Positive and Negative Species Interactions Shape Recruitment Patterns of a Range Expanding Native Alga

Sofie E. Voerman[1,2,3]*[†], Paul E. Gribben[2,3] and Tim M. Glasby[4]

[1] School of Life Sciences, University of Technology Sydney, Sydney, NSW, Australia, [2] Centre for Marine Science and Innovation, School of Biological, Earth and Environmental Sciences, University of New South Wales, Kensington, NSW, Australia, [3] Sydney Institute of Marine Science, Mosman, NSW, Australia, [4] Port Stephens Fisheries Institute, New South Wales Department of Primary Industries, Nelson Bay, NSW, Australia

A species' ability to spread is in part governed by the extent to which recipient habitats either resist, tolerate or promote the species' recruitment. In disturbed marine environments, there is a general trend for the loss of algal canopies, thought to resist invasion, toward algal turf or rock barrens habitat. This study tested whether the spread of the range-expanding native macroalga *Caulerpa filiformis* was resisted by algal canopies but facilitated by algal turf or barrens habitats. Large-scale field surveys generally supported the predicted recruitment patterns, with *C. filiformis* recruits being most abundant on turf (but not barrens) and absent under kelp canopies. However, a discrepancy existed between different structural forms of turf, with the positive association holding true only for geniculate corallines, not filamentous turf. Secondly, a laboratory experiment tested whether the physical structure and/or the sediment-trapping properties of coralline turf influenced the recruitment success of *C. filiformis*. Whilst the structural complexity of turf aided overall recruitment performance (i.e., increased rhizoid production, attachment speed, success, and strength), a positive influence of turf-derived sediment on recruits' growth was less obvious, at least over 10 days. The high morphological plasticity of *C. filiformis* propagules resulted in possible benefits of faster or stronger attachment of more developed propagules being only temporary, and that recruitment may be regulated in accordance with habitat preference. Finally, a field experiment confirmed the observed positive role of turf and the negative influence of algal canopies in the short-term, however, adverse environmental conditions in the longer-term resulted in the loss of most fragments. In conclusion, this study demonstrated the importance of both positive and negative species interactions for the recruitment success of a native alga, suggesting that a shift from kelp to turf algae can initiate further community change.

Keywords: native invader, kelp, barrens, caulerpa, turf, community shifts

INTRODUCTION

Foundation species (those that form for example coral reefs, mangrove, and kelp forests) shape the functioning of entire ecosystems (Stachowicz, 2001). They often support unique communities of high biodiversity and productivity and perform important ecosystem functions including the provision of biotic resistance to invasion (e.g., Moberg and Folke, 1999; Dugan et al., 2011; Lee et al., 2014; Bennett et al., 2016; South and Thomsen, 2016; Gribben et al., 2018; Uyà et al., 2018). However, human disturbances acting at a range of scales are eroding the resistance and resilience of foundation species, often leading to phase shifts (or alternative stable states) in which foundation species are lost or replaced by more stress-tolerant species that may differ in their functioning (Hughes et al., 2007; Norström et al., 2009; Montefalcone et al., 2015; O'Brien and Scheibling, 2018). These resulting alternative communities may then facilitate further community change (Didham et al., 2007; Tylianakis et al., 2008). While the replacement of foundation species by altered communities has received considerable attention, the follow-on consequences of altered communities driving further community change are less well understood.

Globally, marine ecosystems have experienced large losses of large canopy-forming macroalgae such as kelp (Thibaut et al., 2005; Coleman et al., 2008; Voerman et al., 2013; Thomsen et al., 2019; Wernberg et al., 2019). Overgrazing by sea urchins can result in a shift from macroalgae to structurally simpler crustose coralline or bare rock 'barren' habitats (Andrew and Underwood, 1993; Benedetti-Cecchi et al., 1998; Ling, 2008), that can persist for decades (Filbee-Dexter and Scheibling, 2014; Glasby and Gibson, 2020). Alternatively, the loss of macroalgae due to abiotic (e.g., increased temperature, nutrients, sedimentation) or biotic (e.g., overgrazing) disturbances frees up limiting resources such as light and space that can allow for a transition to more stress-tolerant and previously sub-dominant species. For example, loss of kelp can lead to invasive species becoming dominant on rocky reefs (Valentine and Johnson, 2003; Britton−Simmons and Abbott, 2008; Thompson and Schiel, 2012), or lead to a transition to smaller turf-forming algae (hereafter turf) (Airoldi and Beck, 2007; Connell et al., 2008; Moy and Christie, 2012; Filbee-Dexter and Wernberg, 2018; O'Brien and Scheibling, 2018; Straub et al., 2019).

Whilst turf is often regarded as an alternate stable state, it can also promote the recruitment and spread of invaders. For example, turf can promote the recruitment and spread of several invasive macroalgae including *Caulerpa* spp. and *Codium fragile* ssp. *fragile* (Ceccherelli et al., 2002; Watanabe et al., 2009; Gennaro and Piazzi, 2014), although this positive association does not exist for all invasive macroalgae (Arenas et al., 2006; Britton−Simmons and Abbott, 2008). Similarly, recruitment of *Undaria pinnatifida* can be facilitated by removal of native canopies, especially if the understory is dominated by coralline turf (Thompson and Schiel, 2012). This suggests that turf may have important positive interactions by facilitating the proliferation of invasive species. Many native algae are also spreading (e.g.,

Díez et al., 2012; Yesson et al., 2015), but whether they are directly (provision of resources) or indirectly (e.g., via turf) facilitated by the loss of foundation species has not been explored.

Turf habitat can enhance the recruitment of other species via several mechanisms. The physical structure of turf can enhance trapping of vegetative propagules (fragments) of invasive *C. fragile* (Watanabe et al., 2009) or *C. cylindracea* (Bulleri and Benedetti-Cecchi, 2008). The biogeochemical environment created by turf via trapping of nutrient-rich sediment may also benefit rhizoidal algae that are able to utilize increased nutrient concentrations in the sediment (Williams, 1984). We hypothesize that the physical structure will promote propagule attachment, whereas the presence of sediments will contribute to subsequent growth of recruited fragments. To date, however, no studies have parsed the relative importance of sediment properties versus turf physical attributes in facilitating spreading species.

Many of the world's most invasive macrophytes spread vegetatively via asexual fragmentation (Wright, 2005; Williams and Smith, 2007). The recruitment success of macroalgal fragments (i.e., propagules) can be influenced by their quality (van Kleunen et al., 2015; Estrada et al., 2016), the recipient environment (Gribben et al., 2017; Gribben et al., 2018), and the interaction between the two (Bulleri et al., 2018, 2019). For example, larger, more intact fragments such as those with intact rhizoid structures generally show higher recruitment potential (Khou et al., 2007; Wu et al., 2007; Uyà et al., 2018). In addition, in disturbed seagrass habitats, nominally good (with fronds and rhizoids) and poor quality (with fronds but without rhizoids) fragments of *Caulerpa taxifolia* established, whereas only good quality fragments established in healthy seagrass beds (Bulleri et al., 2019). Similarly, we predict that fragments with rhizome + rhizoids structures will have higher recruitment rates and growth because of quicker attachment rates and increased ability to utilize nutrients in sediments trapped by turfs.

