Disentangling the relative effects of structural complexity and substrate composition on fish habitat selection in coral reef environments

By

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Abstract

Identifying features of biogenic habitats (i.e. made of living plants and animals) that attract and retain resident species is a key theme in ecology with important implications for habitat conservation and restoration. Using corals (class *Anthozoa*, phylum *Cnidaria*) —a group of foundational species that provide important habitat for diverse fish communities— as a model biogenic habitat, we designed and tested an integrative method for creating artificial habitat modules to disentangle the relative importance of structural versus compositional features of biogenic habitats hypothesized to affect in the attraction and retention of resident organisms: 3D-SPMC (3D Scan, Print, Mould, Cast; Chapter 2). We then conducted a manipulative field experiment in which we augment a reefscape in Florida, USA over the summer of 2019 with ~ $1m^2$ replicated habitat patches created using artificial (3D-SPMC) and live corals. Here, we evaluated the relative effects of substrate composition (% living coral) and habitat patch structural complexity on the attraction and retention of resident fish species in two environmental contexts ("high" and "low" reefscape structural complexity at the scale of $100m^2$; Chapter 3). We found the 3D-SPMC method performed on par with or better than other techniques widely used to create artificial replicas of biogenic habitats in terms of design accessibility, scalability, and ecological realism. Our experiment revealed that augmenting the structural complexity of habitat patches resulted in greater fish attraction (measured as relative recruitment rate and density of juvenile fishes ≤ 3cm total length [TL]) and retention (measured as relative density of larger-bodied [4-6 cm TL] fishes, and richness of fishes ≤ 6cm TL) in low, but not high complexity environments. We suggest non-intuitive cue use may be driving selection processes to habitat patches in low complexity reefscapes, and/or that predator-prey dynamics may mediate selection in high complexity reefscapes. Substrate composition mediated fish attraction and retention to habitat patches, but in an unexpected way: both were consistently lowest at intermediate (i.e. 50%) compared to low (0%) and high (100%) living coral treatments (i.e. non-linear, concave pattern across % living coral treatments) regardless of reefscape complexity, though the effect was dampened at high background complexity reefscapes. Competition for living substrate patches, indirect cues from con/heterospecifics, and/or taxa- or trait-specific habitat selection may have explained these non-linear patterns. In the context of coral reef degradation and restoration, habitat augmentation will likely increase the attraction and retention of juvenile reef fish, primarily when coral patches are placed in low complexity environments. We recommend further investigation into species and/or trait specific responses that may be driving non-linear relationships between fish recruitment and coral substrate composition, and longer-term studies connecting the retention of recruiting fishes at habitats with variable biogenic substrate composition to adult reef fish assemblages.

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Chapter 1: Introduction

1.1 Biogenic habitat selection

Foundational species are globally prevalent and provide important biogenic habitats to diverse communities (Angelini et al. 2011). Ecosystems where the primary structure-building organisms are foundational species such as forests, grasslands, macroalgae beds, and coral reefs exist in reciprocity with the diverse communities of secondary species that rely on them for habitat; secondary species gain shelter from predation and sites for reproduction, whilst foundational species receive positive ecosystem services in return (like nutrient cycling, bioerosion, and mediating competition or predator-prey dynamics; Webster and Almany 2002, Schöb et al. 2012, Reeves et al. 2020).

A key theme in ecology is identifying habitat characteristics that promote attraction (selection) and retention (subsequent use) by secondary species. For biogenic habitats, these characteristics may be abiotically or biotically derived. In particular, biogenic habitats have two main features that drive habitat selection: 1) three-dimensional complexity (abiotic), and 2) substrate composition (biotic). These features are hypothesized to play a role in enhancing biogenic habitat selection (Öckinger and Smith 2006, Buhl-Mortensen et al. 2010, Lecchini and Nakamura 2013). During the attraction phase, structural complexity provides visual cues and substrate composition provides biochemical cues sensed via olfactory sensory systems, enabling habitat detection and selection (Kingsford et al. 2002, Brooker and Dixson 2016, Coppock et al. 2016). During the retention phase, structural complexity provides shelter from predation and reproduction-site resources while substrate composition affects foraging resources, which promote habitat use and retention (Beukers and Jones 1998, Cheminée et al. 2016, Agudo-Adriani et al. 2016). Also, the local environmental context in which biogenic habitat patches are placed may influence perception of structural complexity and substrate composition features (Mazerolle and Villard 1999, Herse et al. 2017, Bradley et al. 2019). Local environmental context is often measured as ambient vertical relief, which represents structural complexity at a scale of ~100m^2.

In the context of global habitat degradation, more effort is being put into conserving biogenic habitats, restoring them to ecologically functional levels, and understanding community dynamics that may bolster restoration success (Hoekstra et al. 2005, Beck et al. 2011, Jones and Davidson 2016, Katwijk et al. 2016). Re-establishing basic framework habitats through restoration of foundational species has been proven to aid ecosystem recovery by supporting positive feedback loops between foundational and secondary species (Suding et al. 2004, Suykerbuyk et al. 2016). A better understanding of characteristics that attract, and crucially, retain biodiverse assemblages is one of the positive facilitative feedback loops that may be leveraged to better design biogenic habitat restoration (Bekkby et al. 2020). Also, understanding of how habitat restoration may differ in varying environmental contexts will inform optimal placement of restoration activities (Mazerolle and Villard 1999, Gilby et al. 2018, Chase et al. 2019).

1.2 Coral reef ecosystems: model biogenic habitats where fishes are key secondary species

Coral reefs are high-biodiversity topical marine ecosystems, made of sessile coral foundational species (class Anthozoa, phylum Cnidaria), which serve as the primary habitat builders on reefs (Mumby et al. 2007). Although coral reefs cover less than 0.1% of ocean habitats globally, their structurally complex and biodiverse assemblages support nearly one-third of all marine fish species (Spalding and Grenfell 1997, Moberg and Folke 1999). Fish communities play integral roles in coral reef ecosystems by providing key ecosystem functions

(Brandl et al. 2019), regulating food-web dynamics (Holmlund and Hammer 1999), and contributing to reef nutrient regimes (Shantz et al. 2015). Substantial evidence indicates that structural complexity (Graham and Nash 2013, Agudo-Adriani et al. 2016, Darling et al. 2017) and living substrate composition (living coral tissue; Coker et al. 2014, Huntington et al. 2017, Richardson et al. 2020) features enhance reef fish abundance and diversity. The rapid decline of coral dwelling fish after bleaching events (when stress causes living tissue to die) indicates that living coral tissue (rather than the structure provided by coral framework) may be an important attribute of habitat quality (Booth and Beretta 2002) are a major drivers of fish community abundance and diversity. However, the extent to which each feature (complexity vs composition) influences fish community attraction and retention remains unclear.

Coral reefs have been increasingly exposed to chronic disturbances, such as ocean warming and acidification (Levitus et al. 2005, Hoegh-Guldberg et al. 2007, Foster et al. 2016). In the Caribbean and Western Atlantic regions (particularly around developed areas), corals are also exposed to acute disturbances such as disease (Goreau et al. 1998, Green and Bruckner 2000), increased tropical storm magnitude and frequency (Lirman 2003, Cheal et al. 2017), eutrophication (Hunte and Wittenberg 1992, Littler et al. 2006), pollution (Burke and Spalding 2004), and overfishing (Valentine and Heck 2005, Loh et al. 2015). What's more, Caribbean coral cover has been greatly reduced as a result of a phase-shift driven by competitive macroalgae (Maliao et al. 2008), reinforced through the loss of key herbivore species (Mumby et al. 2006, Shantz et al. 2020) and the establishment of invasive species (Lesser and Slattery 2011). In recent decades, the increased rate and magnitude of disturbances have pushed coral reefs into a state of global decline, making them critical ecosystems to understand and protect before they are lost.

1.3 Understanding biogenic habitat selection to inform restoration design

An emerging restoration method for enhancing the density of live coral on reefs is the addition of farmed coral colonies to reef sites, a habitat augmentation process known as 'out-planting" (Rinkevich 2014, Lirman and Schopmeyer 2016). Typically, corals (family *Acroporidae*) are preferred for Caribbean and Western Atlantic restoration, as they are fast-growing and were once the dominant reef-building corals for the region (Young et al. 2012). Moreover, reef fish have been reported to favour *Acroporids,* as their branching growth forms provide habitat structure for visual exposure to conspecifics, a high density of refuges from predators, and indirectly indicate food availability (Coker et al. 2014, González-Rivero et al. 2017). Although coral restoration is now being widely implemented, the majority of studies assessing reef restoration success have focussed on coral growth, survivorship and recruitment (Miller and Barimo 2001, Forsman et al. 2015, Gibbs and Hay 2015). Only a few studies have focused on understanding the effect of coral out-planting on the community dynamics and assemblage of reef-dependent fish species post-restoration (Ladd et al. 2019, Hein et al. 2020).

In recent years, studies have suggested incorporating metrics beyond coral cover (like secondary species' colonization of restored habitat) to better understand the ecological reciprocities that may enhance restoration efforts (Shaver and Silliman 2017, Opel et al. 2017, Ladd et al. 2018, Boström-Einarsson et al. 2020). In systems that are shifting towards algal-dominated states, the high biodiversity provided by an array of trophic groups contributes to positive feedback loop on reefs, whereby herbivorous fish feed on and reduce macroalgal cover, in turn encouraging coral cover, thereby increasing coral growth and habitat space for other fishes across multiple spatial scales (Knowlton and Jackson 2008, Lefcheck et al. 2019, Ladd and Shantz 2020).

On coral reefs, structural complexity and substrate composition features are hypothesized to enhance juvenile reef fish diversity. In the context of habitat restoration, understanding features that enhance attraction and retention to biogenic habitats may provide insights into optimal placements and habitat augmentation configurations. Understanding the relative importance of structural vs. compositional cues that attract juvenile reef fish, and resources that retain them to biogenic habitats, is important as they contribute to ecosystem productivity, and sustain important adult fish assemblages over time (Caselle and Warner 1996, Munday 2001, Morais and Bellwood 2020).

1.4 Research Objectives

Exploration of previous studies has highlighted three major challenges that limit understanding of the processes driving biogenic habitat selection: 1) past methods used to study structural complexity and substrate composition features use artificial habitats modules that do not mimic the structural morphology of biogenic habitats (Sherman 2002, Bortone 2006, Verweij et al. 2006, Nagelkerken and Faunce 2007, Santos et al. 2011, Mercader et al. 2019), are expensive to manufacture or made of materials that are difficult to access (Pérez Pagán and Mercado-Molina 2018, Good 2020), and/or cannot be scaled to create sufficient replicates necessary for a manipulative experiment (Powers et al. 2009, Rutledge et al. 2018), 2) most studies examining attraction cues to biogenic habitat are lab based and lack the realistic context of in situ experiments like environmental context (i.e. reefscape structural complexity measured at ~100m^2, (Lecchini et al. 2005, Brooker and Dixson 2016, Coppock et al. 2016) and 3) manipulative field studies often use study designs that do not fully disentangle structural or substrate composition features, use dead biogenic habitat fragments that may contain dead or dying tissue (potentially providing negative association cues; (Komyakova et al. 2013, Coker et al. 2014), or do not address habitat selection processes over time (i.e. attraction *and* subsequent retention of dependent species vs. just association).

Using coral reefs as model biogenic habitats, we sought to address these gaps by: 1) designing a method for creating artificial habitats to be used in habitat selection cue research that result in modules that are accessible (i.e. in terms of access to materials), affordable, scalable, and morphologically realistic (Chapter 2), and 2) implementing the resulting artificial habitat modules in a manipulative field study in which we fully disentangle the effects of structural complexity and substate composition features on the attraction and retention of fishes to coral reef habitat over time (Chapter 3).

Chapter 2

In this study we aim to: (1) develop a set of metrics by which to evaluate the performance of artificial habitat designs use in habitat selection studies, namely that take into consideration accessibility (material cost, availability and training required), scalability (durability, ease of deployment and reproducibility) and ecology (morphological realism, chemosensory stimulation and environmental impact), (2) develop and describe a new, integrative method which optimizes accessibility, scalability, and ecology by combining inter-disciplinary techniques. (3D-SPMC: three-dimensional Scan, Print, Mould, and Cast), (3) briefly describe its implementation in a field study with the intention of describing deployment considerations, (4) outline the performance of 3D-SPMC (in terms of the three major metrics) compared to other approaches to artificial habitat design, and (5) discuss potential applications of the method.

Chapter 3

In this study we employ the method from Chapter 2 in a manipulative field experiment to understand what features of biogenic coral habitats drive the attraction and retention of juvenile reef fish to habitat patches, and how environmental context may mediate fish-habitat patch relationships. Specifically, we aim to understand: (1) What is the effect of reefscape-scale structural complexity (measured as high vs low relief) on the attraction and retention of reef fishes in the absence of habitat augmentation (i.e. ambient rates of fish attraction and retention)? (2) How does augmenting structural complexity affect the attraction and retention of reef fishes? (3) How does reefscape-scale structural complexity (high vs low relief) mediate the effects of augmenting structural complexity on the attraction and retention of reef fishes? (4) What is the effect of variation in biogenic substrate composition (when holding structural complexity constant) on the attraction and retention of reef fishes? (5) Finally, how does reefscape-scale structural complexity (high vs low relief) mediate the effect of biogenic substrate composition on the attraction and retention of reef fishes?

