-1}) for a 1 min period to remove any remaining plastic particles from the seabed and collect them in the plankton net. Because the seabed at the site with *P. pavonica* consisted of a thin (~5 cm) layer of sediment on top of hard substrate it was not possible to collect sediment samples without resuspending the sediment and dispersing 0.5 mm particles. Therefore, the sediment samples from the *P. pavonica* experiments were excluded from the analyses.

The sediment cores were sieved using 3 mm and 0.25 mm sieves in order to separate most of the sediment from the microplastics. Prior to sieving, the *E. acoroides* specimens were carefully removed from the sediment sample. The sediment samples were oven dried at 60 °C in order to loosen up the sediment and microplastics, and the amount of microplastics was counted directly from the sediment samples. The total fraction of 0.5 mm particles that was retained in the sediment of the measurement section was calculated by dividing the amount of 0.5 mm particles in the three sediment cores with the fraction of the measurement section covered by the sediment cores.

The *E. acoroides* and *P. pavonica* specimens were oven dried at 60 °C for at least 24 h and subsequently grinded into small fragments in order to extract the microplastics from the aboveground structures. Similar to the sediment samples, the amount of microplastics was counted manually. The *S. pistillata* specimens were bleached and washed. During this procedure some small fragments broke off and some of the microplastics were washed out. These were collected and counted separately to be added to the number of particles that were attached to the coral.

2.3. Morphological characterization of the studied species

Given that organism height was nearly equal between the species and replicates (Table S1), differences in trapping rates are expected to be caused by species architecture. In order to determine the effect of species architecture on plastic retention by the aboveground structure of the benthic organisms, the total surface area and surface area to volume ratio were determined (Table S1). Because the studied species were morphologically different, aboveground structure volume and surface area were estimated using different methods.

For the *E. acoroides* canopy, the total volume was estimated by multiplying the canopy height, defined as the mean blade length, by the total area of the measurement section covered by seagrass blades, which was measured from photographs of the top-viewing camera using ImageJ Version 1.53A. The total surface area was measured by multiplying the total length of all blades with the average blade width, which was 1.1 ± 0.1 cm. The surface area of the *E. acoroides* specimens inside the sediment cores was measured separately to obtain the surface area on which the counted plastic particles were trapped.

For *P. pavonica*, the total volume was calculated as the total area covered by the specimen multiplied by its maximum height. The total surface area was determined by breaking the specimens up in small, flat pieces and measuring their total area from photographs. Because the *P. pavonica* specimens from the plastic trapping experiments contained microplastics, these could not be broken up without risking loss of particles. Therefore, the surface area to volume ratio was measured for 4 additional *P. pavonica* specimens with a similar size range as the ones used for the plastic trapping experiments. This was sufficient to yield a linear canopy volume – surface area relation (Fig. S2), which was used to calculate the total surface area and surface area to volume ratio of the *P. pavonica* specimens used in the plastic trapping experiments.

The *S. pistillata* aboveground volume was measured following the same method described for the *P. pavonica* volume above. The surface area was quantified from 3-D models (Lavy et al., 2015). For all corals, at least 20 photographs, covering 360° of the colony, were taken. The images were then uploaded to the Autodesk ReCAP Version 5.0.5.58 software to calculate the surface area of each specimen.

2.4. Plastic stocks in the sediments of central Red Sea seagrass meadows

Concentrations and stocks of environmental plastics in the sediments of four independent central Red Sea seagrass meadows were estimated in order to obtain information on the plastic loads that are naturally trapped in this region, to examine if long-term microplastic sequestration in sediments occurs, as predicted from the processes leading to microplastic retention investigated experimentally in this study. The sediments under macroalgal and scattered corals in the nearshore Central Red Sea are often thin layers over the carbonate bed rock, and are thus not appropriate for long-term burial. Sediment samples were collected and processed as described in Martin et al. (2020), using 1.7 m long corers with a 6.26 cm inner diameter. The sediment cores were sliced in 1 cm thick samples, and 5 random samples from the top 20 cm of each core were processed for microplastic extraction by density separation. Each sediment sample and 700 ml of a 1.5 g cm^{-3} Zinc Chloride solution were added into a Sediment-Microplastic Isolation Unit, manufactured based on the design proposed by Coppock et al. (2017), to allow separation of plastics from sediments by floatation. The supernatant was filtered through a 25 μm nylon mesh and screened under a dissecting microscope in search of plastic. The putative plastic particles were confirmed through chemical characterization using Fourier-Transform Infrared Spectroscopy. Fibers were not counted due to the challenge of confirming their polymeric nature through chemical characterization posed by their small diameter. Relying on a visual characterization only may cause overestimation of their concentrations (Laptenok et al., 2020; Suaria et al., 2020). Moreover, they have not been included in the field experiments either. In general, due to the detection limits of the methodology (see Martin et al., 2020), only plastic pieces larger than 200 μm were considered.