On shallow rocky shores in New South Wales (NSW), Australia, the native green alga *C. filiformis* has become locally more abundant and has spread outside its known historic distribution. Previously described as having a restricted distribution (approximately 200 km of coastline), *C. filiformis* has spread 500 km north of its known traditional range and is now found across > 700 km of coastline (see Glasby et al., 2015 for an overview). *C. filiformis* is the dominant habitat-forming species on many shallow rocky reefs along the coast, where it can form extensive monospecific stands of >1000 m^2 (Glasby et al., 2015; Voerman et al., 2017). The spread of the alga can have large impacts on associated flora and invertebrate fauna (Voerman et al., 2014; Lanham et al., 2015; Voerman, 2017), with weaker effects on herbivorous fish assemblages (Bradley et al., 2018). The mechanisms behind the localized increases in abundance of the alga are unknown (Glasby et al., 2015). However, disturbance to canopies of competing algal species can facilitate the spread of established patches of *C. filiformis* as it is a superior competitor for space (Zhang et al., 2014), and historical losses of a large fucoid around the Sydney metropolitan may have contributed to *C. filiformis'* increased abundance (Glasby et al., 2015). Moreover,

sediment disturbance appears to contribute to the success of the species when occurring on rocky reefs (Voerman et al., 2019), however, the alga is rarely found on sandy substrate itself potentially due to the reduced recruitment on unstable substrate (Voerman et al., 2017). *C. filiformis* reproduces vegetatively via fragmentation (Zhang et al., 2014), which has likely contributed to its current range expansion (Glasby et al., 2015). Fragment morphologies are highly variable, with both fronds with and without rhizome + rhizoid structures present (Khou et al., 2007). Thousands of suspended fragments can be found at a site (Khou et al., 2007), yet how recruitment success may be influenced by propagule quality, or how this may interact with features of the recipient habitat, remains largely unknown.

This study investigated the roles of canopy-forming habitats (kelp and *Sargassum*) and less structured habitats (turf and barrens, which represent degraded habitats in some situations), in the recruitment success of *C. filiformis*. In addition, the mechanisms behind the expected positive role of turf in facilitating *C. filiformis* recruitment were explored, as was the role of propagule quality (i.e., rhizome presence). First, habitat associations of *C. filiformis'* recruits in the field were examined to test the prediction that recruitment is enhanced by turf and reduced by macroalgal canopies. Secondly, a laboratory experiment tested hypotheses about the positive roles of substrate structure on *C. filiformis* attachment success (measured as fragment attachment success, speed and strength) and turf-derived sediment on *C. filiformis* growth. Those positive associations were predicted to be enhanced by the presence of rhizome + rhizoids on *C. filiformis* fragments. Finally, this study further explored the observed habitat associations by experimentally testing the retention success of *C. filiformis* fragments in macroalgal canopies (kelp, *Sargassum*) vs. turf and barren habitats under field conditions.

MATERIALS AND METHODS

Study Species and Sites

Caulerpa filiformis (Suhr) Hering is a green macroalga, with long, thin fronds up to ∼ 70 cm in length (Voerman et al., 2019). Once established, populations consist of a dense network of creeping rhizomes with rhizoid clusters that attach the alga to the substrate (Khou et al., 2007). It has a disjunct distribution along ∼ 700 km of the warm temperate coast of eastern Australia where it occurs primarily subtidal down to ∼ 7 m and also occurs in low intertidal areas (Zhang et al., 2014; Glasby et al., 2015). The alga is principally found on hard (rock) substrate but can also occur on soft (coarse sand) substrate (Voerman et al., 2017). Disturbed fragments (hereafter propagules) predominantly consist of partial or full fronds, with or without a rhizome present, and are predominantly 5–15 cm in frond length (Voerman, unpublished data). *C. filiformis* has a siphonous body structure, which is highly plastic, allowing for rapid growth and creation of new fronds and/or rhizoid structures (Khou et al., 2007), wound healing and fast fragment propagation (Walters and Smith, 1994; Smith and Walters, 1999).

The six sites surveyed (**Figure 1**) encompassed the full distribution of *C. filiformis* in NSW (Glasby et al., 2015) and all contained large beds of *C. filiformis* (Voerman, 2017). All sites were positioned along the exposed coastline, shallow sloping and contained a mixture of the habitats investigated (**Table 1**).

Density of *C. filiformis* Recruits Across Sites and Habitats

To investigate the density of *C. filiformis'* recruits across sites and to test the prediction that recruitment is enhanced by turf habitat and reduced by macroalgal canopies, the six sites were sampled during August–December 2013. Recruits were
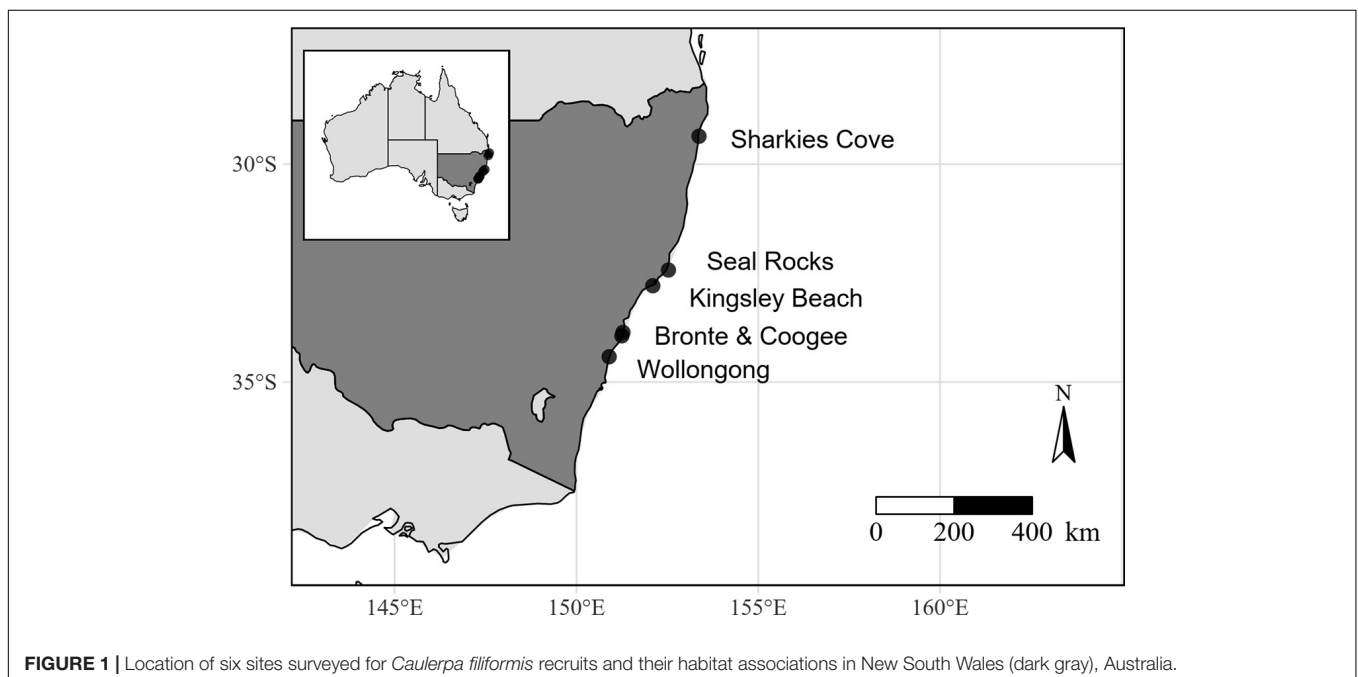

FIGURE 1 | Location of six sites surveyed for *Caulerpa filiformis* recruits and their habitat associations in New South Wales (dark gray), Australia.

TABLE 1 | Recipient habitats investigated for *C. filiformis* recruit density.

Habitat	Description
Barren	Rocky substrate with or without some encrusting algae present and no or very little sediment.
Rock + sand (R + S)	Rocky substrate with a 1–25 cm sediment veneer.
Sand	Sandy substrate outside the rocky reef.
Pebble *	Pebbles < 15 cm diameter
Sessile fauna *	Including barnacles, *Pyura* spp. and sponges.
Geniculate coralline turf (Coralline turf)	Red geniculate coralline algae – predominantly *Corallina* spp. < 5 cm tall, covering > 50% of substrate, often containing sediment. This habitat could also contain some filamentous algae.
Filamentous turf (Fil. turf)	Filamentous brown and green turfing algae < 5 cm tall covering > 50% of substrate, species unidentified, often containing sediment.
Foliose brown algae (Small brown)	Foliose brown algae < 15 cm tall, e.g., *Dictyota* spp., *Zonaria* spp., and *Padina* spp. Sometimes containing small amounts of sediment.
Kelp	80–100% *Ecklonia radiata* canopy cover on rocky reef with some encrusting algae, with or without sessile fauna present. No turf in understory. No or very little sediment.
Sargassum	80–100% *Sargassum* spp. canopy cover over on rocky reef, often with a dense understory of geniculate coralline turf. Sediment presence and abundance variable.