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Chapter 2: 3D-SPMC: An integrative method for enhancing the ecological realism of artificial habitat designs

2.1 Introduction

Biogenic habitats (made of living organisms) are globally prevalent and provide critical resources for other species in high-biodiversity ecosystems (Loh et al., 2019). A major research theme in ecology is identifying attributes of biogenic habitats that enhance their detection and use by organisms, with the goal of predicting how changes in habitat quantity and quality influence resident communities (Mercader et al., 2019; **Fig. 2.1**). While habitat 'quantity' may be estimated as the size, area, or volume of habitat-forming structures (Agudo-Adriani et al., 2016), indicators of habitat 'quality' are more varied and context specific. For example, architectural complexity affects ecological services such as shelter from predation and sites for reproduction and feeding (Cheminée et al., 2016). Species composition of the biogenic habitat also determines the quality of forage resources available to residents (Wilson et al., 2008). Many studies employ artificial habitats (AHs) to isolate and test the role of various structural and compositional features hypothesized to affect biogenic habitat quantity and quality, with responses measured as organism attraction to and use of structures (Smith et al., 2016; Strain et al., 2018).

Extensive background research on existing AH designs and deployment methods reveals several attributes that impact their use in studies seeking to disentangle features affecting biogenic habitat selection: 1) accessibility (resource availability, cost, and training required to work with the AH construction materials and equipment), 2) scalability (durability, module ease of deployment including size and modularity, and reproducibility), and 3) ecology (degree of morphological realism, chemosensory stimulation, and environmental impact; **Table 2.1**).The method presented here stems from experimentation to identify an approach for AH design that would allow us to flexibly manipulate morphological and compositional features hypothesized to affect habitat selection in aquatic ecosystems. Considering existing AH designs used in aquatic research relative to the attributes described above highlighted opportunities for innovation (**Fig. 2.2; Table 2.2**). In particular, some existing AH designs require specialized or expensive materials/equipment, or produce large modules that are challenging to scale 'up' or 'down' to meet the needs of the research. Crucially, many AH designs fall short in their ability to reproduce morphological realism (e.g., structural configuration, surface texture, and colouration; **Fig. 2.2)**, and perform poorly regarding unintended chemosensory stimulation and environmental impact (**Table 2.2**). For example, plastic-based materials have the potential to leach chemicals into the surrounding environment, eliciting a range of chemosensory stimulation responses in surrounding organisms (McCormick et al., 2020), and the physical breakdown of other traditional AH materials (including plastics, thin metal sheets, and line) can lead to the contamination of food webs with micro-debris (Fotopoulou & Karapanagioti, 2019). Alternative biogenic materials (e.g. wood or shell) to construct biodegradable AHs may reduce environmental impacts, but confounding chemical cues associated with these materials and the unknown long-term effects of "degrading" habitat on resident biota make them a poor choice for habitat selection studies (Arvedlund & Kavanagh, 2009; Dixson et al., 2014).

Here we describe 3D-SPMC (three-dimensional Scan, Print, Mould, and Cast), an integrative method for AH design that allows users to isolate and flexibly manipulate compositional and structural elements of biogenic habitats to address research questions regarding habitat selection cues. The method was developed to address the opportunities for innovation outlined above and was also motivated by the lack of pragmatic guidance in published AH research for users seeking to isolate and manipulate structural and compositional features of focal biogenic habitat-forming organisms. After describing the 3D-SPMC method, we

1) briefly describe its implementation in a field study of habitat selection cues for habitat-forming coral, 2) outline its performance (in terms of accessibility, scalability, and ecology) compared to other approaches to AH design, and 3) discuss applications of the method to studying habitat selection cues and informing the design of biogenic habitat restoration projects.

2.2 Description and implementation

Artificial habitat design and construction

3D-SPMC contains five major steps that draw on techniques from engineering (steps 1 and 2), and paleontology and visual art (steps 3-5; Cheah et al., 2005). 3D-scanning and printing are emerging engineering technologies with diverse applications, and molding, casting and 3D assembly are techniques used in paleontology and visual art to replicate designs, conserve the integrity of the original object, and create complex structures.

Here we use staghorn coral (*Acropora cervicornis*), a dominant coral species on Caribbean reefs, as a model habitat-forming organism. Corals are the focus of habitat restoration efforts following decades of decline (Young et al., 2012). Understanding compositional and structural features of corals that attract and retain organisms from the water column to the habitat -a process known as 'recruitment' or 'settlement'(Booth & Beretta, 1994; Ivan Nagelkerken et al., 2015) - can inform the design of restoration projects aiming to restore lost ecological function.

1) *3D scanning and virtual augmentation:* The technique requires that a sample of the biogenic habitat-forming organism being approximated is accessible through field or archival sampling. We obtained a staghorn coral skeleton fragment from the Coral Restoration Foundation (CRF) in Key Largo FL, USA. We intentionally selected a fragment where the

majority of the main structural features were in one plane (**Fig. 2.3A**); although the 3D file can be manipulated to add/remove features (e.g., branches from the coral), this planar form reduced the need for 3D file manipulation. We scanned the fragment using a *2020i Next Engine Desktop 3D Scanner* (NextEngine Inc., Santa Monica, USA) to create a 3D mesh file and manipulated the file using 3D Builder (Microsoft © Application, 2013) to remove all irregularities, ensure high-resolution quality, and create a "water-tight" mesh (remove any "holes" in the file created during scanning). Users that require large and complex AH to address their research question can modularize the process in the 3D file manipulation stage by breaking the design down into smaller separate objects that are assembled into a final product. The design can also be adapted to change proportions of individual components, adjust size ratio, and/or create attachment features. We formatted the resulting 3D-file to create an object with a thin, flat plane running laterally along the edge of the module, which provided a smooth surface for attachment during the mould making process (see Step 3; **Fig. 2.3B)**.

2) 3D printing: We printed the resulting 3D-file using two types of extrusion-based printers, the *Dremel Digilab 3D45* (Dremel DigiLab, Mt Prospect, USA) and the *PRUSA MK 2 & 3* (Prusa Research, Prague, Czech Republic) printers. Both extrude PLA filament (polylactic acid, a common 3D printing filament) by building up consecutive layers of the 3D object, analogous to a hot glue gun extruding liquid plastic that hardens into a firm object. Orienting the object so that the flat plane faced down onto the 3D printer's build-plate reduced the support material required to hold the structure in place, minimizing print-time **(Fig. 2.3C)**. Print time ranged between 3-5 hrs per module (~12 x 3cm), depending on the printer and the number of modules loaded onto the build plate (i.e. total print time of 10-12 hours if three modules were printed at once). Print set-up was an iterative process involving continual monitoring and adjustment for the first few print layers to ensure an established print base. Design flaws created during scanning and file manipulation (step 1) may only become apparent during the printing process (See **Supporting Information A 1.0**).

3) Mould making: To create moulds from which to cast the artificial habitat modules, we first attached the 3D printed corals to a Plexiglass sheet using modeling clay. After coating the entire surface (plexiglass and coral modules) with spray-on *Universal Mold Release* (Smooth-On Inc., Macungie, USA), we brushed on the first layer of *Dragon Skin®10 Medium Series silicone* (Smooth-On Inc., Macungie, USA) onto the 3D printed modules using a 1cm round-tipped paint brush. This first silicone layer was mixed with a few drops of *THI-VEX®* silicone thickener (Smooth-On Inc., Macungie, USA) to help thicken silicone, ensure adhesion to 3D printed modules, and capture fine details of the organisms' morphology in the mould (in our case, polyp-level features of the coral; **Fig. 2.3D**). We poured the next three consecutive layers of silicone onto each mould according to the product's mixing and pouring directions. The entire mould sat untouched in a cool dry area to set for 24 hours. Next, we created a *Plaster of Paris* (Bondex International, Medina County, USA) casing over top by adding layers of heavy duty paper towel coated in a plaster slurry to give the flexible silicone under-mould structural stability (also called a mother mould/bandage shell mould) The entire mould and plaster casing sat untouched in a cool dry area for an additional 24 hours -after which the 3D prints were carefully removed from the silicone layer, resulting in a mould with negative space where the 3D printed corals sat, and a firm support layer

4) Casting: We used *Quikrete® countertop mix* (The Quikrete Companies, Atlanta, USA) concrete, water, and *yellow pigment* (Concrete, Edmonton, Canada) mixed by hand at a ratio of approximately 50:5:1 to approximate the colour of *A. cervicornis*. After lightly coating the moulds with vegetable oil (to act as a mould release) using a 1cm round-tip paint brush, we filled and compressed each mould with the concrete mixture (**Fig. 2.3E**). After a 24hr setting period, we carefully removed casts from the moulds and left them to cure further in a flat, dry area for 24hrs minimum.

5) Assembly and deployment: In our example study region, coral restoration projects typically transplant clusters of 'tripod' shaped *A. cervicornis* to reef environments to enhance coral cover because this shape provides multiple points of attachment to the benthos, increases stability, and exposes the coral to adequate water flow (Hollarsmith et al., 2012). We combined the concrete casts into complex 3D structures that mirrored this tripod shape and size (**Fig. 2.3F**). Assembly involved carefully breaking some of the coral casts into two pieces to create coral "branches", which were attached to original casts using *Apoxie Sculpt Modeling Compound* (Aves, Hudson, USA) and left to set for a minimum of 24hrs. Modules were soaked in sea-water for a minimum of seven days to leach out concrete-associated chemosensory cues before deployment. Modules were transported in large totes to the field site by boat and transferred underwater to experimental plots in milk crates by scuba divers.

2.3 Case Study: Application of 3D-SPMC habitat modules to study fish recruitment cues

We applied artificial corals created via 3D-SPMC in a field experiment to evaluate structural and compositional cues driving juvenile reef fish habitat selection in Key Largo, USA from June-July 2019 (**Supporting Information A 4.0**). The experiment involved placing artificial and living coral modules in replicate 1m^2 clusters at consistent densities (10 corals/cluster) in three treatments representing different percentages of living coral (but equal structural composition) and in two environmental contexts: high complexity seascape (i.e., large variation in vertical relief) and low complexity seascape (i.e., flatter, less variation in vertical relief; N_{total} = 48 clusters). Divers attached habitat clusters to the bottom with the same epoxy used for module assembly (see step 5). Artificial habitat modules were equally easy to deploy compared with living coral fragments and required little additional diver training to affix to the benthos. The modules withstood transportation and under-water handling without damage and remained in place for the entire duration of the two-month study without maintenance or repair.

Following deployment, we conducted SCUBA surveys of the abundance of newly recruited fishes (i.e., <3 cm total length) at each cluster every 1- 4 days over eight weeks. Preliminary results from our study suggests when structural features (i.e., habitat size and morphology) are held constant, recruiting fish show a strong preference for habitats comprising increasing proportions of living coral, but only when the surrounding benthic environment is flat (i.e., low complexity; **Fig. 2.4**). These results suggest a strong interaction between habitat composition and environmental context, with implications for restoration site selection: increasing coral cover at low complexity sites may yield benefits that are not realized at high complexity locations in the same reefscape.

2.4 Relative Performance of 3D-SPMC

By combining desirable attributes from multiple methods for artificial habitat design and construction into a streamlined workflow, 3D-SPMC is likely to perform on par with or better than eight other individual AH materials and designs used in habitat selection studies (**Tables 2.2 and 2.3**). *Accessibility:* Most of the materials and equipment required in steps 1 and 2 of 3D-SPMC are easily obtained through retail in urban centres; however, the 3D printing components require special maintenance (**Table 2.2**). While the baseline costs associated with steps 1 and 2 (3D scanning and printing) of 3D-SPMC are high compared with other approaches (**Table 2.3)**, the cost per AH module decreases substantially with increased production. For example, incorporating printer purchase and printing costs, ten $10cm^3$ modules cost $19.37 CAD each, compared to $0.43 each for 500 modules. Once made, 3D files and prints can be repeatedly edited, re-used, and/or shared, facilitating iterative designs and projects with little financial or time investment. A growing number of online tutorials and training centres offer free training in 3D scanning and printing, making the technology more broadly accessible (See **Supporting Information A 1.2**). While more costly than other moulding materials, *Dragon Skin Series* silicone material (step 3) is strong and elastic, meaning it can be used multiple times to create hundreds of replicates (**Fig. 2.3D**).

Scalability: Scaling AH production to the research question and study design at hand requires modules that are durable, easy to deploy, and easy to reproduce (Bortone, 2006). We chose concrete for our casting material as it is durable in aquatic environments, reducing the potential for short- and long-term changes to the surrounding environment (**Table 2.2**). Other applications of concrete in AH construction result in modules that are large and non-modular, often requiring specialized equipment to deploy (e.g. reef balls; Sherman, 2002), or are created with inflexible moulds that are destroyed during the cast-release process, thus not re-useable (**Table 2.2**). Modularizing the AH structure into simple planar components (step 1) that can later be assembled into replicate, complex 3-dimensional configurations (step 5) makes the 3D-SPMC method more scalable -a major benefit compared to 3D printing complex modules (**Fig S2.1**).

Ecology: While existing designs using concrete only score moderately well in terms of structural realism (**Fig. 2.2, Table 2.2**), the application of 3D scanning and printing (steps 1 and

2) within 3D-SPMC facilitates the creation of biogenic habitat replicas with a high degree of morphological detail. Once cast, concrete is chemically neutral, and thus less likely to cause unanticipated chemosensory stimulation of target and non-target organisms (and less environmental harm). While some previous 3D printing methods to create artificial habitat modules have used biodegradable PLA filament (Tarazi et al., 2019; Wolfe & Mumby, 2020), 3D-SPMC avoids this potential source of aquatic plastic pollution, and mitigates against unintentional chemical cues leaching into the environment.