2.5. Statistical analyses

ANOVAs were used to assess whether species had a significant effect on the retention of 0.5 mm plastic particles in aboveground structures and sediments of the studied biogenic habitats. Before the ANOVAs, normality and homogeneity of variance were assessed using Shapiro-Wilks and Bartlett tests respectively to meet the ANOVA assumptions. Data was log transformed if any of the assumptions were violated and was tested again for both assumptions. The number of 0.5 mm particles in aboveground structures, TKE, and the number of 0.5 mm and 2.5 mm particles in the sediment were log-transformed in order to obtain a normal distribution on the residuals and homogeneity of variance. Comparisons between species and species to control comparisons were assessed with a Tukey-Kramer HSD post hoc test.

3. Results

3.1. Plastic adhesion to the aboveground benthic structures

The fraction of released 0.5 mm particles that were attached to the aboveground structure of the benthic organisms differed approximately one order of magnitude between the species (Fig. 2A, ANOVA $p = 0.012$). *E. acoroides* trapped 0.02% to 0.06% of the released 0.5 mm particles, *P. pavonica* trapped 0.08% to 0.43%, and *S. pistillata* trapped 0.62% to 2.82% of the particles. A higher fraction of 0.5 mm particles was trapped on the *P. pavonica* specimens compared to the *E. acoroides* blades ($p = 0.02$), which are both highly flexible and have smooth surfaces. This indicates that species with a higher surface area to volume ratio (0.37 ± 0.03 and 0.06 ± 0.01 for *P. pavonica* and *E. acoroides* respectively, Table S1) are able to retain a higher number of plastic particles than species with a low surface area to volume ratio. However, the amount of trapped 0.5 mm particles per m^2 surface area is similar (Fig. 2B, $p = 0.99$). The increase particle trapping towards species with a more complex aboveground architecture, i.e., higher surface area to volume ratio, is thus caused by their larger exposed body surface compared to less architecturally complex organisms for a given seabed coverage, rather than differences in organism shape.

A significant number of microplastics were observed to be entangled in *S. pistillata* corallites (Fig. S3). Indeed, a higher fraction of 0.5 mm particles was trapped on the *S. pistillata* specimens compared to *P. pavonica* ($p = 0.02$), which are similar in architectural complexity (surface area to volume ratio of 0.29 ± 0.08 and 0.37 ± 0.03 for *S. pistillata* and *P. pavonica* respectively, Table S1). Given that both species also had similar total surface areas (1127 ± 153 and 1160 ± 458 cm^3 for *S. pistillata* and *P. pavonica* respectively, Table S1), the number of 0.5 mm particles trapped per m^2 surface area is significantly higher for *S. pistillata* (Fig. 2B, $p = 0.02$).