Asterisked habitats were not considered further because habitats were rare (<2% of sampled area).

defined as small individual fragments (<5 cm diameter substrate cover with a maximum of five fronds) that had attached to the substrate (**Figure 2**). Whilst size is not a measure of recruitment, individual fragments of this size have not yet expanded horizontally, and likely represent fragments that have recently attached to the substrate.

Recruits were enumerated in transects (1 m wide, $n = 4$) orientated perpendicular to the shoreline from the low-tide mark to >6 m beyond the edge of the reef (i.e., onto sand). Transects covered a similar depth range (between 0.5 and 6.5 m below low tide level) but varied in length from 30 to 60 m depending on the width of the reef. At two sites (Seal Rocks and Wollongong), transects stopped at 30 m without reaching the end of the reef due to unfavorable sampling conditions. For each recruit encountered, we noted the habitat to which it was attached (see **Table 1** for habitat classifications). New recruits in dense adult *C. filiformis* beds could not be distinguished, so this algal habitat was not sampled.

Information on the relative area of habitats surveyed was used to explain variation in recruit densities. The area of recipient habitat surveyed was estimated as a function of the known percentage cover of each habitat per site quantified from quadrats positioned along the same transects (one 50 × 50 cm quadrat every 3 m, $n = 43 – 95$ per site, see Voerman et al., 2017), multiplied by the area covered by the entire transects surveyed in this study. Recruit density at a site was calculated as a function of the entire rocky reef sampled (i.e., excluding the area covered by adult *C. filiformis* and sand outside the rocky reef). Recruit density per habitat was calculated as a function of the total

FIGURE 2 | Multiple *Caulerpa filiformis* recruits within coralline turf habitat. Image width ~ 40 cm.

area of the individual habitat surveyed at each site (# recruits observed/habitat area surveyed).

ANOVA was used to test for differences in the association of *C. filiformis* recruits among habitats. Only sites with recruits encountered were included in the analysis. Model assumptions were tested with the "GVLMA" package (Pena and Slate, 2014), and adjustments were made to comply with model assumptions when required. Significant treatment effects were further investigated with *Post Hoc* Ls means comparisons ("Lsmeans" package, Lenth, 2016). All statistics were conducted in R version 3.5.1 (R Core Team., 2018).

Effects of Turf Habitat and Propagule Quality on Recruitment

Results from the habitat sampling suggested an important role of turf (geniculate corallines) in promoting fragment recruitment. To explore this further, we investigated whether *C. filiformis* attachment success (attachment speed and strength) and fragment growth (biomass increase and changes in morphology) were related to the physical properties of the turf (structure) and/or the properties of the sediment of the turf-sediment complex. We also tested how these properties interacted with quality (presence or absence of rhizome) of *C. filiformis* propagules.

Seven substrate treatments were created to tease apart the potential effects of substrate structure from the effects of sediment on *C. filiformis* attachment and growth (**Table 2**). Treatments with physical structure (either natural or artificial) were predicted to enhance *C. filiformis* attachment and a treatment with turf-derived sediment was predicted to enhance subsequent growth of *C. filiformis*. To investigate the effect of propagule quality on recruitment performance, two types of *C. filiformis* fragments were used; high-quality propagules consisting of fragments with rhizome and rhizoids present or low-quality propagules where

TABLE 2 | Substrate treatments and abbreviations.

Treatment	Abbreviation	Structure	Sediment	Prediction	
				Attachment	Growth
Rock with natural turf containing sediment	R + T + S	Natural	Yes	+	+
Rock with natural turf, sediment removed	R + T − S	Natural	No	+	0
Rock	R	No	No	0	0
Rock with turf removed (procedural control)	R − T	No	No	0	0
Artificial turf	Artificial T	Artificial	No	+	0
Artificial rock	Artificial R	No	No	0	0
Sand	S	No	No	−	0

Predictions indicate the predicted relative performance (negative −; neutral 0; positive +) of attachment or growth of C. filiformis propagules among treatments.

rhizomes were removed. The two types of propagules were added separately to each of the treatments listed in **Table 2**. The general prediction for high quality propagules (with rhizome and rhizoids) vs. low quality fragments was that attachment would be enhanced relative to low quality propagules for all treatments, while growth would be enhanced only in treatments with turf-derived sediment.

Substrate treatments were created by collecting small (5–10 cm widest diameter) rocks, either with ($n = 30$) or without ($n = 10$) turf cover. Rocks were collected from the shallow subtidal region at Seal Rocks (−32.431° S, 152.525° E) and transported in seawater to the research facility at DPI Port Stephens. Rocks were kept in large, aerated tanks with flow through estuarine water (∼34 ppt) and kept under 12:12 h light:dark cycle at ambient temperature (∼25–30°C daily max) for 4 days until the start of the experiment. Turf consisted of numerous species < 5 cm tall but was dominated (>50% cover) by geniculate corallines. In the laboratory, all sediment was removed from the turf-sediment matrix from rocks with turf to create the R + T − S treatment, or mixed, and re-introduced in naturally occurring amounts to rocks with turf to form the R + T + S treatment. To form the R − T treatment, rocks with turf were carefully cleared of vegetation with a heavy-duty tile brush. Naturally bare rocks were not treated and formed the R treatment. Artificial rock consisted of a kitchen tile with the ceramic side facing upwards. This side consisted of an even surface with small-scale pores and a fish-scale pattern with ±1 mm surface relief. A 4 mm thick heavy-duty scouring pad (70 nylon and 30% polyester© MrClean) was glued onto artificial rock to create the artificial R + T treatment. Coarse sand was sourced adjacent to the rocks, and a 2 cm thick layer was created to form the S treatment. Habitat treatments were placed in shallow plastic trays (150 × 95 × 60 mm) with openings added on the sides to allow for water flow. Each treatment was added to a large tank ($n = 10$ large tanks, seven habitat treatments/tank) to create a randomized block design.

Intact *C. filiformis* was collected from Newcastle (−32.926° S, 151.793° E) from large boulders around the low tide mark and transported to the laboratory in seawater, where propagule quality types were created by pruning the rhizome and rhizoids. Fronds were 8–15 cm in length. High quality propagules consisted of a frond with 2 cm rhizome attached to it each with 2–4 rhizoid clusters. Low quality propagules consisted of only a frond. After pruning, all propagules were kept suspended in aerated seawater with constant flow for 48 h to allow for wounds to heal which takes < 48 h (Goddard and Dawes, 1983). Number of rhizoid clusters and wet weight was determined prior to the start of the experiment for later growth analysis for all fragments individually. Rhizomes constitute a very low proportion of propagule biomass, and initial fragment weight did not differ between substrate or propagule quality treatments at the start of the experiment ($F_{6,55} = 0.85$, $p > 0.4$ and $F_{1,55} = 1.46$, $p > 0.1$ respectively, mean fragment weight 122 ± 6 g). A single fragment was then placed in the center of its allocated substrate treatment ($n = 5$ replicate trays per Substrate × Propagule quality combination), with random distribution of propagule quality across tanks. Tanks were kept under the same conditions as described above for 12 days.

Attachment speed (days to attach) was assessed by carefully shaking the treatment tray every second day and checking for movement vs. attachment of the fragments. On the final day of the experiment (day 10), attachment strength was measured by attaching a clasp with two wooden stirring sticks to all the rhizoids to evenly distribute the force over the fragment attached to a pull balance. Once fragments were removed, change biomass (wet weight) and production of new attachment points (# rhizoid clusters) from the start of the experiment were determined. From the attachment strength measure and the known number of rhizoid clusters, we determined the force per attachment point. The effects of Substrate and Propagule quality on attachment speed, strength (entire fragment and individual rhizoids estimates), and growth (change in total wet weight and rhizoid cluster production) were tested with general linear models with tank as blocking factor and type II ANOVA tests ("Car" package, Fox et al., 2016) using methods as described above. Fragments that had not attached were excluded from tests for attachment speed and strength but not growth analysis.