2.5 Discussion

Application to habitat restoration research and design

Restoration planning has only recently started to include metrics of ecosystem function (Suding & Hobbs, 2009), and/or focus on key species that may accomplish broader co-beneficial goals of restoration (Jones & Davidson, 2016; Ladd et al., 2018; Peterson et al., 2003). Information on key structural and compositional attributes of biogenic habitats that promote habitat selection and use by resident species is essential for conservation and restoration planning; manipulative field and laboratory experiments using this method to create artificial habitats (such as in the experiment described above) can provide insights into the composition and optimal placement of biogenic habitats to bolster ecosystem function and sustainability (Ferrario et al., 2016). As seen in our case study, habitat composition affects fish recruitment, but environmental context also mediates the direction and magnitude of ecological response. Crucially, we only detected this effect by using 3D-SPMC to create modules for an experimental design in which we replicated a high degree of morphological realism across habitat modules varying in material composition (live coral vs concrete). In some aquatic ecosystems, employing artificial structures in restoration itself has resulted in increased fish recruitment (Green et al., 2015; Harding & Mann, 2001) they are no substitute for the suite of ecosystem services created by living biogenic habitats (e.g. Bruno et al., 2019; Côté & Darling, 2010; **Supporting Information A 3.0**).

Application to habitat selection research

A persistent challenge for testing habitat selection cues has been designing habitat modules that enable researchers to isolate and manipulate structural and compositional attributes, thus disentangling their relative influence on the habitat selection process (Coker et al., 2012; Harborne et al., 2011). 3D-SPMC offers a flexible means to design AH modules that manipulate structure and composition of focal biogenic habitat-forming organisms, and could be employed to provide insights into factors affecting habitat selection by resident biota in environments ranging from coastal oyster reefs and mangroves (Beck et al., 2011; Ellis & Bell, 2004), to woody vegetation in freshwater bodies, to mesophotic glass sponge reefs (Dunham et al., 2018).

Scale is an important consideration when designing AHs for selection cue studies; the scale of the ecological process being examined and the type(s) of cues to be manipulated influences decisions around study type (i.e., i*n situ* vs *ex situ*) and duration, focal habitat size and configuration, and response variable selection (see **Supporting Information A 5.0** for a list of key research design questions the researcher should address in selecting appropriate AH configuration). We used coral fragment-sized modules in dense clusters at a scale which fish recruitment is likely to vary, that mimics the design of reef restoration projects, and because recent evidence suggests fine-scale morphology affects larger-scale ecological processes (Urbina-Barreto et al., 2020). However, 3D-SPMC could be used to create larger and/or more complex habitat patches by generating larger 3D prints (and mould/casts), increasing habitat complexity in the assembly phase by combining multiple casts into a single module, and/or combining multiple habitat modules into a final structure. While the effect of patch size on species colonization and habitat use has been relatively well studied compared to habitat composition (Bohnsack et al., 1994) our method allows researchers to incorporate both aspects into their study design to evaluate habitat composition characteristics.

By manipulating the composition of casting material (step 4), researchers can use 3D-SPMC to study compositional features hypothesized to affect chemosensory stimulation. For example, studies aiming to study predator, prey, and competitor detection by focal organisms could directly incorporate homogenized tissue, body fluids, or key chemical components (e.g. pheromones, hormones) of con- and hetero-specifics into the casting material. One could also test multiple recruitment cue responses (Huijbers et al., 2012) by deploying AHs in combination with other cues (i.e. acoustic cues).

3D-SPMC could also be used to study epi-biotic habitat colonization by invertebrates like corals, sponge, or oyster spats by altering the configuration and/or casting composition of the AH modules. For example, oyster shells incorporated into structure provided attractant cues to larval oyster and saw higher spat recruitment (Ortego, 2006).Ceramic modules with tighter surface-pore densities may reduce biofouling and/or enhance targeted species-specific settlement (Johari et al., 2010). Companies are already creating “ecologically active” concrete materials that modify composition and surface texture to support specific marine fauna and flora (Perkol-Finkel & Sella, 2014), lowers the carbon footprint of artificial habitat construction (Dennis et al., 2018), and addresses the concern of concrete waste in aquatic ecosystems (Cooke et al., 2020). One could even consider expanding and adapting this method to test biofilm or anti-biofouling coatings that reduce or promote targeted biotic build-up (Tamburri et al., 2008).

This method can also be adapted to evaluate the structural characteristics of soft-bodied biogenic habitat-forming organisms such as sea-fans and seagrasses by using flexible casting material or 3D printing using flexible or biogenic printing material (Wangpraseurt et al., 2020; Yirmibesoglu et al., 2018), with implications to bio-mechanic studies and the contribution of biogenic organisms to shoreline protection (Christianen et al., 2013). Note that specialized printers may be a more expensive option that may limit affordability and accessibility.

Evidence across ecosystems suggest both composition and structural complexity contribute to biogenic habitat quality, impacting the ecological understanding and conservation implications for multiple secondary species (Gardiner et al., 2018; Harborne et al., 2011). Ultimately, more studies in controlled and natural settings are needed to draw conclusions about habitat selection ecology and potential restoration implications; 3D-SPMC is an integrative and adaptable method which meets this need.

Table 2.1 Descriptions for key attributes affecting the performance of Artificial Habitat (AH) module designs for aquatic research, and associated criteria for low (orange), moderate (yellow), and high (green) performance for components of each attribute.

Attribute	Sub-attribute	Definition	Performance Categories
Accessibility	Resource Availability	Ease of acquiring resources (both the materials and equipment) needed for AH design and construction	Green: both material and equipment easily obtained through common commercial retail facilities located in urban centres. Yellow: either the material or equipment requires special ordering, shipping, and maintenance Orange: both material and equipment obtainable only through experts or custom ordered
	Cost	Monetary cost required to assemble a $1m^3$ module (see Table 3)	Green: <200$ CAD Yellow: 200-500$ CAD Orange: >500$ CAD
	Training Required	Training with a proficient user required to use the tools necessary for the three phases of AH creation: design, construction, deployment.	Green: no phase requires substantial training Yellow: one phase requires training Orange: >2 phases require training
Scalability	Durability	Potential for an AH to persist in an aquatic environment with minimal degradation (dependent on material type *and* deployment method)	Green: low likelihood of replacement needed over a year-long experiment (1 time) Yellow: moderate likelihood of replacement needed over a year-long experiment (2-3 times) Orange: high likelihood of replacement needed over a year-long experiment (>3 times)
	Ease of Deployment	Effort required to affix and maintain AH in an aquatic environment (dependent on five factors, with the following states associated with high performance: final model modularizable [yes, modularizable], final model weight/volume [low weight/small volume], buoyancy [negative buoyancy], personnel needed [few personnel], and affixation time [short time to affix])	Green: high performance for all factors Yellow: high performance for 3-4 of the factors Orange: high performance for 2 or fewer of the factors
	Ease of Reproduction	Time required to construct all replicate AH modules needed for the study from design, to construction, to deployment phases.	Green: most required modules created in two weeks Yellow: most required modules created in one month Orange: most required modules created in more than one month
Ecology	Morphological Realism	Degree to which AH modules mimics the structural shape and colour of the target biogenic habitat-forming organism	Green: matches both structural shape and colour of the target organism Yellow: either structural shape or colour matching with target organism Orange: low structural shape and no colour matching
	Chemosensory Stimulation	Extent to which AH material releases chemical cues eliciting an olfactory induced avoidance response to targeted biota	Green: limited or no evidence of stimulation-induced avoidance response Yellow: some or lagged evidence of stimulation-induced avoidance response Orange: strong or immediately observable stimulation-induced avoidance response Grey: unknown stimulation/avoidance response
	Environmental Impact	Extent to which AH material may alter the surrounding chemical and physical environment, in the short-term via persistence/dissolution in the environment and long-term via bioaccumulation in food webs.	Green: no or limited short-term or long-term influence on environmental conditions Yellow: no short-term influence on environmental; long-term environmental effects likely Orange: both short-term and long-term effects on surrounding environmental conditions likely Grey: unknown environmental effects over short or long term

Table 2.2 Performance of common artificial habitat (AH) types used in aquatic research, given by their construction materials and the habitats they are designed to mimic, relative to three groups of metrics (accessibility, scalability, and ecology). Orange = poor, yellow = moderate, and green = high performance; grey = unknown. Detailed descriptions of each metric and performance criteria are provided in Table 1. CR = Coral Reef, OR = Oyster Reef, M = Mangrove, S = Seagrass Bed, UF = Unspecified Freshwater habitat, OA = other aquatic habitats. Bold text = example studies highlighted in Figure 2. Thick black borders indicate characteristics of existing methods integrated into 3D-SPMC.

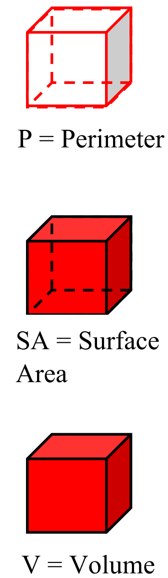
AH Type		Accessibility			Scalability			Ecology		
Material	Habitat	Resource availability	Cost	Training required	Durability	Ease of Deployment	Ease of Reproduction	Morphological Realism	Chemosensory stimulation	Environmental Impact
Plastic*	CR[1], OR[2], OA[3], M[4], S[5], **UF**[6]	green	yellow	green	yellow	green	green	orange	orange	orange
3D prints (PLA plastic)	**CR**[7]	yellow	orange	yellow	yellow	yellow	yellow	green	yellow	yellow
Biogenic	OR[8], **M**[9], UF[10]	green	green	green	yellow	green	yellow	green	grey	green
Line/nets†	CR[11], OR[12], **OA**[13]	green	green	green	orange	yellow	green	orange	yellow	yellow
Metal	CR[14], OR[15], **M**[16], OA[17]	green	green	green	yellow	green	green	orange	yellow	yellow
Rocks/ rubble††	CR[18], **OR**[19], OA[20]	green	green	green	green	green	green	orange	green	green
Ceramics	CR[21], UF[22], **OA**[23]	yellow	orange	yellow	green	green	yellow	yellow	green	green
Concrete	**CR**[24], OR[25], OA[26], M[27], S[28], US[29]	green	green	green	green	yellow	green	yellow	green	green

*Refers to unmolded plastics like plastic sheeting or PVC (Polyvinyl Chloride) pipes and moulded plastic like plastic cones or plastic seagrass.
†line/nets refer to synthetic, wire or cotton line.
†† We include rocky reef habitats in our qualitative analysis as they exist along a gradient of non-biogenic to biogenic habitats in aquatic ecosystems by supporting invertebrate and plant recruitment

[1](Bortone et al., 1994; Oren & Benayahu, 1997), [2] (Coen & Luckenbach, 2000), [3](Mercader et al., 2019), [4](I. Nagelkerken & Faunce, 2007; Verweij et al., 2006), [5](Mercader et al., 2019), [6](Moring & Nicholson, 1994.; Santos et al., 2011), [7](Pérez Pagán & Mercado-Molina, 2018; Ruhl & Dixson, 2019; Trilsbeck et al., 2019), [8](Coen & Luckenbach, 2000; Powers et al., 2009; Rutledge et al., 2018; Walles et al., 2016), [9](Breitburg, 1992; Ellis & Bell, 2004; Laegdsgaard & Johnson, 2001), [10](Moring & Nicholson, 1994), [11](Oren & Benayahu, 1997; Sherman, 2002), [12](Xu et al., 2017), [13](Charbonnel et al., 2011), [14](Scarcella et al., 2015), [15](Mercader et al., 2019), [16](Verweij et al., 2006), [17](Burt et al., 2009; Charbonnel et al., 2011; Cresson et al., 2019), [18](Powers et al., 2009), [19](Mercader et al., 2019), [20](Charbonnel et al., 2011; Cresson et al., 2019), [21](Trilsbeck et al., 2019; Umar et al., 2015), [22](Santos et al., 2011), [23] (Brotto & Araujo, 2001), [24](Oren & Benayahu, 1997; Scarcella et al., 2015; Sherman, 2002; Talbot et al., 1978), [25](Coen & Luckenbach, 2000), [26](Charbonnel et al., 2011; Cresson et al., 2019; Mercader et al., 2019), [27](I. Nagelkerken & Faunce, 2007), [28](Mercader et al., 2019), [29](Moring & Nicholson, 1994.; Santos et al., 2011)

Table 2.3: Cost associated with creating a $1m^3$ structure using the 3D-SPMC method and eight other materials commonly used for AH design. The amount of material required for each design depends on the material type and its method of use, as indicated by red shading in the diagram below (P = Perimeter, SA = Surface Area, V = Volume).