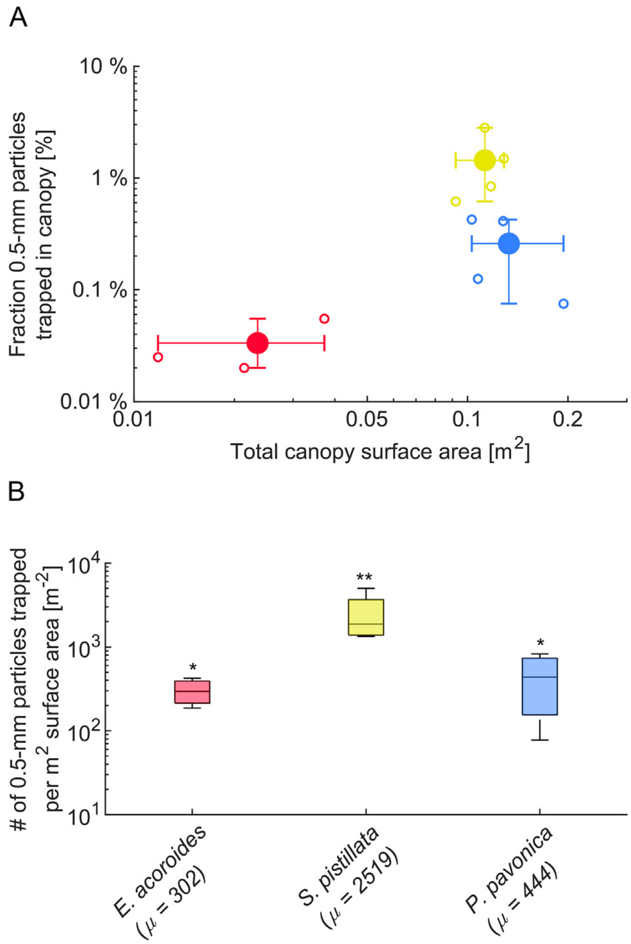

Fig. 2. A: Total canopy surface area against the fraction of 0.5 mm particles that were trapped on the canopy. Circles represent individual measurements and dots + error bars represent the means ± maximum/minimum. B: Boxplot (whiskers are min-max, boxes are between 1st and 3rd quantile, and lines are medians) of number of trapped 0.5 mm particles per m^2 canopy surface area, asterisks indicate groups that are statistically similar.

This indicates that surface properties, such as the presence of corallites for *S. pistillata*, influence microplastic retention in aboveground benthic structures.

In most of the experimental runs no 2.5 mm were particles trapped in the benthic structure. Two *E. acoroides* replicates contained one 2.5 mm particle, resulting in an overall trapping rate of 0.1 ± 0.12% and one *S. pistillata* specimen contained seven, resulting in an overall trapping rate of 0.33 ± 0.65%. There was however no apparent relation with species identity or aboveground architectural characteristics.

3.2. Plastic retention in the sediment

In general, the fraction of 0.5 mm particles that was trapped in the sediment (0.81–7.86% for *E. acoroides* and 16.58–22.04% for *S. pistillata*) was one to two orders of magnitude higher than the amount that was trapped in the aboveground structure (respectively 0.02–0.06% and 0.62–2.82%). This identifies the sediment as the main sink for microplastics in the studied biogenic habitats. The latter is confirmed by our measurements on environmental plastics >200 μm, which were indeed found in the sediments of central Red Sea seagrass meadows at concentrations of 13.4 ± 6.0 items kg^{-1} ($n = 20$ processed samples). Particularly, a mean of 1450 ± 900 pieces of plastics m^{-2} (corresponding to 80 ± 70 mg m^{-2}) are estimated stocked in the top 20 cm of sediments in the four sampled meadows (Table 2).

The fraction of 0.5 mm particles trapped in the sediment declines exponentially with increasing near-bed TKE (Fig. 3A, $R^2 = 0.93$). This decline is irrespective of the presence or absence of the studied species, as both the fraction of 0.5 mm particles trapped in the sediment for both the control experiments and *E. acoroides* and *S. pistillata* measurements follow the same relation with near-bed TKE. Thus, hydrodynamic conditions determine the extent to which microplastics may accumulate in the sediment. The near-bed TKE for *E. acoroides* and *P. pavonica* did not differ significantly from the near-bed TKE in the control experiments (Fig. 3B, p = 0.99 and 0.91 for *E. acoroides* and *P. pavonica* respectively). Neither did the fraction of 0.5 mm particles trapped in the sediment ($p = 0.99$ for *E. acoroides*). In contrast, the near-bed TKE for *S. pistillata* was an order of magnitude lower than for the control experiments (means ±SD respectively 0.14 ± 0.09 and 1.36 ± 1.08 J m^{-3}, $p = 0.01$), and the amount of trapped 0.5 mm particles was an order of magnitude higher ($p = 0.001$) indicating that rigid benthic structures are able to significantly reduce hydrodynamic energy and thereby facilitate the trapping of microplastics in the sediment.