Effects of Habitats on Fragment Retention

A field experiment was designed to determine whether recruit density patterns observed in the field sampling were explained by differences in fragment retention among habitats, i.e., retention on turf > *Sargassum* spp. > kelp and barren. At Malabar, Sydney (−33.966° S, 151.255° E), we placed fragments in either canopy-forming habitats (*Sargassum* and kelp) or in less structured habitats (turf and barren), which in some situations may represent degraded conditions. The experiment was conducted twice, once in January 2015 and again in January 2016. In each habitat, plots were created ($n = 8$ plots for turf and *Sargassum* in 2015, and $n = 4$ plots for kelp and barren in 2015 and all habitats in 2016). Plots consisted of four stainless steel bolts on each corner of a 25 × 25 cm plastic mesh (25 × 25 mm mesh size; ©Gardenmaster). Individual plots were placed in interspersed

patches of habitat, each $> 4\,\mathrm{m}^2$, but kelp plots were all positioned inside the same large kelp patch ($> 40\,\mathrm{m}^2$), with plots $> 2\mathrm{m}$ apart. Plots were positioned on horizontal surfaces at depths of 1.5 – 3 m below low tide and >50 cm from any edge of the habitat patch. The turf treatment consisted of a natural assemblage of a dense cover dominated by red geniculate coralline algae ($>75\%$ cover) and with some filamentous turf (species unidentified), all < 5 cm tall. Kelp, *Sargassum* and barren habitats were as described in **Table 1**.

Caulerpa filiformis was collected from a patch at the same site and transported to the lab where we created fragments consisting of single, unbranched, blades, each 10 cm in length, similar to the "poor quality" fragment type in the section above. Fragments were kept in aerated ocean water with constant flow at a 12:12 h light:dark cycle at 21°C for 3 days to allow for wound healing, after which intact fragments were transported back to the site where they were added to the plots. Fragments were placed in the plots (five fragments/plot in 2015 and seven fragments/plot in 2016) and loosely attached to the mesh with two thin (<0.5 mm wide) strips of duct tape. Although this method excluded potential differences in fragment entrapment, it could test for differences in fragment retention and recruitment potential among habitats.

In 2015, plots were revisited every 3 – 6 days during the first 2 weeks, and then every 2 weeks until the experiment stopped after 8 weeks due to the loss of most fragments. In 2016, plots were revisited every 2 days, ocean conditions permitting, and ran for 3 weeks. During every visit, the number of fragments still present was counted. Differences in fragment retention among habitats were tested with ANOVA tests for each sampling date with using methods as described above. As fragment retention was very low, other response variables such as growth rate could not be investigated.

A measure of ocean conditions (max. wave height) was used to test for associations with *C. filiformis* fragment retention over time. Wave data recorded by the Sydney offshore Waverider buoy located at 33.772° S; 151.409° E ($\sim$26 km NE of Malabar) were collected and provided by the Manly Hydraulics Laboratory (see **Supplementary Material II**).

RESULTS

Density of Recruits Across Sites and Habitats

Canopies of kelp and *Sargassum* were abundant at all sites except Kingsley Beach (**Figure 3**). Habitats of turf (coralline and filamentous forms) and barrens were abundant at all sites except Sharkies Cove (**Figure 3**). Adult *C. filiformis* covered large parts of the reef at Kingsley Beach, Bronte, and Coogee (47, 36, and 33% of rocky reef area surveyed respectively, **Figure 3**), but was less abundant at Sharkies Cove, Seal Rocks and Wollongong (14, 6, and 9% of rocky reef area surveyed respectively, **Figure 3**).

Caulerpa filiformis recruits were found at four of the six reefs sampled and absent from Sharkies Cove and Kingsley Beach. The average density of recruits on the rocky reef at the four sites with recruits present was 9 ($\pm$2) per 100 m^2, with the highest density of 13 individuals per 100 m^2 at Seal Rocks and Wollongong.

Recruits were found across a broad range of habitats, but in most habitats the density was low ($<0.2\,\mathrm{m}^{-2}$) (**Figure 4**). Recruit density in the structurally complex geniculate coralline habitat was significantly greater than in all other habitats ($F_{7,20} = 7.154$, $p < 0.001$; **Figure 4**). There was no indication that recruit density was enhanced in filamentous forms of turf (**Figure 4**). Recruits were generally rare in barrens and *Sargassum* habitat (**Figure 4**). Any recruits in barrens were always in association with small-scale substrate relief, such as small crevices, cracks, and folds. No recruits were found on sand, rock with a sediment veneer, or in kelp habitat (**Figure 4**).

The Role of Substrate and Propagule Quality on *C. filiformis* Recruitment

Attachment success of fragments across all treatments at the end of the 10-day experiment was high for substrates containing three-dimensional structure (artificial turf, R + T – S and R + T + S) and on Sand (90 – 100%), but less so on hard substrates lacking three-dimensional structure (Artificial R, R, R – T; 20–70%). Attachment speed varied significantly among substrates (**Figure 5A**), with the same patterns among substrates for both the low- and high-quality propagules (**Table 3**). Overall, fragments on R + T (with or without sediment) attached the quickest (4 days), followed by Artificial Rock and Artificial Turf (**Figure 5A**). Fragments on Sand took the longest to attach (10 days). Fragment attachment strength and rhizoid cluster attachment strength differed among substrates (**Figures 5B,C**), but no differences between propagules of low of high quality were found (**Table 3**). Attachment strength of *C. filiformis* propagules was significantly less on substrates lacking three-dimensional complexity (artificial R, R, R – T) or structural integrity (Sand) (**Figure 5B**). Attachment strength of rhizoid clusters followed similar patterns among substrates but only some *post hoc* comparisons were significant, due to the large variation in rhizoid attachment (**Figure 5C**).

Overall growth rates were not related to Substrate type (**Table 4**) but were higher for high quality propagules compared to without rhizoids respectively (**Table 4** and **Figure 6**).

Fragments with rhizome removed (low quality) had increased production of rhizoid clusters compared to the rhizome intact (high quality) treatments (**Table 4** and **Figure 6**). By the end of the experiment, the final numbers of rhizoid clusters did not differ with propagule quality (**Table 4**), but were greater on natural turf substrata, particularly on turf with sediment present (**Figure 7**).

Recruitment Across Different Habitats

Recruitment success differed among habitats (see **Supplementary Material I** for ANOVA test results), but patterns were not consistent over time and did not always follow those predicted.