Material	Cost (CAD$)	Design
1-inch polyvinyl chloride (PVC) pipe	14.28	P
Acrylic sheet	456.32	SA
3D printing polylactic Acid (PLA) filament – 100% infill	37500.00	V
3D printing polylactic Acid (PLA) filament – 15% infill	5625.00	V
Oyster shells	20.00	V
Polypropylene line	11.80	P
Nylon mesh	28.47	SA
Stainless steel mesh	33.33	SA
Galvanized steel sheet	113.75	SA
Quarry rocks	129.58	V
Clay	1534.58	V
Cinder blocks	151.96	V
Pre-made concrete mix	143.84	V



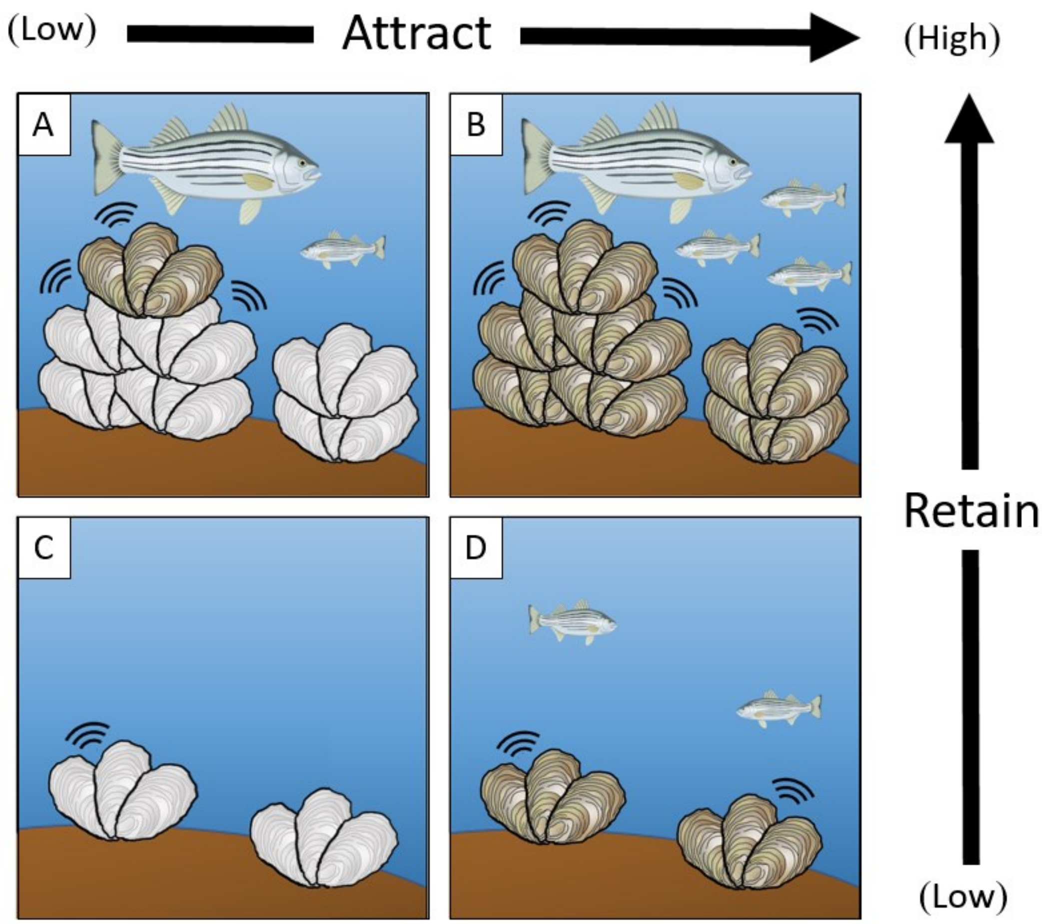


Fig. 2.1: The structure and composition of biogenic habitats (e.g. oyster reef, family *Ostriedae*) affect their selection and use by resident biota (e.g. Striped bass, *Morone saxatilis*). Composition mediates a range of visual, auditory, and chemosensory cues that attract resident species. Structural features influence the amount and type of shelter space and foraging resources available, influencing species retention. Studies integrating ecologically realistic artificial habitats (white oysters) with live biogenic habitat (grey oysters) are a useful tool for disentangling the relative influence of features affecting habitat selection (i.e., attraction) and use (i.e. retention). (A) Complex structural features and limited compositional cues are hypothesized to attract resident organisms at low rates, but retain organisms once attracted. (B) Complex structural features and high compositional cues are hypothesized to attract and retain species at high rates. (C) Few structural features or compositional cues are hypothesized to result in low species attraction and retention. (D) Few structural features but high compositional cues are hypothesized to attract organisms at high rates but retain few organisms that are attracted.

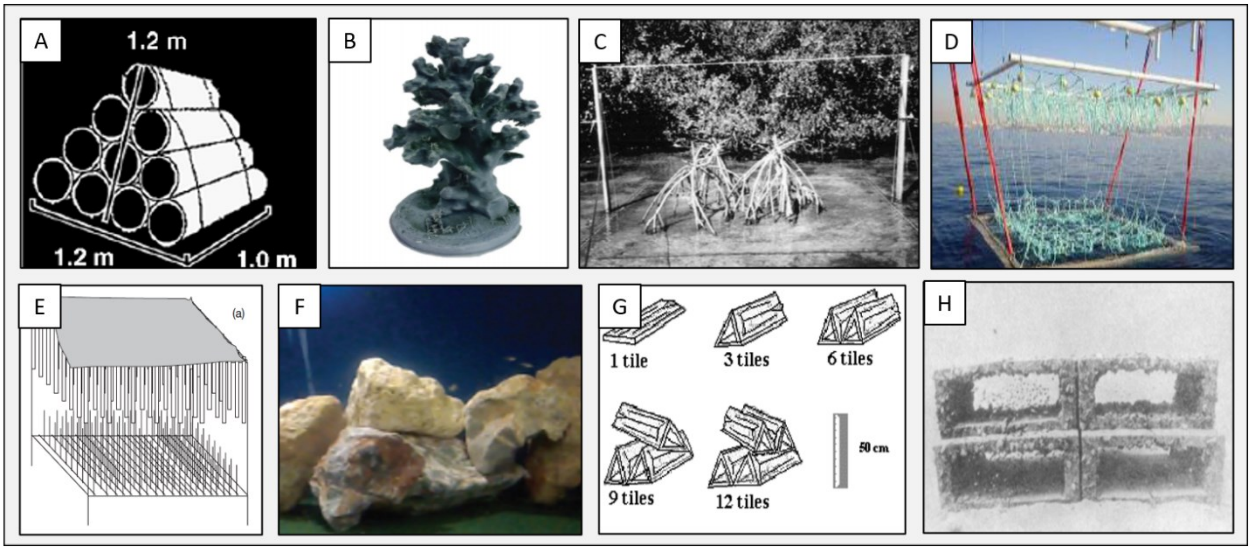


Fig 2.2 A wide variety of materials and configurations have been used to create artificial habitat modules in aquatic environments. Here we illustrate examples of materials and their common designs presented in Table 2: (A) A plastic PVC pyramid simulating freshwater reservoir habitat (Santos et al., 2011), (B) 3D printed plastic module (Plastic polylactic acid filament) simulating coral species (Ruhl & Dixson, 2019) (C) Mangrove prop root bundles simulating complex mangrove habitat (Ellis & Bell, 2004), (D) Line "floating rope" structures simulating restored *Posidonia oceanica* (Neptune grass) beds (Charbonnel et al., 2011) (E) Plastic PVC pipe and metal iron rods module simulating mangrove roots and seagrass leaves, respectively (Verweij et al., 2006) (F) Rocks/rubble simulating coastal nursery habitat (Mercader et al., 2019) (G) Ceramic tiles simulating coastal habitat (Brotto & Araujo, 2001) (H) Concrete blocks with varying hole sizes simulating coral reefs (Talbot et al., 1978)

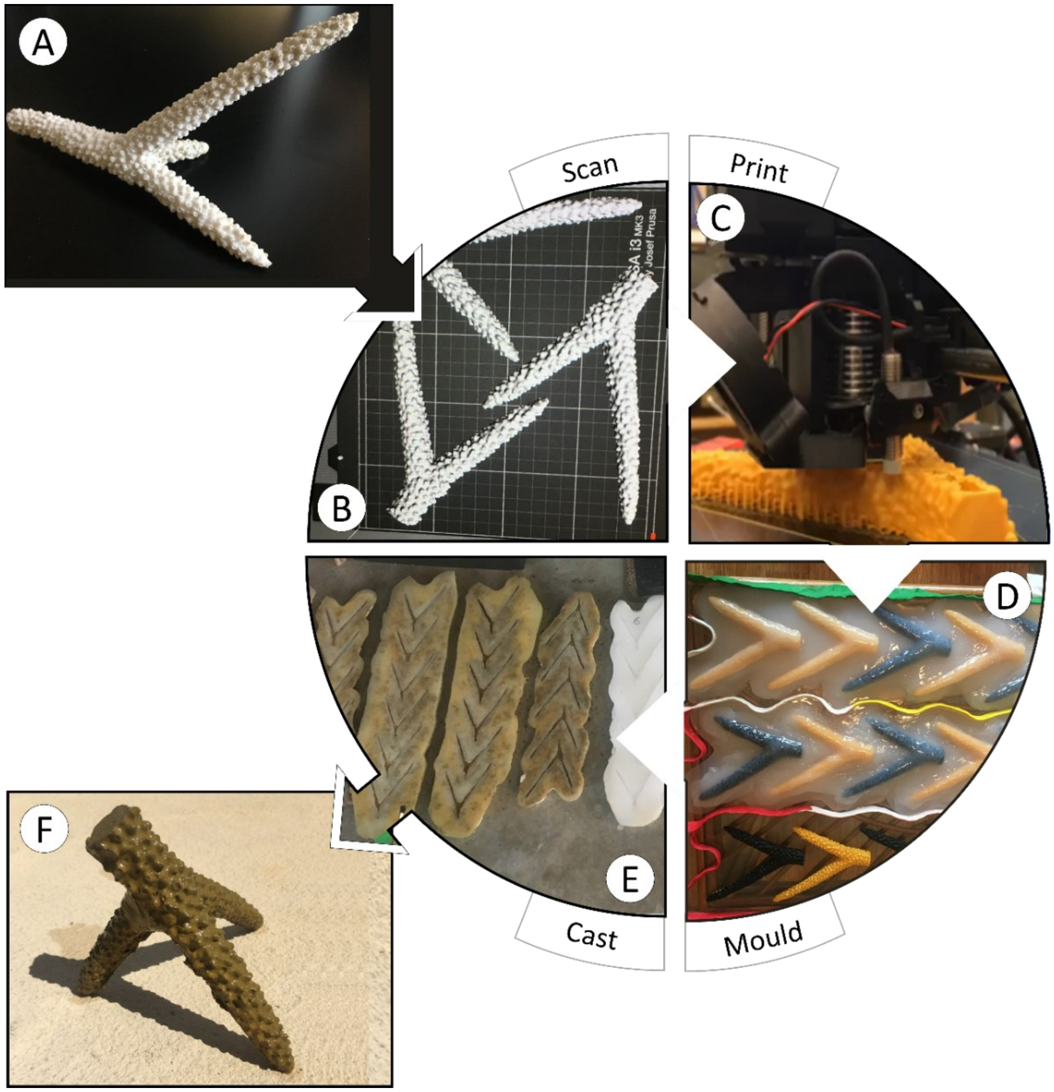


Fig 2.3 (A) Fragment of the focal biogenic habitat-forming organism is selected for 3D-scanning; here a coral skeleton fragment of *Acropora cervicornis* (staghorn coral) with a flat, Y-shape branch. (B) 3D file created by scanning the fragment from Fig 3A, which can be manipulated further to alter/augment structural features and complexity. (C) Multiple copies of the 3D file are printed using PLA filament and extrusion printers. (D) Consecutive layers of silicone mould material are poured over duplicated 3D prints; plaster casings (not shown) are made for each silicone mould to enhance the mould's structural stability (E) The resulting silicone moulds are lined with vegetable oil to act as a mould release and then filled with desired casting material; here, pigmented concrete. (F) Concrete casts are assembled into final, more complex artificial habitat modules; here a tripod shaped artificial coral for deployment in clusters in a field experiment (see Figure 2.4).

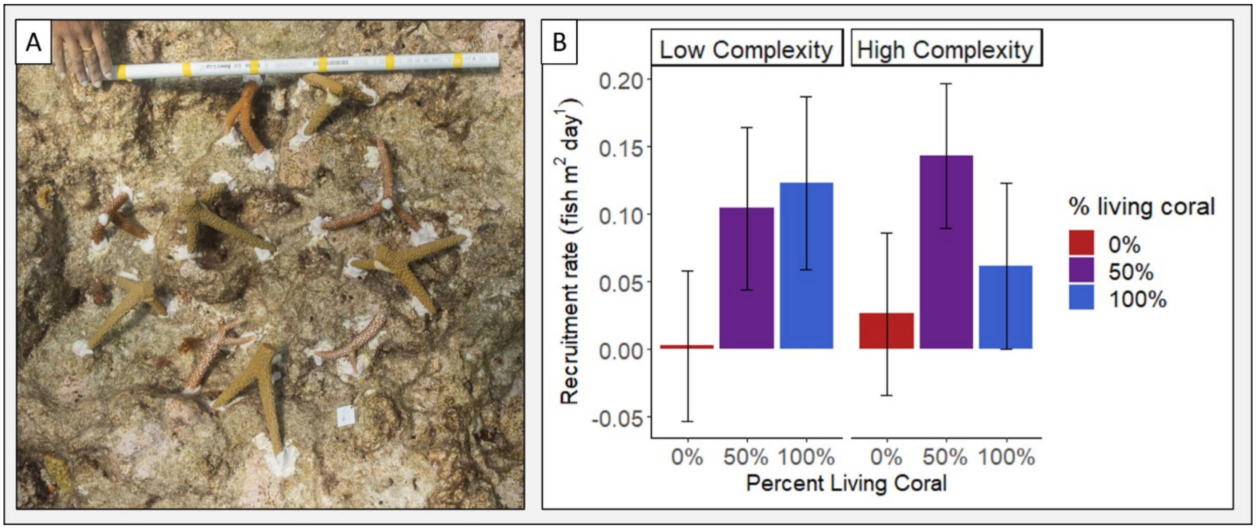


Fig 2.4 (A) Example coral reef habitat patch comprised of five artificial coral habitat modules created via 3D-SPMC, and five living corals (i.e. 50% living coral in the patch) deployed in a replicated *in situ* experiment in FL, USA to test the effect of live coral content (i.e. %) within reef habitat patches, while controlling for structural habitat complexity, on reef fish recruitment in areas of high or low seascape structural complexity. (B) Mean recruitment rate (±S.E., N = 16) of fish associated with the habitat patches in three treatment of % living coral (i.e. ratio of artificial coral to live coral modules, $n_{treatment}$ = 12): 0% = 0 living coral/10 artificial coral, 50% = 5 living coral/5 artificial coral, l, 100% = 10 living coral/0 artificial coral, control = 0 living coral/0 artificial coral.