No 2.5 mm plastic particles were present in the sediment of the control experiments, and the fraction of 2.5 mm particles that was trapped in the sediment for the benthic structure experiments was generally lower than the fraction of 0.5 mm plastic particles and highly variable (Fig. 4, $p = 0.05$). Similar to 0.5 mm particles, *S. pistillata* was able to trap a higher fraction than *E. acoroides* (means respectively 12.9 and 2.22%, $p = 0.03$). While 0.5 mm particles were found lodged in the sediment matrix in all sediment cores, i.e., distributed over the entire length of the flume channel, the 2.5 mm particles were only observed to settle in the wakes of the *S. pistillata* specimens and *E. acoroides* shoots without entering the sediment matrix, rendering them prone to resuspension. The median sediment grain size at the experimental location for *S. pistillata* and *E. acoroides* was 0.89 mm, i.e. larger than the 0.5 mm particles but smaller than the 2.5 mm particles. This suggests that sediment grain size in relation to the size of microplastics plays a fundamental role in microplastic retention in the seabed.

4. Discussion

4.1. Controls on plastic accumulation on aboveground benthic structures

This study provides experimental evidence that the potential of nearshore coastal biogenic habitats to serve as sinks for microplastics in the marine environment (see Fig. 5 for a conceptual model of the mechanisms involved). Architectural complexity and species cuticle

Table 2
Geographic coordinates and dominant species of the 4 seagrass meadows sampled for environmental microplastics. For each core, 5 random samples from the top 20 cm were processed and mean concentrations and stocks of environmental plastics were calculated.

Core ID	Coordinates (lat; long)	Species	Mean ±SE concentration (n kg^{-1}), n = 5 per core	Stocks (mg m^{-2})
1	22°56′2″; 38°52′49″	*Cymodocea* sp.	0	0
2	22°55′53″; 38°53′21″	*Halophila stipulacea*	0	0
3	22°22′51″; 39°07′54″	*Thalassodendron ciliatum*	27.5 ±11.8	281
4	22°16′53″; 39°05′07″	*Halophila stipulacea*	26.2 ± 19	24

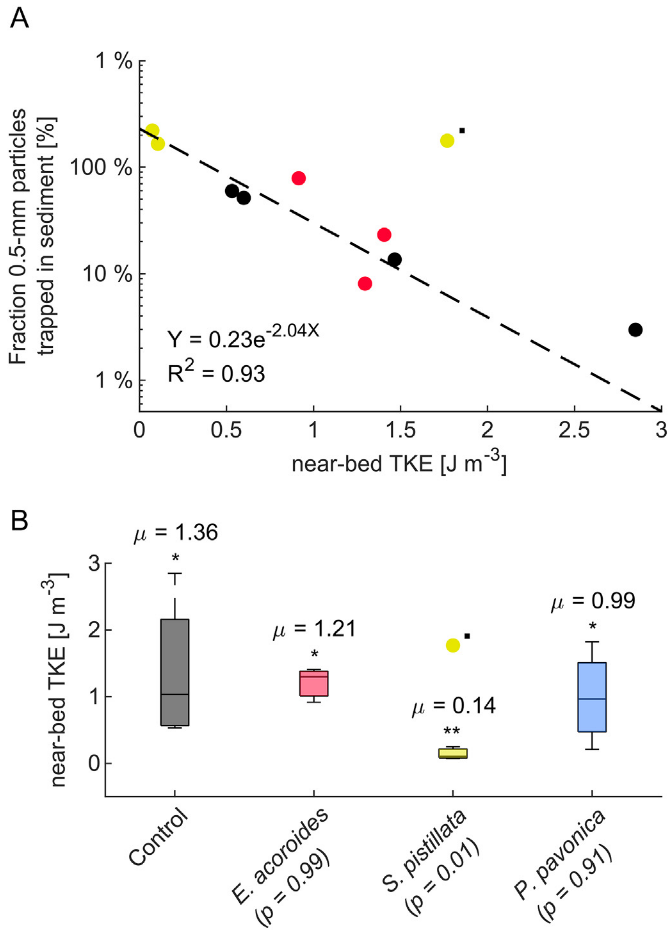

Fig. 3. A: Near-bed turbulent kinetic energy (TKE) against the fraction of 0.5 mm particles that were trapped on the sediment, colors correspond do species as indicated in B. B: Boxplot of species specific effects on near-bed TKE. *P*-values between brackets are from Tukey HSD post-hoc tests comparing the studied species with the control experiments on bare sediment. Asterisks indicate groups that are statistically similar. One outlier of *S. pistillata* (indicated with a black square) was excluded from the regression in A and statistical tests in B. In this replicate the specimens were less tall (see Table S1, replicate 4), hence the acoustic Doppler velocimeter possibly measured the flow above the near-bed layer where TKE is strongly reduced.

characteristics were identified as key contributors to plastic adhesion to benthic structures. Architecturally complex species, such as *P. pavonica*, provide a larger exposed body surface for a given seabed coverage.