For the 2015 experiment, nearly all fragments (90%) were retained in the turf habitat during the first 12 days. Retention was reduced in kelp and *Sargassum* habitat (50 and 54%) but was lowest on barrens, with only $\sim$20% of fragments remaining after 12 days (**Figure 8A**). However, this pattern reversed after 14 days, with the loss of all propagules from turf, and minimal further loss from the other habitats (**Figure 8A**). This resulted in *Sargassum*
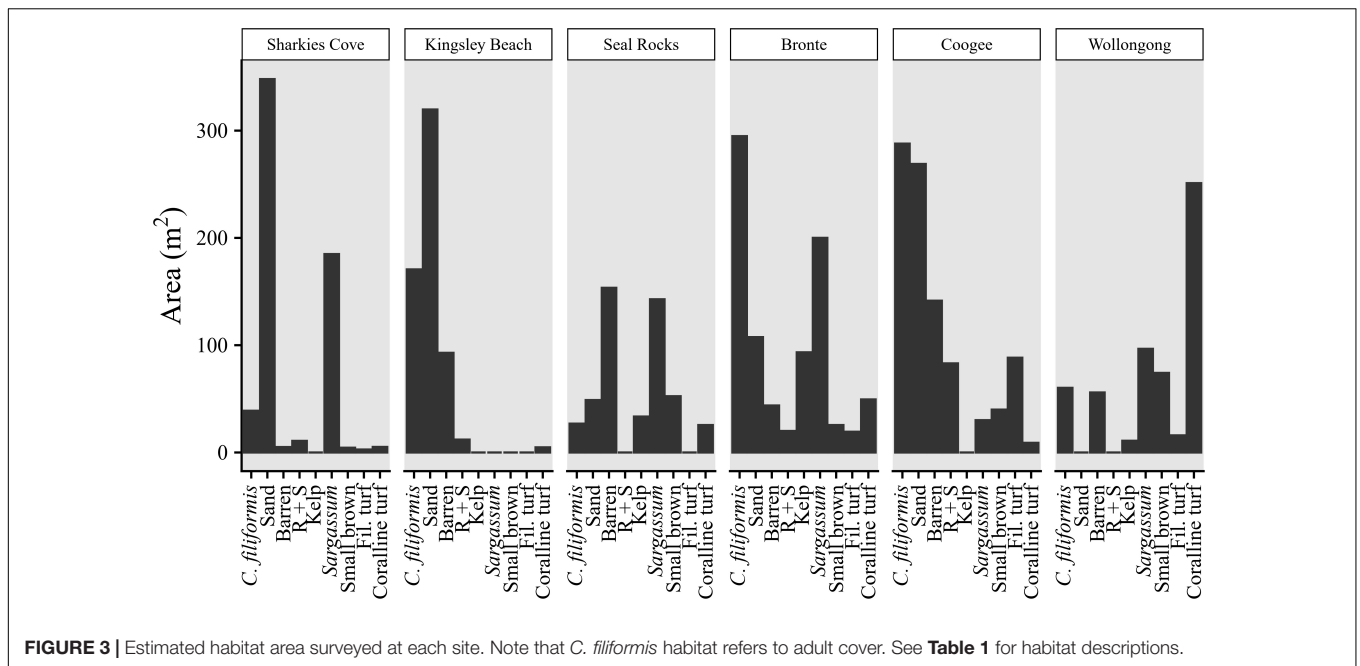
FIGURE 3 | Estimated habitat area surveyed at each site. Note that *C. filiformis* habitat refers to adult cover. See **Table 1** for habitat descriptions.

and kelp habitats having higher overall retention success than turf and barrens. This event coincided with a change from a period of low to moderate swell (up to 1 m) to high swell events (>1.5 m) (**Supplementary Material II**). During this subsequent period of frequent, intense swell, overall propagule retention was

very low, with nearly all fragments being dislodged after 2 months of experimentation.

Similarly, the 2016 experiment was characterized by frequent high swell periods (**Supplementary Material II**). Again, overall fragment retention was low, and most fragments were lost after less than 20 days (**Figure 8B**). As observed in the previous year, even though overall success was low, *Sargassum* habitat showed higher fragment retention rates than any of the other habitats investigated at most sampling times during this high-swell period.
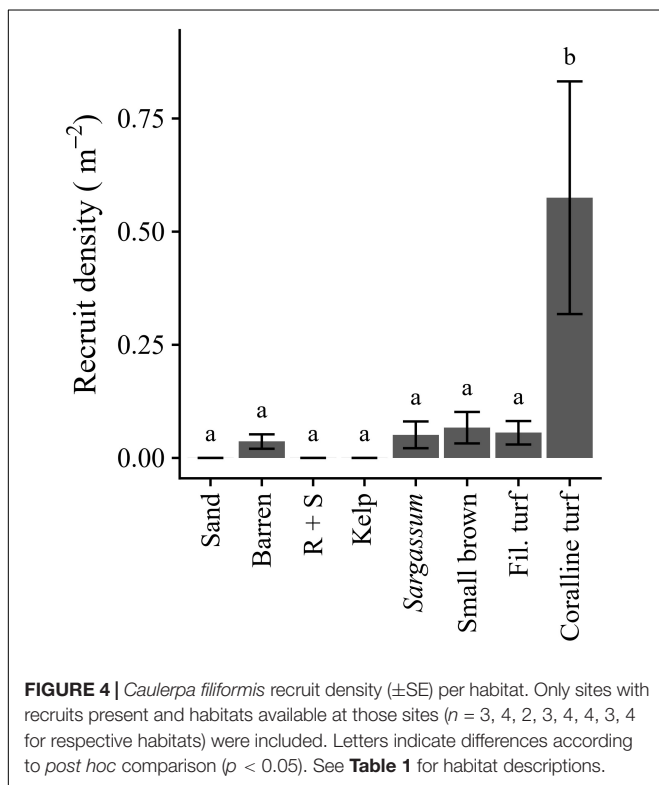
DISCUSSION

Here, we investigated if turf and barrens habitats (which in some situations are considered degraded habitats) facilitate the spread of a previously sub-dominant community member. Surveys and experiments showed that recruitment of the rapidly spreading native macroalga *C. filiformis* was consistently higher in algal turf compared to other native habitats due to the provision of a superior surface for attachment. There was no evidence that *C. filiformis* was colonizing barrens habitats.

The Role of Habitat Suitability in Shaping *C. filiformis* Recruitment Success

A species' potential spread is governed in part by the availability of suitable habitat for recruitment. The absence of suitable habitat may therefore explain the absence of *C. filiformis* recruits at two of the six sites investigated here. At Kingsley Beach, large parts of the reef were covered by dense adult stands of *C. filiformis* possibly limiting the quantity of space available for recruitment, while other reef areas were low-quality habitat for propagule attachment (predominantly barrens) as defined in

FIGURE 4 | *Caulerpa filiformis* recruit density (±SE) per habitat. Only sites with recruits present and habitats available at those sites (n = 3, 4, 2, 3, 4, 4, 3, 4 for respective habitats) were included. Letters indicate differences according to *post hoc* comparison ($p < 0.05$). See **Table 1** for habitat descriptions.

FIGURE 5 | Attachment speed (days to attach) **(A)**, attachment strength (N) of entire fragment **(B)** and average attachment strength (N) per rhizoid cluster **(C)**, averaged over levels of Propagule quality. Only fragments that had attached within 10 days of experimentation were included in the analysis. N = 10, 2, 7, 4, 10, 10, 10 for habitats Sand, Artificial Rock, R, R – T, Artificial Turf, R + T – S and R + T + S respectively. Letters indicate differences according to *post hoc* comparison (p < 0.05). No *post hoc* comparison is available for the Artificial Rock treatment, as only two fragments had attached at the end of the 10 days experimental period. R, rock; T, turf; S, sediment. Error bars represent SE.
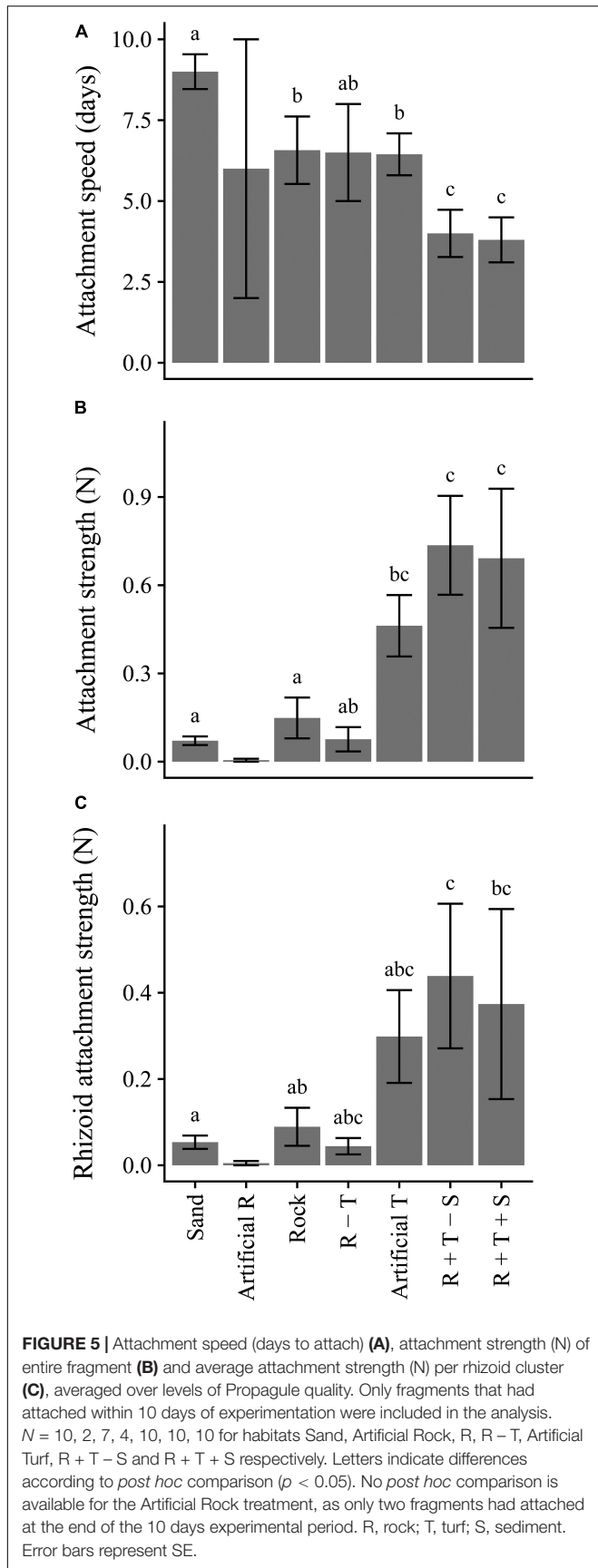
TABLE 3 | ANOVA (type II) test results on attachment performance (attachment speed, fragment- and estimated rhizoid attachment strength) for factors Substrate type and Propagule quality and their interaction measured at the end of the 10 days experimental period, with Aquarium added as blocking factor.