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2.7 Supporting Information, A

1.0 Considerations when using 3D printing technology

1.1 3D scanning and Printing

Different 3D scanners are designed for different purposes, with trade-offs between the size of the objects that can be scanned and the resolution of the scan. For example, some scanners are designed to scan objects as large as cars and may not capture fine-scale details of a biogenic habitat sample. Scanning biogenic objects requires the focal sample to be the appropriate size for a given 3D scanner (i.e., within the spatial limitations of a scanner) that provides the necessary resolution of morphological features. As mentioned in the main text of Chapter 2, these seeming limitations can be remedied by modularizing the 3D scanning and printing process to scan individual components to later assemble during the file manipulation phase or once printed. Based on trials using various 3D scanners, we recommend scanning systems that capture micro-habitat detail when creating AH to test habitat selection cues. The *2020i Next Engine Desktop 3D Scanner* required little manipulation after scanning and upheld ecological integrity of the design shape. A variety of 3D printers were used to test printing capabilities and features. The first printers tested were the *Form II resin printer* (**Fig. S1A**) and the *Stratasys J750 printer* (**Fig. S1B**). The main advantages of these printers are their ability to print objects with extremely high resolution. However, these printers and printing materials are often more expensive, and an impractical solution to reducing cost and increasing scalability. Extrusion-based printers and printing material are more accessible and affordable. They also have the option of easily changing printing material filament, making them adaptable (**Fig. S1C**).

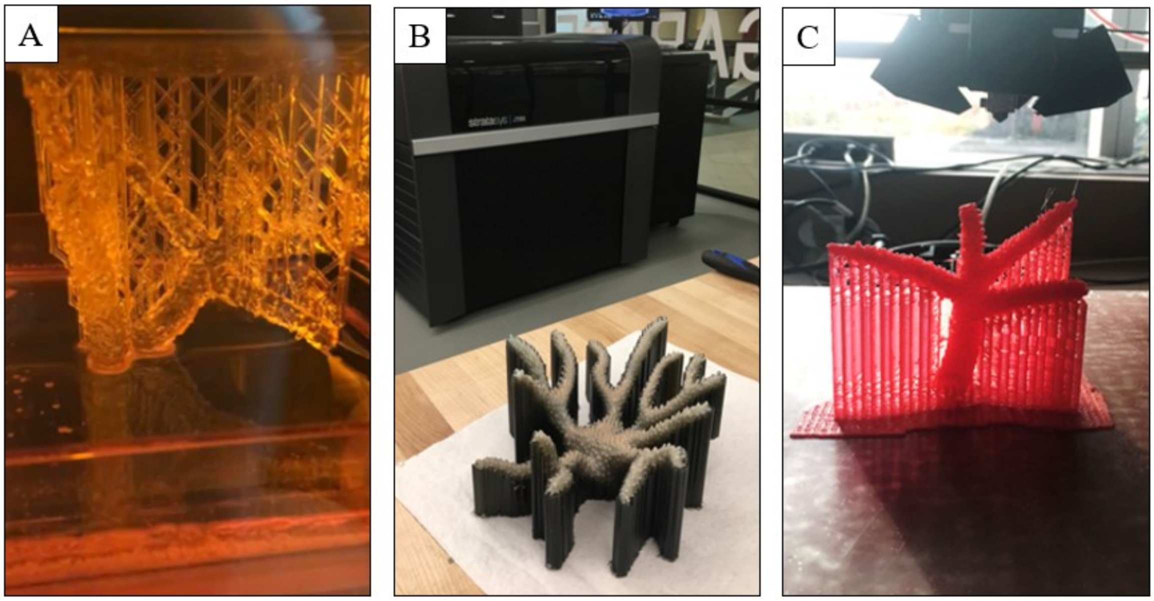

Fig. S2.1 (A) 3D print from a *Formlabs Form II* resin printer, figure showing high-resolution print quality but limited in cost and availability of printer material (B) 3D printing from a *Stratasys j750* printer, figure showing high-resolution print quality but limited in cost and availability of printer material. (C) A complex 3D print using a basic extrusion-based printer, figure showing more material dedicated towards support material than the print itself.

1.2 Links for online tutorials and 3D model databases

Tinkercad: https://www.tinkercad.com/

Thingiverse: https://www.thingiverse.com/

Ocean Agency coral 3D files: https://www.theoceanagency.org/ocean-image-bank

Smithsonian 3D Digitization: https://3d.si.edu/corals

2.0 Further description of artificial habitat materials and their relation to accessibility, scalability, and ecology performance attributes in Table 1

2.1 Accessibility

2.1.a Resource availability:

Materials that score highly in terms of resource availability criteria are plastics, biogenic materials, line/nets, metal, rocks/rubble, and concrete. Plastics are easily obtainable from commercial retailers in urban centers and thus are widely used to create AHs. Some examples of plastic AHs are PVC plates to enhance larval coral settlement (Oren and Benayahu 1997), PVC pipes to mimic mangrove prop roots (Verweij et al. 2006, Nagelkerken and Faunce 2007; **Fig. 2A & E)** and plastic leaves to imitate *Thalassia testudinum* (turtlegrass) in artificial seagrass beds (Verweij et al. 2006). Biogenic materials score highly as they were some of the first artificial habitats used in artificial habitats (D'itri 2018) due to their wide availability, and are thus still used to date (Ellis and Bell 2004, Walles et al. 2016). 3D prints score moderately as some types of 3D printing material or printing equipment may be more difficult to access. For example, although the capacity to 3D print has increased dramatically over the past few decades (Kumar et al. 2016), printers and printing material are still fairly inaccessible outside commercial retailers in urban centres (Trilsbeck et al. 2019). Ceramics score moderately because although their construction material (clay) is widely available, their main limitations lie in the additional equipment required in post-production processes, such as kilns. Additionally, specialized ceramic 3D printers and printing filament may be difficult to access depending on your location and project budget (Lee et al. 2017).

2.1.b Cost:

Materials with highest performance (lowest costs) include biogenic materials (e.g., oyster shells), line/nets (polypropylene line & nylon mesh), metal (stainless-steel mesh and galvanized steel sheet), rocks/rubble and concrete. Rocks and rubble have been favoured due to low costs, or simply used opportunistically at no cost (Lima et al. 2019). Plastics generally have a wide price range, with cheaper plastics often favoured due to their low cost (and associated accessibility) and low training requirements, thus scoring moderately. Materials with highest associated costs (and lowest cost performance) are 3D prints and ceramics. The cost of 3D printing was calculated for material needed to create a solid $1m^3$ block (100% infill) as well as a partially solid block (15% infill) as prints are most often made using a partial infill, greatly reducing material demands and associated costs. 3D printing is the most expensive option, however costs are decreasing as the technology and materials become more available globally (Trilsbeck et al. 2019). The range of printing materials now available to 3D print includes biodegradable plastic, ceramics, and even sandstone (Lee et al. 2017), however these specialized materials increase production and post-processing costs. A growing demand for 3D printing technology has allowed individuals to contract companies or institutions for 3D prints, or to spread the cost of a 3D printer over several modules -thus reducing associated costs. Note that the cost estimates in Table 2 are only those associated with material, and do not include equipment required for construction. Those would also vary depending on design/construction method.

2.1.c Training required:

Most materials score highly as they require little training in the three phases of AH creation (design, construction, and deployment). Plastics, biogenic material, line/nets, metal, rocks/rubble and concrete are readily accessible and come ready-to-use. 3D printing scores moderately as there is a significant time investment in scanning, file manipulation and print supervision needed to ensure high-quality printing (Trilsbeck et al. 2019). The availability of 3D printing resources and training may be more easily overcome at institutions with digital technology centres that have trained staff (Behm et al. 2018). However, once initial investments are made, and 3D files are created, it is a design type that reduces in cost over time as files can be made available on free file-sharing services, and the cost per unit decreases as more modules are printed. These files are also shareable among networks or even globally on file-sharing servers such as thingiverse.com, increasing it's potential to be used by those that don't necessarily have file-creation training or equipment.

2.2. Scalable

2.2.a Durability:

Rocks/rubble, concrete, and ceramics score highest as they are all substances that are relatively stable in aquatic environments (Umar et al. 2015). Concrete in particular is a versatile material that can be used in conjunction with other materials for module stabilization (Nagelkerken and Faunce 2007, Biggs 2013), making it a strong contender for artificial habitat (AH) construction in a variety of shapes, sizes and amalgamations. Plastic, 3D prints, biogenic materials and metal score moderately as certain types or configurations are more durable than others, but more broadly have been shown to break down via wave action and exposure to sunlight. For example, oyster shells are often used in oyster reef restoration as they are easily accessible and have been found to promote larval oyster recruitment (Nestlerode et al. 2007). However, if the loose shells are not properly amalgamated within a supportive structure, they can quickly scatter or become buried in sediment (Lukens and Selberg 2004), making them less likely to persist in an aquatic environment without degradation (La Peyre et al. 2014). 3D printing material impacts module durability: typical PLA-printed modules would have lower durability in aquatic environments compared wish high quality, UV bonded polymer material or 3D printed ceramic modules. Lines and nets score poorly as they are most often used in suspension and/or in conjunction with reef balls/concrete blocks (Sherman 2002), making them susceptible to tearing and detachment due to wave action or boat propeller cuts. Note that durability (a modules persistence in the environment) depends on material type but also deployment method).

2.2.b Ease of deployment:

Plastics, biogenic material, rocks, metal, and concrete have high performance under this metric as they are negatively buoyant and depending on the module type need little adhesive material, supports, and personnel to affix to the benthos in aquatic environments. Additionally, AHs deployed using these materials typically don't take up much volume or weight, making them logistically easier to deploy by wading, vessels and/or scuba divers (i.e., fewer personnel and less time needed for deployment). Line and nets score moderately as they are typically positively buoyant material, requiring extra deployment attention to be properly affixed to substrate or to the AH module in use. Concrete also scores as only somewhat meeting this requirement as it is a heavy material, often deployed in large blocks (Moring and Nicholson 1994., Bortone et al. 1994) reef balls (Sherman 2002), or complex modules, making it more resource intensive in volume and personnel capacity to deploy. To conserve printing material and print time, 3D prints are often printed with a hollow or partially hollow infill, resulting in hollow space that makes them positively buoyant, difficult to deploy/affix to bottom substrate and more likely to float away from AH area to become aquatic debris. However, most 3D-printed AHs are small enough that they can be easily affixed by one person, reducing time and effort to deploy, thus score moderately.

2.2.c Ease of Reproduction:

Plastics, line/nets, metal, rocks/rubble, and concrete score high as most modules using these materials can be made relatively quickly (i.e., within two weeks). Biogenic material scores moderately as there are finite biogenic resources available for AH creation, potentially limiting the time needed to obtain resources to construct and deploy habitat modules. Ceramics score moderately because they may be limited in terms of the time required to properly dry and kiln-fire ceramic work before deployment.

2.3 Ecology

2.3.a Morphological realism:

Biogenic material and 3D printing have the highest metric performance in this category. The former due to its obvious biogenic origins (**Fig 2C**) and the latter due to its potential as a tool to create highly morphological realistic modules (**Fig 2B**; Mohammed 2016). 3D scanning and printing technology has already been rudimentarily tested in aquatic habitats (Ruhl and Dixson 2019), with the ability to create extremely high-resolution micro-habitat characteristics such as coral polyps on a coral head (**Fig. 3C**). Plastics, line/nets, metal and rock score moderately, as they are often used to create AHs with low morphological similarity to biogenic habitat (Lima et al. 2019) such as simplistic PVC or tile modules (Brotto and Araujo 2001; **Fig. 2A**). Other simplistic modules are often made using concrete. For example, studies using concrete most often deploy them as simple concrete blocks (Talbot 1965, Sherman 2002, Cresson et al. 2019; **Fig. 2H**) or stacked modules (Santos et al. 2011) that has little morphological similarity to biogenic habitat. In some cases, metal mesh has been favoured due to its malleability and ability to be manipulated into complex forms. However, this attribute has mainly been used to hold together conglomerate materials like shells/rubble to create modular AHs (Scarcella et al. 2015). Ceramic AHs have been deployed in pyramid tile-modules to test habitat complexity (Brotto and Araujo 2001; **Fig. G**), as simple stand-alone tiles to test benthic (i.e. seafloor) assemblage recruitment (Umar et al. 2015), and even created using specialized ceramic 3D printers (Mohammed 2016, Trilsbeck et al. 2019).