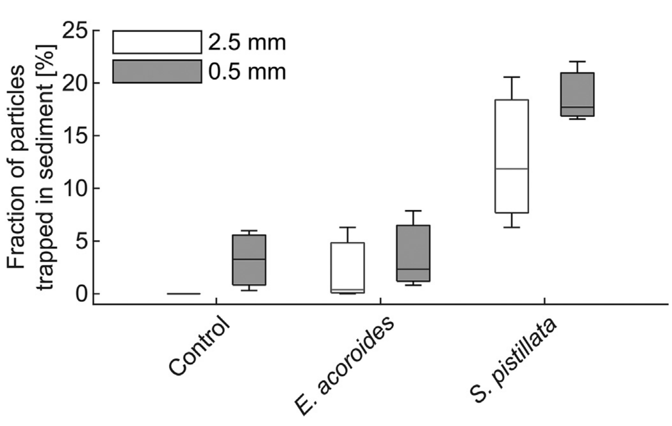

Fig. 4. Boxplot (min-max, 1st and 3rd quantiles, and median) of the fraction of 0.5 mm and 2.5 mm particles trapped in the sediment.

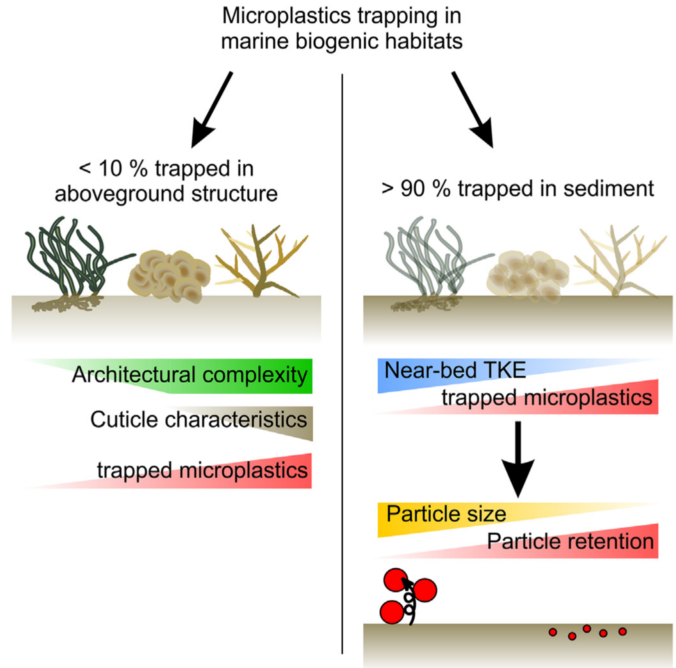

Fig. 5. Overview of plastic trapping and retention mechanisms in biogenic habitats and their underneath sediments.

Hence, they retain a higher number of plastic particles in their aboveground body compared species with a smaller aboveground body surface for the same seabed coverage, such as *E. acoroides*. The number of particles trapped per m^2 of aboveground body area however did not change with architectural complexity, indicating that it does not influence plastic trapping efficiency. *S. pistillata* retained more microplastic particles in its aboveground body compared to *P. pavonica*, which is similar in size and architectural complexity. Experiments were conducted during daytime, when polyps are generally retracted. This indicates that cuticle characteristics, in this case the presence of corallites, influence microplastic trapping efficiency by physical entanglement on the surfaces of benthic organisms.