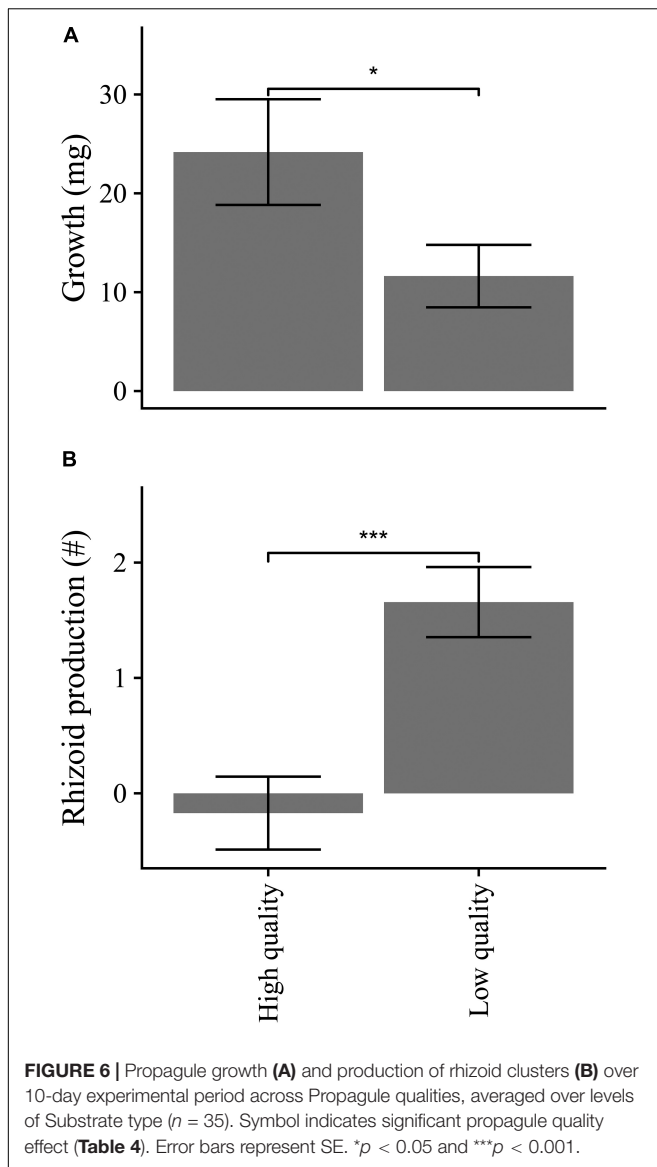| Variable	Factor	SS	Df	F	p
Attachment	Aquarium	12.906	1	2.713	0.108
speed (days	Substrate type	186.371	6	6.530	**<0.001**
till first	Propagule quality	2.069	1	0.435	0.514
attachment)	S × P	58.337	5	2.453	0.051
	Residuals	180.760	38		
Recruit	Aquarium	0.317	1	3.946	0.054
attachment	Substrate type	3.136	6	6.348	**<0.001**
strength (N)	Propagule quality	0.0135	1	0.195	0.684
(sqrt)	S × P	0.222	5	0.540	0.735
	Residuals	3.043	38		
Rhizoid cluster	Aquarium	0. 133	1	1.700	0.200
attachment	Substrate type	1. 334	6	2.853	**0.022**
strength (N)	Propagule quality	0. 070	1	0.899	0.349
(sqrt)	S × P	0. 226	5	0.581	0.714
	Residuals	2.955	38		

Only fragments that had attached were included in the analysis. Significant p-values are indicated in bold (p < 0.05).

TABLE 4 | ANOVA (type II) test results on growth performance (change in total wet weight, production of rhizoid clusters, and final rhizoid number) for factors Substrate type and Propagule quality and their interaction over the 10 days experimental period, with Aquarium added as blocking factor.

Variable	Factor	SS	Df	F	p
Growth (g) (Δ wet	Aquarium	117	1	0.184	0.669
weight)	Substrate type	4823	6	1.266	0.288
	Propagule quality	2751	1	4.331	**0.042**
	S × P	6112	6	1.604	0.164
	Residuals	34934	55		
Production rhizoid	Aquarium	7.314	1	2.765	0.102
clusters (#)	Substrate type	67.771	6	4.270	**0.001**
	Propagule quality	57.447	1	21.717	**0.001**
	S × P	8.183	6	0.516	0.794
	Residuals	145.486	55		
Final # rhizoid	Aquarium	7.314	1	2.765	0.102
clusters	Substrate type	67.771	6	4.270	**0.01**
	Propagule quality	0.616	1	0.233	0.631
	S × P	8.183	6	0.516	0.794
	Residuals	145.486	55		

N = 5 propagules per treatment level. Significant p-values are indicated in bold (p < 0.05).

the laboratory experiment. Similarly, at Sharkies Cove, recruits may have not been observed due to the absence of high-quality habitat for recruitment (turf) as defined in the laboratory and field experiments. However, the relatively low abundance of adult *C. filiformis* may have simultaneously reduced propagule supply at this site.

FIGURE 6 | Propagule growth **(A)** and production of rhizoid clusters **(B)** over 10-day experimental period across Propagule qualities, averaged over levels of Substrate type (n = 35). Symbol indicates significant propagule quality effect (**Table 4**). Error bars represent SE. $^*p < 0.05$ and $^{***}p < 0.001$.

FIGURE 7 | Production of rhizoid clusters (± SE) over 10-day experimental period across substrata, averaged over levels of Propagule quality (n = 10). Different letters indicate significant differences between levels of Substrate ($p < 0.05$). R, rock; T, turf; S, sediment.