2.3.b Chemosensory stimulation:

Rocks/rubble, ceramics and concrete all score with high performance as there is little evidence indicating chemosensory stimulation by secondary organisms. 3D prints score moderately as those made of plastics face the same chemosensory response considerations as other plastics, while those made of ceramic likely have negligible effect. Initial laboratory studies indicate that fish behaviour is not impacted by 3D printed objects (in terms of time spent in 3D printed habitats; Ruhl and Dixson 2019), however we caution that more studies on a diverse assemblage of fish over long periods of time would need to occur to have confidence in deploying 3D printed plastic modules in the field. Line/nets score moderately in this category as their composition and design may vary and influence aquatic organisms differently (i.e., synthetic vs organic fibre lines). Metal also scores moderately due to the variability of metal types and forms employed as AHs. For example, iron ions released during oxidation can actually increase primary productivity in the immediate surroundings (Layman et al. 2016), however the type of metal and its treatment are important considerations as certain compounds may impair physiological and behavioural response in surrounding organisms (Weis et al. 2001, Sovová et al. 2014). Plastics score poorly due to the growing body of evidence linking micro and nano-plastic effects on aquatic species physiology and behaviour through emitted chemosensory stimulation and nano-particle consumption (Wegner et al. 2012, Cedervall et al. 2012). Biogenic material scores as unknown as they may contain cues associated with the once-living organism, potentially confounding study results aiming to disentangle the effect of living organisms and structure on habitat selection. For example, in a study examining larval oyster recruitment to living and artificial oyster reefs, Walles et al. (2016) used bags of living oysters to mimic a natural reef and bags of oyster shells to mimic an artificial reef and found higher oyster larval recruitment at natural reefs. This could be due to the chemosensory ability of larvae to detect chemical cues of conspecifics (Tamburri et al. 2008) or by the soundscape cues associated with living oyster reefs (Lillis et al. 2013), but could also be due to negative habitat cues associated with degraded habitat (Dixson et al. 2014), making it difficult to disentangle which cues are driving a habitat selection response.

2.3.c Environmental Impact:

Biogenic material scores highly as they do not have a degrading effect to the surrounding chemical and physical environment in the short-term. Rocks/rubble, and concrete and ceramics have a similar chemical composition to rocky substrates (Dennis et al. 2018) thus score highly. Ceramics have the potential to reduce epifaunal biofouling in aquatic environments due to material pore-tightening during the firing process. These qualities make concrete a high-performance material for AH construction. 3D prints score moderately as there is growing research and availability of biodegradable printing material, however the break-down process in an aquatic environment still runs the risk of creating harmful marine debris and/or contribute to aquatic microplastic pollution (Reichert et al 2018). One of the first 3D printed reefs was made using a specialized 3D printer and patented sandstone printing material (SOI 2012). While this has lower environmental impact, it remains inaccessible and expensive for researchers or restoration managers. Line/nets and metal score moderately as they do not necessarily pose an immediate threat to their local chemical and physical environment from short-term degradation, however if dislodged or unattended, run the risk of being extremely harmful to aquatic and non-aquatic wildlife via entanglement, or bio-accumulation over the long-term (Read et al. 2006, Bergmann et al. 2015). While some plastics have been favoured due to their low toxicity when dissolved in water (Baine 2001, Wolfe and Mumby 2020) or corrosion resistance (Lima et al. 2019), there are many plastics that release chemicals harmful to marine biota (Sherman and Spieler 2006), or breakdown in harsh ocean conditions (Hudson 1993). Furthermore, the deployment of plastics in aquatic environments further contribute to the aquatic plastic pollution crisis (Sigler 2014), making plastics an undesirable material to continue using in AH deployment and why it is ranked poorly.

3.0 Further discussion on using AHs for restoration design purposes:

3.1 *Defining restoration success:*

Restoration "success" is determined by meeting specific restoration goals and thus success metrics vary from project to project. For example, restoration goals using AHs in aquatic ecosystems could be multi-dimensional to include direct benefits such as enhancing settlement surface area, local production, fisheries production,(Miller 2002, Powers et al. 2009) and/or increasing biodiversity (Epstein et al. 2003, France and Duffy 2006). They can also include indirect service-related goals such as water quality and public health concerns (Coen and Luckenbach 2000), anti-trawling deterrents (Jensen et al. 2000), or reflect passive values such as knowledge that habitats are conserved for future generations (Whitmarsh et al. 2008). Restoration success is clearly dependent on the local context, thereby directly dependent on holistic monitoring of pre-defined success metrics (Ruiz-Jaen and Mitchell Aide 2005). A holistic monitoring process includes initial and continued involvement from a variety stake-holder groups that incorporates socio-environmental approaches (Wortley et al. 2013, Belhassen et al. 2017), a process often overlooked by restoration researchers and/or practitioners.

In addition to monitoring, restoration success may be determined relative to a reference baseline, pre-disturbance information can be established based on historical data and/or indigenous knowledge that surpass records in western science (Koehler 2009, Ens et al. 2012). However, even when controlling for these factors, studies employing AHs do not typically report on the “success” of an AH in meeting any design criteria, as they are often focussed on a particular aspect of using the AH to study a specific phenomenon -such as its ability to promote ecological characteristics like recruitment or biodiversity (Sale 1991, Sherman and Spieler 2006, Powers et al. 2009, Walles et al. 2016, Ruhl and Dixson 2019) enhancing fisheries production (Seaman 2007, Whitmarsh et al. 2008, Beck et al. 2011). The wide variety of purposes, contexts and designs in which AHs are deployed make it difficult to evaluate the performance of AHs in a standardized way (Baine 2001). It is our hope that methods such as the one described in this paper can offer a way to standardize AH comparisons when applied to restoration planning.

3.2 Cautionary Management:

One of the most common uses of artificial structures in aquatic systems is the use of Fish Aggregating Devices (FAD). FADs are structures that heterogenized the pelagic seascape to offer water-column aggregation space. They are one of the oldest technologies used by fishermen, with indigenous design, technologies and usage pre-dating the relatively recent interest in FADs for commercial fisheries and western science (Bortone 2006, Raju et al. 2016), where they are most often deployed to enhance fisheries (Castro et al. 2002).While FADs certainly show evidence of aggregating surrounding species, this calls into question whether they are simply attracting species to a novel habitat vs. enhancing the production of the habitat and its surrounding area. The "attraction vs. production" debate is a long-standing question of whether artificial structures simply re-distribute already existing species in the area (attraction) or increase an area's carrying capacity by enhancing juvenile recruitment and retention (production). Two of the biggest cautions of using FADs in habitat selection studies or restoration activities is that they typically fall into the former category of attracting biomass, rather than increasing ecosystem productivity, and when employed simply as a fishing device, FADs may be used to exploit surrounding species (Seaman 2007).

While Artificial habitats serve a unique role in enhancing ecosystem function and resilience, a focus on only habitat replacement may lead to passivity in conservation, over-exploitation of newly attracted species and an over-reliance on technological solutions rather than addressing necessary systematic changes. No number of studies can protect against the chronic effects of climate change, but local action can still make a difference to protect key local species, transfer resilience to ecosystems, and act as a buffer to degradation (Côté and Darling 2010, Bruno et al. 2019). Therefore, we strongly recommend against using 3D-SPMC for wide-scale restoration, rather as a tool to identify important features of habitat and the contexts in which they matter. We recognize that ecosystem restoration is a participatory political process to also repair human-environment relationships which serves to resist the colonial and capitalistic systems which dismantle that relationship (Fox et al. 2017) and contributes further to habitat degradation.

4.0 Case Study Details

Living corals were obtained by collaborators at the Coral Restoration Foundation from their Carysfort Reef offshore coral nursery and were cut to the same length as the artificial coral fragments (12cm).

5.0 Pragmatic considerations for the planning phase:

The following is a set of reflective questions designed for users to consider before using the 3D-SPMC method. It reflects the design process and questions we encountered during the methodology development. The following is divided into 2 parts: Part 1: Project Objectives, and Part 2: 3D-SPMC Steps and Considerations.

Part 1: Project Objectives

1. Identify: what are you using the method for?
    a. Habitat Cue Study
        i. What is the goal of your research?
        i. What response metric will you measure?
        ii. At what scale does this ecological process occur?
        iii. What is the appropriate scale/size of the artificial module that matches that ecological process?
    b. Inform Restoration Design
        i. What is the goal of your Restoration Program?
        ii. How will employing this method provide information on:
            - Optimal design and placement of living or artificial habitats?

- What percent living biogenic habitat is needed for colonizing organisms to detect and use habitat?

2. Pragmatics:
    a. Site selection:
        i. Where will this project take place? (lab vs. field)
        ii. How will you access field sites and transport modules there?
        iii. Depending on size of final module: does it need to be modularized and built in-situ? How will they be affixed? Plan placement.
    b. Collaborators & Resources:
        i. Who has similar goals to yours, or is already working on something similar?
        ii. What kind of time/resources are at their disposal already?
    c. Time & Money:
        i. What is your project budget?
        ii. What is the timescale of your project? How many modules will you need to make in that time frame? (taking into account the time needed for printing, and drying in the mould making and casting steps)
        iii. What is the minimum unit of replications for your project (including extras in case any break) and do they fit the time and budget parameters?
    d. Space:
        i. Do you have a reliably dry workspace for the moulding and casting stages?
        ii. Is there somewhere to store concrete casts while they are curing?

iii. Where will casts be pre-soaked prior to deployment?

Part 2: 3D-SPMC Steps and Considerations:

1. Scanning & Virtual Augmentation:
    a. Are there already 3D files available on any of the 3D file databases? Check:
        i. Tinkercad (https://www.tinkercad.com), Thingiverse (https://www.thingiverse.com), Pinshape (https://pinshape.com)
        ii. Coral specific: Coral image bank, Smithsonian coral database (https://3d.si.edu/corals)
    b. Do you need to edit the file to meet your needs? If so, some of the common 3D editing softwares are:
        i. freeCAD (https://www.freecadweb.org), Microsoft 3D Builder, Meshlab (https://www.meshlab.net), Tinkercad (https://www.tinkercad.com)

        *note: on some databases you can filter objects by shape and file type. Depending what kind of 3D editing software available to you, this may be necessary

        ii. Check what software your own institution, collaborators, colleagues already have access to.
        iii. Are there easily accessible tutorials for the software you want to use?
        iv. Are there digital educators you can consult (i.e. digital scholarship libraries, engineering makerspaces, 3D design contractors)?

        *note: when it comes to 3D models, there are many ways to skin the cat. Depending on your proficiency with learning new software, the time you have to learn a new technique, often seeing what the people around you already use and have access to is a good choice.

2. 3D Printing:
    a. Printing Resources
        i. Which printers are available to use? Good places to start: engineering faculties, libraries (public or institutional), research labs that do re-constructive morphology (medical, paleontological).
        ii. Depending on your budget, you may be able to out-source the printing to a 3D printing contractor. These private businesses are becoming more popular, and may even be able to help during the design phase.
    b. Printer considerations
        i. What is the print area of the “build plate” (the area the print is being printed onto) and the volume of the area you can print?
        ii. If you require a bigger module than the build area/volume, you may need to go back to Step 1 and modularize your 3D file into components that can be assembled post-printing or post-casting
        iii. What kind of printing material are you using? What size of filament is compatible with your 3D printer?
        iv. What kind of infill will you need for your print? (0-100%)? In the 3D-SPMC method you likely don’t need a solid object (this saves on printing material and printing time) We recommend looking at the different print options for the printer in use and using a lower infill (0-15%).

v. How many 3D files can you upload to the build plate? For small 3D files or large build plates, you may be able to fit more than 1 3D file on the build plate. This may slightly increase the print time, but it is a more efficient way of reproducing numerous 3D prints at once.

*note: Again, there are many printers now available on the market, with a variety of printing techniques. If you are new to this, we recommend consulting with experts who have already done this. Even though it is a relatively simple process when you get used to it, there will inevitably be troubleshooting involved once you begin.

3. Mould Making:
   a. Mould material
      i. How many times do you want to re-use your flexible mould? We recommend *Dragon Skin Silicone* moulding material for its longevity and high-resolution capture of fine-scale details, but there are other options available: silicone from caulking and dish soap, silicone from caulking and cornstarch. (Keep in mind that often these lower-budget moulds may be best suited for proto-typing but may not withhold multiple casts, nor be flexible enough to capture fine-scale details.)
   b. Mould design
      i. What shape is your 3D-print? Can you orient many prints in a planar area? How you orient the 3D prints on the moulding surface will

represent a trade-off between conserving moulding material and leaving enough space between casts that you don’t damage them in the removal process.

ii. Depending on the final module shape, you may decide to place the 3D print flush on the moulding surface, or use clay to lift the 3D print to create a small gap.

4. Casting

a. Material

i. Depending on your research questions/module size, we recommend prototyping your cast to see how they look and withstand underwater. Other considerations: At what depth will they be deployed; how will that affect colour attenuation? Is it a turbid environment; does colour not matter as much?

ii. Mould release is sold as a specific product (by *Viking plastics* and other companies. In our experience and consultations, a neutral vegetable oil is a far cheaper and more effective alternative. *Be sure to pre-soak your modules pre-deployment to release any cues associated with the mould release and casting materials*

b. Space

i. Do you have a covered/dry area to process the casts and let them dry fully? Concrete becomes stronger over time as it cures -the longer you let the modules cure pre-deployment the better (particularly for high wave action/current locations)

ii. Even though it is not necessary, having fans blowing at a low, slow speed over casts will help dry faster (particularly in humid environments)

5. Assembly & Deployment
    a. Assembly
        i. How complex are the modules? Do they need multiple attachment points?
        ii. If designed to be modularizable, can the modules be designed to "inter-lock" to conserve attachment material? (i.e., create locking points in the design stage)
        iii. Other forms of attachment to consider in the assembly phase: concrete, cement, ceramic that is then fired.
    b. Deployment
        c. How much does each module weigh? When considering replication, will all modules be able to be transported at once?
        d. If modular, what is the final weight/volume of the module? Does it make sense to transport the module fully constructed or in parts?