In this study only passive microplastic uptake by nearshore biogenic habitats is considered. Active uptake by suspension-feeding may however exacerbate plastic accumulation on benthic structures in addition to passive retainment, especially under high flow conditions which promotes microplastic ingestion and impairs surface adhesion due to frequent particle resuspension within the flow boundary layer (Lim et al., 2020). Previous studies have reported plastic ingestion rates of suspension-feeding benthic organisms ranging from 2 to 40% of the removal rates due to surface adhesion (Arossa et al., 2019; Corona et al., 2020; Martin et al., 2019c). However, given that the benthic structures only contained <10% of the total load of trapped microplastics, active uptake and adhesion likely only plays a minor role in total microplastic trapping (i.e., both on the aboveground structure and in the sediment) in habitats formed by suspension-feeding organisms.

4.2. Controls on plastic accumulation in sediments

Sediment was observed to be the major microplastic sink, trapping 1–2 orders of magnitude more microplastics than what was found in the aboveground portion of the studied organisms. Hydrodynamic conditions, and in particular the near-bed TKE, determined the settling of microplastics in the sediment. This confirms previously observed sediment-like behavior of plastic particles with considerably higher density than seawater in an unvegetated ecosystem (Forsberg et al., 2020). In the case of biogenic habitats, sediment settlement and entrainment is governed by the near-bed TKE (Tinoco and Coco, 2018; Yang et al., 2016), which in turn is affected by energy dissipation by physical obstacles represented by benthic organisms. Thus, the decreasing fraction of microplastics trapped in the sediment with increasing near-bed TKE observed in this study shows that plastic particles behave similarly to other natural suspended particles. While this study is limited to unidirectional currents, the prevailing process in biogenic habitats sheltered from waves, similar mechanisms are expected for wave exposed habitats given that the hydrodynamic processes leading to particle trapping and entrainment in biogenic habitats are similar (Tinoco and Coco, 2018; Yang et al., 2016). Net horizontal transport of particles in the near-bed zone is however limited to wave asymmetry induced particle transport or transport by residual currents. Therefore, even in wave exposed environments unidirectional currents are important for the transport and accumulation of microplastics. However, waves are generally more efficient in generating near-bed TKE than currents, especially under flexible canopies, reducing the flow velocity needed for particle resuspension (de Smit et al., 2020). Therefore, the addition of waves may reduce particle trapping rates by hampering sedimentation and increasing the likelihood of resuspension.

Corals, and probably other rigid and architecturally complex aboveground structures, provide the largest near-bed TKE reduction and therefore retained the highest number of microplastics in the sediment. Sediments adjacent to coral reefs have indeed been identified as major microplastic sinks (Jeyasanta et al., 2020). In contrast, *E. acoroides* did not prompt increased microplastic retention in the sediment compared to the unvegetated control experiment, as the near-bed TKE was similar. Previous observations have indeed shown that seagrasses and macroalgae did not accumulate more microplastics in their sediments than adjacent unvegetated areas (Cozzolino et al., 2020), though a larger plastic accumulation in seagrass meadows compared to bare sediments has also been observed (Huang et al., 2020). This may be explained by the low seagrass density, 80 $\pm$ 36 shoots m^{-2} in this study and 312 $\pm$ 132 shoots m^{-2} in Cozzolino et al., 2020, which impairs their near-bed flow attenuating effect. Indeed, concentrations of environmental microplastics >200 μm in the seagrass meadows sampled in the central Red Sea and in those sampled by Cozzolino et al. (2020), were both very low (13.4 $\pm$ 6 and 2.8 $\pm$ 1.0 items kg^{-1} excluding fibers, respectively). Denser seagrass meadows that are able to significantly reduce near-bed TKE may instead accumulate larger numbers of microplastics than less dense seagrass (de los Santos et al., 2021). The role of the canopy in reducing the near-bed TKE and enhancing plastic deposition and accumulation in sediments is further demonstrated by the large quantities of plastics found in the sediments of *S. pistillata*, that consistently reduced the near-bed flow velocity and TKE compared to the less rigid canopies of seagrasses and macroalgae. Structural complexity is a key trait for the nursery function of a coastal habitat (Heck et al., 2003; Lefcheck et al., 2019), and canopy stiffness is a key trait for coastal protection services (Bouma et al., 2005). Therefore, the most valuable ecosystems in terms of nursery and coastal protection services also are those with the highest potential of accumulating large amounts of microplastics, thereby removing them from the pelagic food web, although possibly accessible to infauna.