Habitat suitability varies with the recipient biotic community, that can either resist, tolerate or promote macroalgal recruitment (Scheibling and Melady, 2008; Hughes, 2010; Burek et al., 2018; Layton et al., 2019). As predicted, relatively few *C. filiformis* recruits were found under algal canopies, which supports the notion that intact habitat-formers resist invasion, although response to different canopies varied. No recruits were found under kelp canopies, and similarly recruits were not retained under kelp when experimentally added in the field. Kelps are especially efficient in taking up available light limiting the potential for many other macroalgae to persist (Kennelly, 1987b; Valentine and Johnson, 2003; Clark et al., 2004) and/or the continual physical sweeping of fronds at wave-swept shores and the abrasion caused can remove benthic organisms (Kennelly, 1987b; Irving and Connell, 2006; Hughes, 2010) and may simultaneously inhibit the supply and recruitment of *C. filiformis* propagules to the substrate. Unlike for kelp, there was not
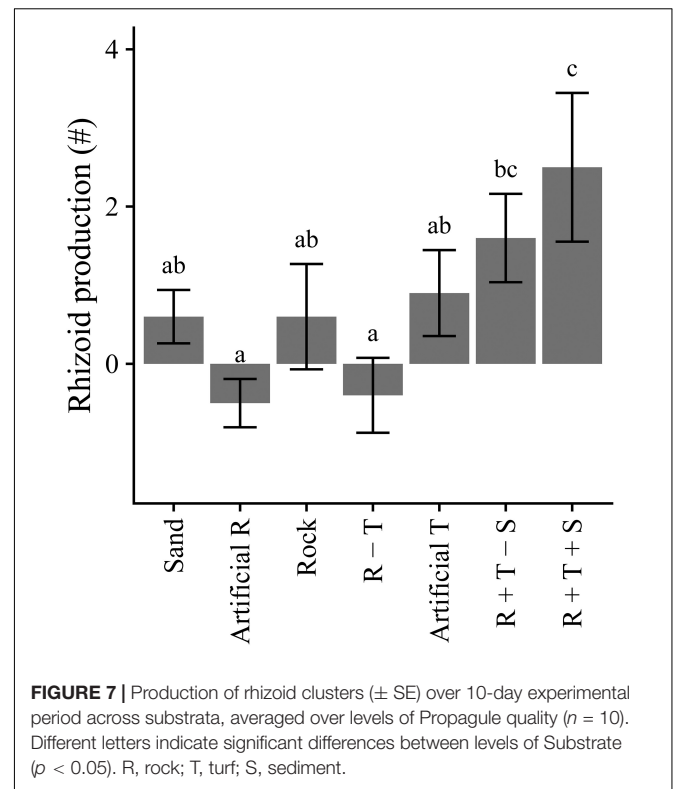
a consistent negative association between the smaller canopy-forming *Sargassum* habitat and *C. filiformis* recruits. Although the arrival of propagules may be restricted by *Sargassum* canopies (Arenas et al., 2006), the presence of scattered understory turf amongst *Sargassum* habitat likely facilitated retention and recruitment success of *C. filiformis* propagules.

Field observations showed a clear distinction in *C. filiformis* recruitment between different types of turf, with higher recruitment in communities dominated by geniculate corallines, but not filamentous turf. Although the two types of turf can co-occur, our results support the importance of distinguishing the morphologies of the assemblage often collectively termed "turf" (e.g., Connell et al., 2014; O'Brien and Scheibling, 2018). The discrepancy in their respective roles in shaping *C. filiformis'* recruitment patterns likely results from variation in the provision of suitable substrate for attachment by either form of turf. While geniculate coralline algae provide complex three-dimensional rigid surface created by their calcium carbonate deposits, filamentous turf does not. How altered relative abundance of geniculate coralline vs. filamentous forms affect invaders recruitment success – or more broadly species interactions in general – is an interesting area of further study, especially if the relative abundances of the two are expected to change due to further environmental change (Hepburn et al., 2011; Short et al., 2014).

The density of *C. filiformis* recruits was greater on geniculate coralline turf compared to any other habitat present, and this was remarkably consistent across sites. Habitat suitability of coralline turf was also demonstrated by our field experiment, albeit
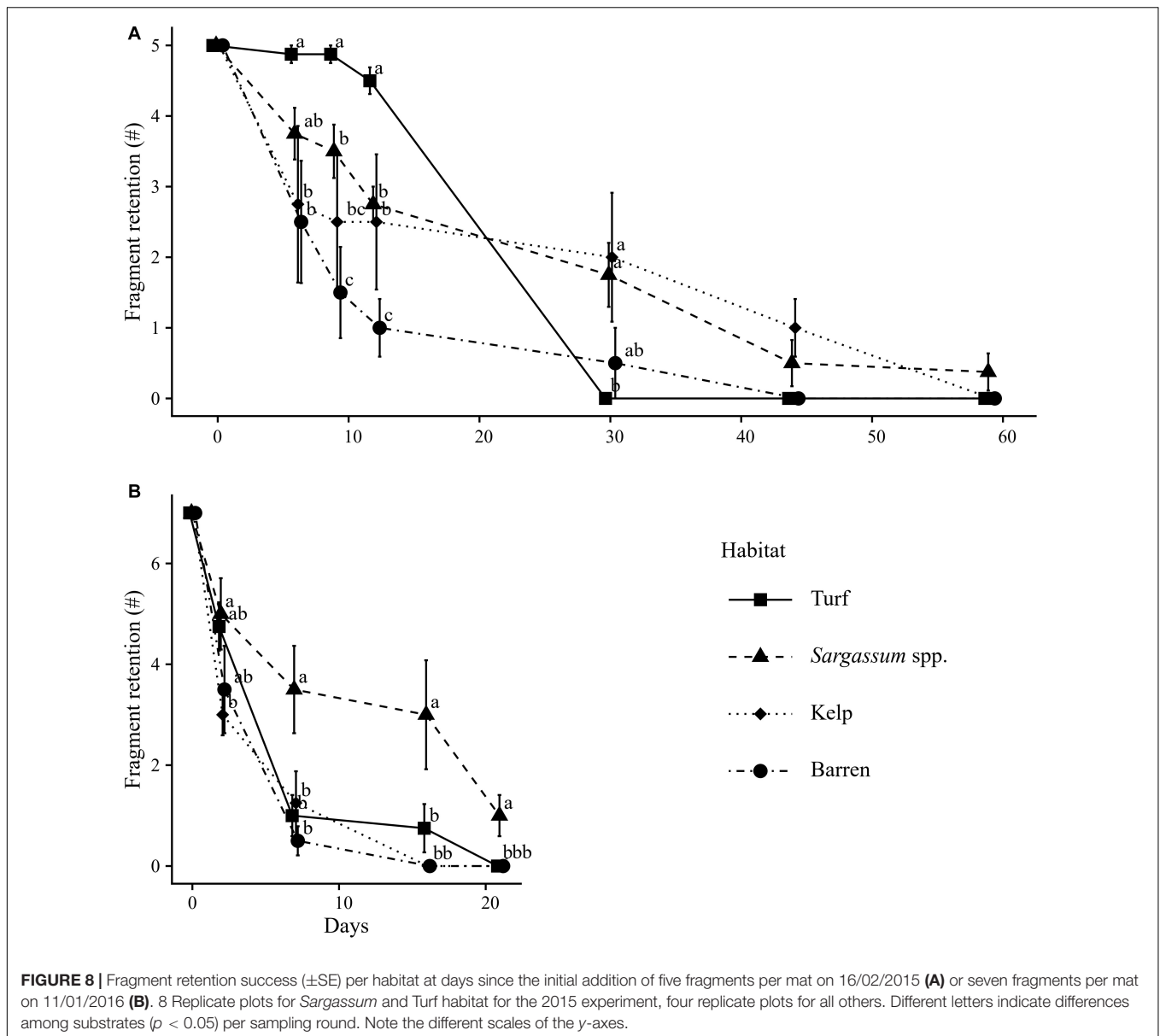
FIGURE 8 | Fragment retention success (±SE) per habitat at days since the initial addition of five fragments per mat on 16/02/2015 **(A)** or seven fragments per mat on 11/01/2016 **(B)**. 8 Replicate plots for *Sargassum* and Turf habitat for the 2015 experiment, four replicate plots for all others. Different letters indicate differences among substrates ($p < 0.05$) per sampling round. Note the different scales of the y-axes.

only under benign weather conditions, and in the laboratory experiment which demonstrated how turf facilitated *C. filiformis'* recruitment. Several studies have proposed the positive role of turf in trapping propagules of vegetatively spreading species including those from the genera *Caulerpa, Dictyota,* and *Codium* (Ceccherelli et al., 2002; Herren et al., 2006; Bulleri and Benedetti-Cecchi, 2008; Watanabe et al., 2009). Our laboratory experiment results also indicate a subsequent facilitation of *Caulerpa* recruitment, created by a combination of more successful, faster and stronger attachment of propagules. Increased attachment performance resulted from the structure turf provides, as indicated by the similar attachment on artificial turf substrata that mimicked the structural complexity of algal turf. The increased attachment strength on turf substrata was not solely a result of increased number of attachment points following increased

rhizoid production, but also increased attachment strength per rhizoid cluster. The latter may have resulted from increased time to attach resulting from faster attachment speed on turf, as increased attachment time allows for stronger attachment (Khou et al., 2007), or because of the mechanical properties of the turf allowing for stronger attachment per attachment point *per se.*

Although rhizoid production was highest in the presence of turf and sediment, there was no evidence for the role of turf-sediment in promoting *C. filiformis'* recruitment success (attachment success, speed or strength) or the hypothesized subsequent growth. Similarly, Bulleri and Benedetti-Cecchi (2008) found no effects of turf-derived sediment on the recruitment success or size of *C. cylindracea* after 45 days in the field. Equally, no changes in growth rates of already established individuals of *C. filiformis* were observed under the influence of

turf-derived sediment over an 8 week period in the laboratory (Voerman, 2017).