*note: Keep in mind your study objectives; is there a way to deploy modules that mimic biogenic habitats or restoration efforts in your study area? (i.e., some coral restoration practitioners affix coral fragments to the benthos with nails and zip-ties vs. *epoxy*)

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Chapter 3: Disentangling the roles of complexity and composition in mediating species attraction and retention to biogenic habitats

3.1 Introduction

Biogenic habitats created by foundational species provide critical resources which support high-biodiversity ecosystems (Steneck et al. 2002, Bellwood et al. 2004, Angelini et al. 2011) Identifying characteristics of biogenic habitats that attract and retain secondary species (i.e. species that selectively use biogenic habitats) is a key theme in ecology with important implications for habitat conservation and restoration (Peterson et al. 2003, Halpern et al. 2007). The extent to which secondary organisms use particular biogenic habitats has mainly been predicted as a function of habitat "quantity", typically described as the size, area or volume of habitat-forming species (Zuckerberg and Porter 2010, Agudo-Adriani et al. 2016). Habitat "quality" is also likely important to habitat selection, but is often vaguely defined, more varied, or is context specific. Habitat selection theory suggests the strength of cues generated by features indicating high "quality" habitat will increase the likelihood that individuals will be attracted to that habitat (Stamps et al. 2005), while the resources available at the habitat dictate which species will subsequently be retained at (i.e., use) the habitat once it is selected (Bonin et al. 2009). For biogenic habitats, two main features are hypothesized to describe habitat "quality", which influence their detection (attraction) and use (retention) by secondary organisms: (1) their substrate composition (i.e., biochemical features) and, (2) their structural complexity (i.e. three-dimensional features; **Fig 3.1**). Secondary organisms may simultaneously use visual, acoustic and/or olfactory cues provided by substrate composition and complexity to detect and navigate towards suitable habitats across spatial scales, and then make use of resources from compositional and structural complexity features to retain to habitats once found (Lecchini et al. 2005b, Arvedlund and Kavanagh 2010, Huijbers et al. 2012, Zimmer et al. 2016).

The substrate composition (i.e. biochemical features) of habitat-forming species attracts organisms via stimulation of their olfactory sensory systems (Atema et al. 2002, Gratwicke and Speight 2005). Biochemical features are especially important for open communities such as marine, plant, and insect communities that have a dispersive life stage and rely on olfactory senses to navigate towards habitat (Almany 2003). Substrate composition may also influence the retention of secondary species after they are attracted by enhancing foraging resources, either directly through consumption of habitat-forming species' tissue or indirectly by enhancing opportunities to feed on epi-biotic organisms colonizing the biogenic habitat (Lindsey et al. 2006, Brooker et al. 2013). For example, secondary species recruitment to oyster reefs is likely enhanced by attraction to the olfactory cues given off by living oysters and then retained via multiple positive ecological interactions with living oyster reefs such as enhanced foraging resources of colonizing epi-biotic organisms (Powers et al. 2009, Reeves et al. 2020).

The structural complexity created by foundational species' three-dimensional morphology provides visual cues that enhance the attraction of secondary organisms to biogenic habitats (Almany 2003). Structural complexity also provides important features that drive species retention by providing shelter from predators, enhanced foraging resources and reproduction sites (Hixon and Beets 1993, Graham and Nash 2013). The association between secondary organisms and structurally complex habitats has been well documented across multiple ecosystems and contexts including many marine habitats (Carr 1989, Laegdsgaard and Johnson 2001, Gratwicke and Speight 2005, Beck et al. 2011, Cheminée et al. 2016, Dunham et al. 2018, McNeil et al. 2021) forests (Ellwood and Foster 2004, Ellison et al. 2005, Toenies et al. 2018), and grasslands (Öckinger and Smith 2006, Meyer et al. 2009, Peters et al. 2016) to name a few.

Elucidating the relative influence of compositional and structural features driving species' attraction and retention to biogenic habitats may increase our understanding of positive ecological feedback loops between foundational species and secondary organisms, particularly important in the context of global habitat degradation and restoration (Ellison et al. 2005, Milazzo et al. 2019). Studies spanning multiple ecosystems would benefit from understanding the distinct processes that affect habitat characteristics that enhance selection, providing insights into how these characteristics could be incorporated into restoration planning. These insights may identify particular features of foundational species to selectively use in restoration (Suding et al. 2004, Suykerbuyk et al. 2016, Shaver and Silliman 2017, Ladd et al. 2018, Reeves et al. 2020) or influence placement of restoration projects (Hale and Swearer 2017), both of which may enhance selection and use by secondary organisms and thus positive feedback loops that increase restoration success.

However, many studies seeking to disentangle drivers of species' selection to biogenic habitats have been conducted *in vitro*, lacking the realistic considerations of *in situ* experiments like measuring ecological metrics across time (attraction and retention) or accounting for other environmental factors. Moreover, *in situ* studies may confound variation in habitat structural complexity and substrate composition (i.e., the two factors are correlated across biogenic habitat structures; Johansson and Ehrlén 2003, Summerville et al. 2005, Komyakova et al. 2013), or involve habitat augmentation with dead fragments of foundational species that are structurally realistic (Lindahl et al. 2001, Noonan et al. 2012, Coker et al. 2012), but risk releasing cues indicating "poor" quality habitat (i.e., from biochemical features indicating dead/dying habitat; Dixson et al. 2014). Neither study design is equipped to fully disentangle the relative effects of structural and compositional features on organism attraction and retention. Approaches to artificial habitat design used in selection experiments can also introduce other unintended (and potentially negative) cues into the environment (Good 2020, Ruhl and Dixson 2019, McCormick et al. 2020), and may pose additional risk in terms of environmental contamination (Reichert et al. 2018, Fotopoulou and Karapanagioti 2019).

In situ studies that manipulate structural and compositional features independently must also address the potential influence of environmental context (or, large-scale structural complexity) on species attraction and retention to local biotic habitat patches (Buhl-Mortensen et al. 2010, Darling et al. 2017). In particular, habitat quality at larger scales (i.e., $\geq 100m^2$; which we refer to as “background structural complexity”) may influence the attraction and retention of secondary species to habitat patches at more localized scales (i.e., 1-10m^2). As a result, the placement of biogenic habitat patches within a given background structural complexity may render them functionally distinct from each other, as identical habitat patches in different environmental contexts may alter how a habitat patch may attract and retain secondary organisms (Brickhill et al. 2005, Bradley et al. 2019). Generally, habitat selection models assume that if individuals face increased costs (i.e., increased risk of predation or loss of future fitness) when searching for habitat patches embedded within “low quality” environmental contexts, they may be less selective (Stamps and Krishnan 2005), particularly during the initial habitat selection phase (Ward 1987, Booth and Hixon 1999). Alternatively, the “habitat desert” hypothesis predicts preferred selection of “high quality” habitats in a habitat-limited landscape, indicating that “high quality” habitat patches (i.e., defined by their structural and compositional features) in “low quality” environments may see higher attraction and retention.

Here we use corals (class *Anthozoa*, phylum *Cnidaria*), a group of foundational species that provide important habitat for diverse communities of fishes, as a model system in which to disentangle the relative influence of compositional and structural features (the two main aspects of habitat quality) in attracting and retaining secondary organisms to biogenic habitat. Coral reefs are globally important, high-biodiversity ecosystems, which provide critical ecosystem services (Spalding and Grenfell 1997, Pratchett et al. 2014), have cultural and economic significance (Hoegh-Guldberg et al. 2007, Lachs and Oñate-Casado 2020), and support nearly a third of all fish species (Moberg and Folke 1999). Decades of coral decline due to chronic and acute disturbances such as ocean temperature rise (Resplandy et al. 2019), acidification (Sunday et al. 2017), coastal development, eutrophication (Hughes et al. 2003, D'Angelo and Wiedenmann 2014), increased frequency of tropical storms (Lirman 2003), overfishing (Roberts 1995), and coral disease (Green and Bruckner 2000) have also spurred global efforts for restoration, primarily by adding live corals back to degraded reefs (a process called 'out-planting'; Lirman and Schopmeyer 2016). Loss of biogenic coral cover has non-linear impacts to secondary organisms; it is estimated that 62% of fish species decline in abundance following loss of coral habitats (Wilson et al. 2006). Efforts to restore these biogenic habitats have shown varying outcomes of success (Basconi et al. 2020, Ware et al. 2020), based mainly on metrics of coral health and survival (Woesik et al. 2021). Evidence suggests metrics beyond coral survival, such as fish density and biodiversity, should be used to evaluate restoration success (Ruiz-Jaen and Mitchell Aide 2005, Boström-Einarsson et al. 2020) because of the benefits that enhanced fish density and biodiversity provide across multiple spatial scales via fish-derived nutrient provisioning to corals (Shantz et al. 2015) and grazing of competitive macroalgae (Ladd et al. 2018, Lefcheck et al. 2019).

Reef fish recruitment (or 'settlement'), the process whereby pelagic fish larvae move from the water column onto coral reef habitats benthic (i.e. seafloor) habitats as juveniles, is a key ecological process for community biomass production on coral reefs (Victor 1983, Forrester 1990) and can also be used as a measure of ecosystem productivity (McClanahan and Graham 2005, Morais and Bellwood 2020), and thus also a metric of coral reef restoration success. About half of all reef fish species associate closely with corals as juveniles (i.e. use coral habitat patches at the scale of ~1m^2; (Caselle and Warner 1996, Munday 2001, Feary et al. 2007), with evidence for strong selection of shelter and foraging resources provided by corals over multiple spatial and temporal scales (Doherty and Fowler 1994, Coker et al. 2012). However, conflicting findings from studies investigating habitat selection by fish recruits to corals suggest there are likely complex processes involving both substrate composition, structural complexity, and local environmental context driving habitat selection processes (Hadfield and Paul 2001, Coker et al. 2012, Nagelkerken et al. 2015). A majority of these studies (both lab- and field-based) focus on fish association or orientation with coral habitats, without identifying the mechanisms driving attraction *and* retention to these biogenic habitat patches.

To fully isolate the roles structural complexity and substrate composition play in driving fish attraction and retention to coral habitats, we use a recent methodological advance in artificial habitat creation (Garg and Green 2021; in review) within an *in situ* experiment on reef environments in the Florida Keys. Specifically, the structural complexity of coral habitat patches provide visual cues that attract juvenile reef fish (Agudo-Adriani et al. 2016), and shelter from predation (an ecological resource) that retains them (González-Rivero et al. 2017), while the biochemical features of living coral provide olfactory cues that attract juvenile reef fish (Brooker and Dixson 2016), and enhanced foraging resources that retain them (Brandl et al. 2015; for more details on reef fish attraction and retention see **Supporting Information B**). We tracked four metrics of reef fish recruitment on environments augmented with habitat patches containing structurally identical but compositionally distinct (i.e. varying proportions of living and artificial coral tissue) coral over a 50 day period when juvenile fishes may be strongly affected by habitat features: 1) recruitment rate of small-bodied juvenile reef fish (<3cm total length [TL]) in the first 10 days after habitat augmentation as a proxy for the initial attraction phase of fishes from the water column to reef habitats, because juvenile reef fish densities to novel structures have been observed to asymptote within 10 days post-deployment (Shulman et al. 1983, Almany 2003; "relative recruitment rate"), 2) density of small-bodied juvenile reef fish (<3cm TL) from day 10-50 of the experiment as a proxy for the late attraction phase when juvenile fish are still showing some selection among habitat patches (MacPherson et al 1997; "relative recruit density"), 3) density of larger-bodied juvenile reef fish (4-6cm TL) in the last three days of the experiment as a proxy for retention of individuals that have settled and subsequently grown using resources at each habitat patch (Goatley and Bellwood 2016; "relative final density"), and 4) species richness of all juvenile reef fish species (1-6cm TL) over the entire study period as a proxy for the level of retained biodiversity supported on each patch type ("relative species richness"; **Fig 3.2**). We also situated the experiment in two environments (>20m apart) that represent "low" and "high" structural complexity at a reefscape-scale to investigate the influence of environmental context on the relationship between secondary species' habitat use (attraction and retention) and the substrate composition and structural complexity features of augmented coral habitat patches.