4.3. Sediment as a permanent sink for microplastics

A relatively high fraction of plastic particles was trapped considering that the portion of the seabed enclosed within the field flume was only 0.5 m in length. It is therefore likely that spatially extensive biogenic habitats are able to capture all microplastics present in the water flowing through their aboveground structure, under favorable hydrodynamic conditions. The accumulation of microplastics in biogenic habitats appears to be determined by 1) the likelihood that microplastics in the water column encounter an aboveground benthic structure, and 2) the capacity of biogenic habitats to trap particles in their aboveground structures and retain these particles in their sediments. The former depends on flow dynamics. For example, a high flow velocity over a biogenic habitat may induce flow separation and reduce the frontal area of flexible benthic structures (Järvelä, 2005), thereby potentially reducing microplastic accumulation (de los Santos et al., 2021; Järvelä, 2005; Peralta et al., 2008). The results of this study suggest that the latter is a direct function of near-bed TKE reduction by the benthic structure and the sediment particle size in relation to the microplastic particle size, as a larger fraction of 0.5 mm particles was retained in the sediment compared to 2.5 mm particles.

The observed influence of microplastic particle size on particle retention is likely the result of hiding-exposure mechanisms occurring in sediment mixtures consisting of multiple particle sizes. The smaller particles are sheltered, i.e. "hidden", by larger particles, which in turn are exposed. Such sheltering increases the erosion resistance of the finer sediment fraction and decreases that of the coarser fraction (Einstein, 1950). Given that low-density particles such as microplastics by definition have a low erosion resistance, sheltering by larger sediment particles may be of pivotal importance to microplastic retention in the sediment, eventually leading to their burial. The assessment that seagrass sediments contained a mean of 80 $\pm$ 70 mg plastics m^{-2} within the top 20 cm of sediments, provides evidence that the processes experimentally resolved in the field experiments are indeed in operation in the Red Sea, leading seagrass meadows to act as sinks for microplastics there. Indeed, 1 m^2 of seagrass meadow contains as much microplastic stock within the top 20 cm as 8 ha of Red Sea surface waters, where the mean concentration is about 1 g km^{-2} (Martí et al., 2017).

While the results of this study suggest that coarser sediment particles have a higher potential to retain smaller microplastic particles, other studies report either no differences in microplastic concentration with grain size, or a higher concentration in finer sediments or sediments with high organic matter content (see Harris, 2020 for a review). The in situ hydrodynamic control used in this study disentangles hydrodynamic conditions from sediment properties. In natural systems however, fine sediments and sediments with high organic matter content generally occur in depositional environments with calm hydrodynamic conditions. Hence, while these sediments have a lower microplastic retention potential, the hydrodynamic conditions promote microplastic settlement. On the other hand, coarse sediments have a higher microplastic retention potential but are often accompanied by higher flow or wave strength, preventing the settlement of microplastics even though they are favorable for microplastic retention from a purely sedimentary perspective. It is therefore crucial to consider both microplastic trapping mechanisms observed from controlled experiments, and observations on microplastic concentrations in the environment, combined with information on hydrodynamics, in order to correctly interpret the microplastic trapping and retention potential of nearshore biogenic habitats.

4.4. Conclusions

Biogenic habitats bring high value to coastal ecosystems, acting as sinks for organic carbon in their sediments, partly driven by the role of their canopies in trapping seston particles (Duarte et al., 2013). We experimentally demonstrated that seagrass, macroalgae and corals facilitate microplastic accumulation, and burial in the underneath sediment. This adds to the recently demonstrated role of mangroves as significant sinks for microplastics (Martin et al., 2019b). The studied biogenic habitats facilitate microplastic trapping in two ways: 1) adhesion of particles to their canopy, which is positively correlated to architectural complexity and cuticle characteristics, and 2) promoting microplastic settlement on the sediment, which accounted for >90% of the trapped particles and is positively related to the ability of the biogenic habitat to reduce near-bed TKE. This settlement may result in permanent trapping when plastic particles are of similar size or smaller than the sediment grain size though hiding-exposure mechanisms. The most valuable biogenic habitats in terms of nursery and coastal protection surfaces are thus also the ones with the highest potential to accumulate large amounts of microplastics, mainly in their sediments, removing them from the pelagic food web.