The Role of Propagule Quality in Shaping *C. filiformis* Recruitment Success

The presence of rhizome and rhizoid structures can aid recruitment success of vegetatively spreading algae (Smith and Walters, 1999; Khou et al., 2007; Uyà et al., 2018), although their importance may vary across habitats (Uyà et al., 2018; Bulleri et al., 2019). The overall lack of difference in recruitment success (attachment success, speed or strength) between low and high quality *C. filiformis* propagules observed in this study is likely a result of the high plasticity of the alga aided by its siphonous body structure that allows for a high capacity to rapidly reallocate resources (Vroom and Smith, 2001). Low quality propagules (without rhizomes and rhizoids) quickly grew rhizoid clusters, such that at the end of the 10 days experiment the two types of propagules had similar numbers of rhizoids. However, fragments with rhizoids present did show higher growth rates, irrespective of habitat. Increased growth may be due to high-quality propagules being able to direct energy toward photosynthesis and growth without first having to invest in rhizoid production for attachment. High quality propagule driven increased growth rates may in turn increase competitive strength for limited space in the field over the short-term. Results also revealed a clear differentiation in rates of production and/or maintenance of rhizoid clusters among substrata, with highest investment on natural turf substrata, especially R + T + S, while other substrata showed low rhizoid production or even rhizoid loss. Rhizoid production is inhibited when fragments are kept in solution and only form when in contact with a substratum (Khou et al., 2007). We propose substrate types can similarly either stimulate energy investment toward the creation or maintenance of rhizoid clusters or alternatively away from this allowing for facultative recruitment depending on habitat type. The mechanisms behind the observed differentiation in rhizoid investment are unclear. Allelopathy has been suggested to explain the role of coralline turf in the settlement of kelp sporelings (Denboh et al., 1997), and chemical cues from crustose coralline algae drastically enhance settlement coral larvae in tropical systems (Dixson et al., 2014). Perhaps similar mechanisms can explain the increased rhizoid investment and subsequent attachment of *C. filiformis* propagules on coralline turf.

The Influence of Wave Action in *C. filiformis* Recruitment Success

Patterns of *C. filiformis* fragment retention from our field experiment suggested that differences among habitats may be related to oceanic swell. Specifically, under relatively benign swell conditions, retention in turf habitat was greater than that in other habitats and least in kelp and barren habitats, which agrees with our observations of the distribution of recruits in the field. The predominantly negative association of fragment retention with canopy formers reversed under challenging environmental conditions (i.e., increased swell). Larger species of macroalgae can buffer near-ground wave action (Masteller et al., 2015), with

ameliorating effects becoming more beneficial when conditions become more severe (Hughes, 2010; O'Brien and Scheibling, 2018). However, high wave action events are simultaneously responsible for the creation (Smith et al., 2004; Watanabe et al., 2009) and potentially the dispersal of propagules. Whilst rough conditions generate fragments, we found that benign conditions promote recruitment. Thus, although retention was enhanced under canopies when abiotic conditions became challenging, ultimately it is a poor-quality recruitment habitat. Wave action and low attachment strength on sand (as per our laboratory experiment) also likely explains the absence of adult *C. filiformis* stands on large sandy stretches along the exposed shoreline of NSW but not in sheltered bays (Glasby et al., 2015; Voerman et al., 2017).

IMPLICATIONS AND CONCLUSION

Turf is considered a normal component of the mosaic of shallow rocky reef habitats in NSW (Underwood et al., 1991; Andrew and Underwood, 1993), however, turf may also represent degraded conditions where has resulted from the loss of canopy-forming algae (Airoldi and Beck, 2007; Filbee-Dexter and Wernberg, 2018). There are increasing concerns about losses of the kelp *Ecklonia radiata* due to ocean warming (Wernberg et al., 2018), while the expanding distribution of *C. filiformis* is close to the northern distribution limit of *E. radiata* in NSW where temperatures are most likely to exceed the tolerance of kelp and where there are increasing negative effects of tropical herbivorous fish (Vergés et al., 2014; Glasby et al., 2015; Wernberg et al., 2018). The loss of the large fucoid *Phyllospora comosa* (not present in our sites at time of study) from the Sydney region (Coleman et al., 2008) has similarly been proposed as a potential mechanism behind the spread of *C. filiformis* (Glasby et al., 2015). Any loss of canopy formers will likely benefit the spread of *C. filiformis* if they are replaced by turf, but not if replaced by barrens. This may be exacerbated as turf inhibits the recruitment of many sexually reproducing macroalgae including the kelp *E. radiata* (Kennelly, 1987a; Burek et al., 2018; Layton et al., 2019) and several fucoids (e.g., O'Brien and Scheibling, 2018). Species that, indeed, are important in resisting *C. filiformis* recruitment (this study) and its subsequent horizontal spread (Zhang et al., 2014; Voerman et al., 2017). Our results suggest that turfing habitat is an important facilitator of *C. filiformis,* and where turfs represent an alternate state previously dominated by canopy forming habitat (e.g., Feehan et al., 2019; Layton et al., 2019), they may act as a transitional habitat for further community change by promoting the recruitment of *C. filiformis*. While the replacement of canopy forming algae with turf can have large implications for the functioning and productivity of coastal systems (Filbee-Dexter and Wernberg, 2018), this may be exacerbated by coralline turf facilitating the colonization of *C. filiformis*. For example, dominance by *C. filiformis*, which is structurally and functionally very different from other native habitats in terms of forming dense meadows without a large canopy, potentially enhancing sediment trapping and having chemical defense, has been linked to dramatic changes associated flora and fauna relatively to

other native habitats (Voerman et al., 2014; Lanham et al., 2015; Voerman, 2017; Voerman et al., 2017).

In conclusion, positive and negative species interactions define the recruitment success of the native alga *C. filiformis*. Whilst turf is often considered an alternative state, geniculate coralline turfing habitats also promote the recruitment of invasive algae, in our case, *C. filiformis,* which has been termed a 'native-invader.' The extensive spread of *C. filiformis* represents a clear challenge to ecological communities on rocky reefs on which it is becoming locally more abundant. However, our results indicate that recruitment success, and therefore its impacts, is promoted by the loss of algal canopies. Thus, environmental managers may be able to identify reefs at particular risk from the spread to *C. filiformis*.

DATA AVAILABILITY STATEMENT

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

AUTHOR CONTRIBUTIONS

SV, PG, and TG designed the study and wrote the manuscript. SV executed the work and analyzed the data. All the authors contributed to the article and approved the submitted version.

SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fmars.2021.594447/full#supplementary-material

Supplementary Material I | ANOVA (Type II) test results in retention success among recipient habitats. Eight replicate plots for Sargassum and turf during the 2015 experiment, and four replicate plots for all other treatments.

Supplementary Material II | Max wave height recorded by the Office of Environment and Heritage's (OEH) Sydney offshore Waverider buoy during the fragment-retention experiments in 2015 and 2016. Wave data was collected and provided by the Manly Hydraulics Laboratory.

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