CRediT authorship contribution statement

Jaco C. de Smit: Conceptualization, Methodology, Formal analysis, Investigation, Data curation, Visualization, Writing – Original Draft. **Andrea Anton:** Methodology, Investigation, Statistical analysis, Writing – Review & Editing. **Cecilia Martin:** Methodology, Investigation, Writing – Review & Editing. **Susann Rossbach:** Methodology, Investigation, Writing – Review & Editing. **Tjeerd J. Bouma:** Conceptualization, Writing – Review & Editing, Funding acquisition, Project administration. **Carlos M. Duarte:** Conceptualization, Writing – Review & Editing, Funding acquisition, Project administration.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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AppendixA

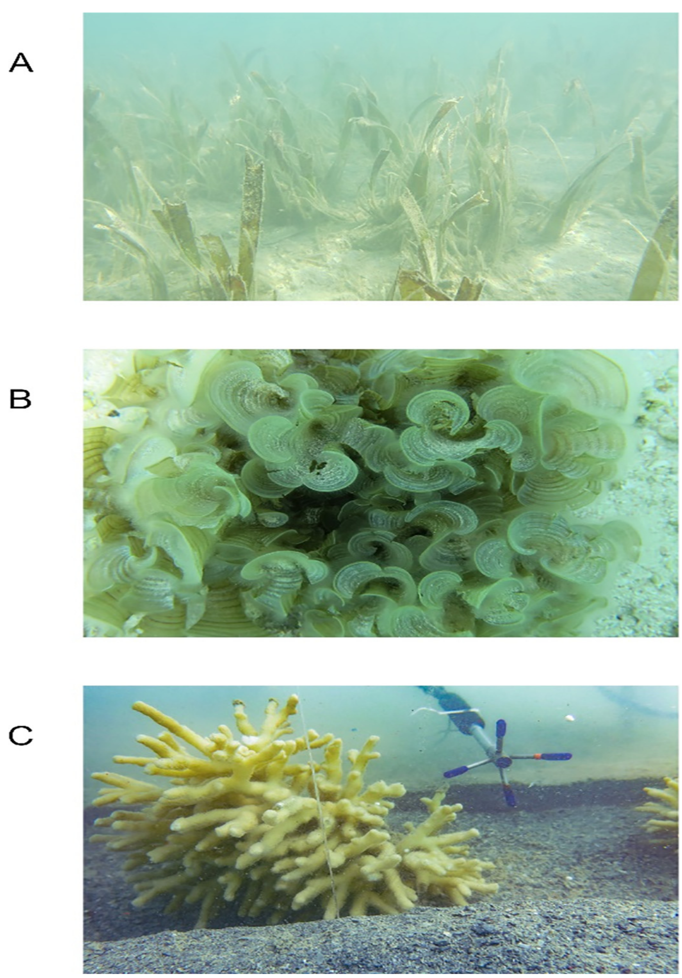

Figure A1. The benthic organisms used in the field flume experiments. A: *Enhalus acoroides*, B: *Padina pavonica*, C: *Stylophora pistillata*.

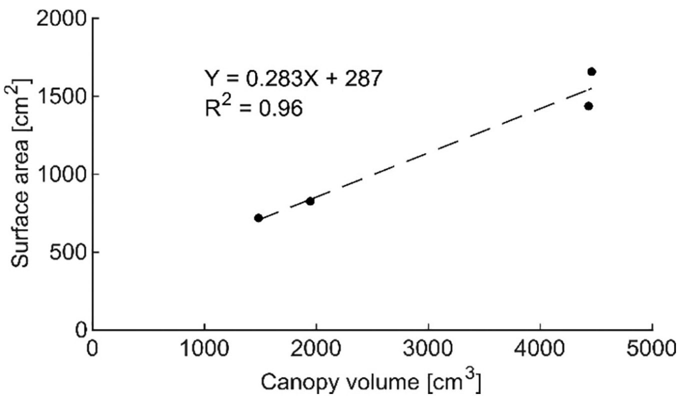

Figure A2. Canopy volume – surface area relation for *P. pavonica* used to calculate total surface area and surface area to volume ratio for the *P. pavonica* specimens used in the field flume experiments.

Figure A3. Plastic retention on the surface of a *S. pistillata* specimen. Red dots are 0.5 mm plastic particles.

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