We used this study design to answer five questions, several of which have multiple alternative hypotheses based on the trade-offs juvenile fishes face during habitat selection (including: risk of predation from higher search times, potential loss of future fitness, shelter from physical stress, and immediate needs like food and shelter resources [Stamps et al. 2005]; see **Table 3.1** for proposed mechanisms and cited literature): (1) What is the effect of environmental context (i.e., reefscape-scale structural complexity; high vs low relief) on the attraction and retention of reef fishes (measured as our four metrics recruitment) in the absence of habitat augmentation (i.e. ambient rates of fish attraction and retention)? We hypothesize that both attraction and retention would be greater overall in high complexity reefscapes due to existing broad availability of structurally complex shelter sites (**Table 3.1**). (2) How does augmenting structural complexity affect recruitment? We hypothesize that both attraction and retention would be greater overall when structural complexity is augmented via adding habitat patches due to increasing structural complexity (**Table 3.1**). (3) How does reefscape-scale structural complexity (high vs low relief) mediate the effects of augmenting structural complexity on recruitment? We hypothesize attraction may either be: a) greater to structures in low complexity reefscapes where visual cues are relatively stronger or b) greater to structures in high complexity reefscapes where visual cues are dampened, and that retention would be greater overall to structures in high complexity areas due to the cumulative enhanced and diversified resources (**Table 3.1**) (4) What is the effect of variation in biogenic substrate composition (when holding structural complexity constant) on recruitment? We hypothesize that attraction and retention would be greater overall to habitats with higher proportions of living substrate, but that there may be enhanced attraction and retention to habitats with lower proportions of living substrate in the late attraction/retention phase if living substrate habitats are filled quickly, or show species specific associations to habitat composition (**Table 3.1**). (5) Finally, how does reefscape-scale structural complexity (high vs low relief) mediate the effect of biogenic substrate composition on species attraction and retention? We hypothesize attraction and retention may: a) be greater to structures with higher proportions of living substrate in high relief areas compared to low relief areas, as they contain strong structural and biochemical cues to attract recruits and have enhanced resources for them to use, b) show no preferential association to structures with varying proportions of living substrate in low relief areas due to high exposure to predators, or c) show no preferential association to structures with varying proportions of living substrate in high relief areas as they are embedded in an environmental context with existing diverse shelter options **(Table 3.1**)

3.2 Methods

3.2.1 Experimental design and site selection

To evaluate the relative influence of substrate composition and structural complexity on attraction and retention of fishes to reefs, we conducted an *in situ* habitat augmentation experiment in which we manipulated substrate composition while controlling for substrate complexity (**Fig 3.2**). Habitat patches were comprised of different proportions of living *Acropora cervicornis* (staghorn) coral fragments and structurally similar artificial corals at consistent densities on natural reefs. Artificial corals were designed and constructed using 3D-SPMC (3D scanning, printing, molding and concrete casting), a protocol for creating artificial habitat modules that closely match the detailed morphology of focal biogenic organisms as well as manipulate substrate composition of the modules (Garg and Green, 2021; in review).

Each habitat patch consisted of a dense 1x1m^2 cluster of 10 'coral fragments', with experimental treatments representing patches comprised of increasing proportion of living: artificial coral in each cluster of corals: 0% (0 living corals, 10 artificial corals), 30% (3 living corals, 7 artificial corals), 50% (5 living corals, 5 artificial corals), 70% (7 living corals, 3 artificial corals), and 100% (10 living corals, 0 artificial corals; **Fig 3.3D**). The density and area of our habitat patches (10 corals in a tight cluster, each living and artificial coral out-plant ~12cm tall) were consistent with methods employed by reef restoration practitioners within the study region in the upper Florida Keys. All living *A. cervicornis* corals were obtained from the Coral Restoration Foundation offshore nursery at Carysfort Reef, FL, USA.

Habitat patches were added to four 24x16m^2 experimental plots at Carysfort Reef in the Florida Keys National Marine Sanctuary (USA) where no previous restoration had been done (**Fig 3.3A**). To take into consideration the influence of the reefscape structural complexity on habitat selection by juvenile fish, two plots were located in high complexity habitats within the larger reef (mean relief of the reef framework ≈ 3m), and two plots in low complexity locations (mean relief of the reef framework ≈ 0.5m; **Fig 3.3B**) spaced at ~22m distances from one another. In each plot we also selected areas of similar size to our habitat patches in which we did not add habitat modules to serve as controls for the effect of adding habitat structure to the environment (i.e., indicative of ambient fish recruitment and habitat use in the area). The number of replicate habitat patches and control patches (i.e., no structure added) in each treatment were equally represented and randomly distributed within each study plot, ensuring a minimum 4m distance between each patch (n = 16 per treatment; **Fig 3.3C**). With help from staff and interns at the Coral Restoration Foundation, we 'out-planted' (i.e. affixed to the seafloor) all habitat patches in an intensive two-day period on June 3rd and 4th 2019. Corals were affixed to the benthos using a small amount of *Apoxie Sculpt* (approx. 10g/coral fragment), consistent with restoration methodologies used by restoration practitioners in the Florida Keys (**Fig 3.3D**).

3.2.2 Data collection

We visually surveyed all habitat patches and control patches (i.e., no structure added) for fishes 6 cm TL and smaller every 1-2 days for the first 10 days post-deployment (June 5th - June 15th 2019), then every 3-6 days for the following four-weeks (June 20th-July 28th 2019) while scuba diving. Surveys included identifying each individual fish to species and estimating their total length (nearest 1cm) within a $1m^2$ area around each coral cluster. Each patch was surveyed for two minutes; the first minute from a distance of 2m to record any fish in the water column and the second minute from a distance of 0.5m to record cryptobenthic fishes (those closely associated with the habitat substrate on the benthos). All in-water work was approved by the Florida Keys National Marine Sanctuary under permit number FKNMS-2019-033 and University of Alberta AUP #00003176.

3.2.3 Data analysis

All data manipulation and statistical analyses were conducted in R Version 4.0.2 (RStudio Team 2020). To capture habitat attraction and retention by fish at the scale of our experimental patches, we first filtered our survey data to exclude roving shoals or schools of fish that were in transit on the reef (i.e. present at the focal patches for less than 30 seconds and clearly swimming to another part of the reef during an observation). We also excluded from our analyses the first survey post-habitat deployment to avoid capturing recruitment patterns attributed to disturbance caused by the large number of divers present in the water during the habitat module deployments.

Effect of reefscape complexity on ambient fish recruitment

We first examined the effect of reefscape structural complexity (measured as “high” or “low” relief) on the magnitude of fish recruitment in our study plots by comparing recruitment rate (6 visits, n = 96), mean density (10 visits, n = 160), final density (3 visits, n = 48) and species richness (16 visits, n = 256) at the control patches (i.e. no added living or artificial coral) between low and high complexity areas (n = 16; 8 patches in high complexity plots, 8 patches in low complexity plots using a Welch's two sample t-test for recruitment rate and non-parametric Wilcoxon tests for mean density, final density, and species richness.

Effects of habitat patch complexity and composition on fish recruitment

To evaluate how reefscape structural complexity ('low' vs 'high' relief) influenced relationships between fish recruitment and habitat patch quality, we first standardized all of our response variables (calculations described in more detail below: recruitment rate, recruit density, final density, and species richness) for each experimental habitat patch relative to ambient recruitment measured at the control patches (i.e., where no habitat was added) in each study plot. Specifically, we calculated relative response metrics by taking the difference between an observation at an experimental habitat patch on a given sample day and the mean value of control patch in the same background complexity on that day (i.e. a metric of 2 fish m^2 on experimental patch *a* in plot A at time t_1 - mean metric of 3 fish m^2 for control patches in plot A&B [plots with the same background complexity] at time t_1 = relative metric of -1 fish m^2 on experimental patch *a* in plot A at time t_1). Thus, all of our response variables are expressed relative to 0 (representing 'baseline' levels in plots with no added structure), allowing us to evaluate the direction and magnitude of changes attributed to adding structure separately from the effects of modifying habitat composition (% live coral) in low and high relief environments.

We then examined the combined effects of substrate composition (% living coral), and background complexity (low vs high relief) on the attraction (measured as relative recruitment rate and relative density) and retention (measured as final density and species richness) of fishes to experimental habitat patches through linear mixed effect models (LMMs using the lme4 package; Bates et al 2015) and generalized linear mixed effect models (GLMMs using the glmmTMB package; Brooks et al 2017). We also conducted post-hoc analyses in which we calculated significance p-values for pairwise comparisons from our models using estimated marginal means (using the emmeans package; Lenth 2021). Our response metric calculations and corresponding modeling analyses were as follows:

Attraction metric 1: relative recruitment rate

We calculated relative recruitment rate as the difference in density of fishes ≤ 3 cm total length (TL; i.e. the size below which fish recruit from the water column to substrate; (Komyakova and Swearer 2019) at each patch between consecutive visits divided by the number of days between those visits for the first 10 days of the experiment (6 visits; n = 640; **Fig 3.2; Fig 3.4A**) To examine the combined effects of substrate composition (% living coral) and reefscape complexity (low vs high relief) on relative fish recruitment rate to the habitat patches, we first fit a generalized least squares model to determine the optimal auto-correlation structure using Akaike's Information Criterion (Zuur et al. 2009). The top model identified by smallest AIC value had an AR1 autoregressive variance-covariance which allows heteroscedastic variances and non-independence of observations through time (based off visual examination of heteroscedasticity over time; **Appendix A, Fig A3.1**; Pinheiro and Bates 2000). We then fit linear mixed effect models (using AR1 autoregressive structure) with substrate composition treatment (% living coral) and reefscape complexity (low vs. high relief) as interacting categorical fixed effects. We compared models with and without visit (n=6) and plot (n=4) as random intercepts to take into account the spatial and temporal hierarchical data structure using Akaike's Information Criterion (Bolker et al. 2009, Zuur et al. 2009). Plot did not explain any additional variance in the model and was dropped from the final model (**Table A3.1**). Model adequacies were assessed using visual examination of residual plots.

Attraction metric 2: relative density

To examine the combined effects of substrate composition (% living coral) and reefscape complexity (high vs low relief) on the relative density of recruit-sized fishes (≤ 3 cm TL) after the initial recruitment phase (10 visits, n = 800; **Fig 3.2**; **Fig 3.5A**), we fit a generalized linear mixed effect model where relative density of fish recruits (response variable with a gamma distribution) at the habitat patches was predicted by composition treatment (% living coral) and reefscape complexity (low vs. high relief) as interacting categorical fixed effects. Prior to constructing our model, we added a constant value of 6 to our response metric to meet gamma distribution requirements of positive continuous data (Dobson and Barnett 2018). We compared models with and without visit (n=10) and plot (n=4) as random intercepts to take into account the spatial and temporal hierarchical data structure using Akaike's Information Criterion (Bolker et al. 2009, Zuur et al. 2009). Both plot and visit explained significant variance in the model and were both included in the final model (**Table A3.1**). We assessed model adequacy via visual examination of model residuals and tests for uniformity, outliers, and dispersion generated using the package DHARMa (Hartig 2020). Although some evidence of non-uniformity was present (KS test, p = 5.436e-05), all other assumptions were met.

Retention metric 1: relative final density

We calculated the average density of large fish recruits (4-6 cm TL) observed during the last three visits of the experiment (n = 240; **Fig 3.2**; **Fig 3.6A**; response variable termed 'final density') as a proxy for inferred retention of recruit-sized fishes that stay and grow in each habitat patch. To examine the effect of substrate composition and reefscape complexity on final fish density we fit a generalized linear mixed effect model where final fish density (response variable with a gamma distribution) was predicted by patch composition treatment (% living coral) and reefscape complexity (low v high relief) as interacting categorical fixed effects. Prior to constructing our model, we added a constant value of five to our response metric to meet gamma distribution requirements of positive continuous data (Dobson and Barnett 2018). We compared models with and without visit (n=3) and plot (n=4) as random intercepts to take into account the spatial and temporal hierarchical data structure using Akaike's Information Criterion (Bolker et al. 2009, Zuur et al. 2009). Plot did not explain any additional variance in the model and was therefore dropped from the final model (**Table A3.1**). Models with and without visit as a random effect performed comparably (ΔAIC <2); since it is ill-advised to include random effects with too few levels (n = 3 visits; Bolker et al. 2009), and since models performed comparably, the random effect visit was dropped from the final model. The final model was thus a generalized linear model with a gamma distribution (and no random effects; **Table A3.1**). We assessed model adequacy via visual examination of model residuals and tests for uniformity, outliers, and dispersion generated via the package DHARMa (Hartig 2020). Although some evidence of non-uniformity (KS test, p = 0.00275) and outliers (p = 0.000772) was present, all other assumptions were met and performed better in model assessment tests than the GLMM with visit as a random effect.

Retention metric 2: relative species richness

To examine the combined effects of substrate composition and reefscape complexity on the relative species richness of all juvenile and grown fishes (i.e. ≤ 6 cm) at the habitat patches over the study period (16 visits, n = 1280; **Fig 3.2**; **Fig 3.7A**), we fit a generalized linear mixed effect model where relative species richness (response variable with gamma distribution) was predicted by patch composition treatment (% living coral) and reefscape complexity (low vs. high relief) as interacting categorical fixed effects. Prior to constructing our model, we added a constant value of 3 to our response metric to meet gamma distribution requirements of positive continuous data (Dobson and Barnett 2018). We compared models with and without visit (n=16) and plot (n=4) as random intercepts to take into account the spatial and temporal hierarchical data structure using Akaike's Information Criterion (Bolker et al. 2009, Zuur et al. 2009). Plot did not explain any additional variance in the model and was dropped from the final model (**Table A3.1**). We assessed model adequacy via visual examination of model residuals and tests for uniformity, outliers, and overdispersion generated via the package DHARMa (Hartig 2020), with no significant deviation in any of the model assessment tests.

3.3 Results

Effect of reefscape complexity on ambient fish recruitment

In line with our hypothesis, the density of juvenile fishes on control patches during the late attraction phase (Days 10-50) was significantly lower in low (1.68 ± 2.05 fish m^2 [mean ± SD]) versus high (3.08 ± 3.81 fish m^2) relief environments ($W = 2460$, p = 0.01; **Fig A3.2B, Table A3.2**). Contrary to our hypotheses, fish recruitment rate in the first 10 days did not differ significantly between low (0.14 ± 1.80 fish m^2 d^{-1}) and high (0.10 ± 2.21 fish m2 d-1) relief areas (t = 0.08, p = 0.94; **Fig A3.2A, Table A3.2**), nor did final density of larger-bodied (i.e. grown) fish in the last three visits (low relief; 1.54 ± 1.74 fish $m^{2;}$ high relief; 3.00 ± 3.62 fish $m^{2\,;}$ W = 228, $p = 0.21$; **Fig A3.2C, Table A3.2**) and species richness of juvenile and grown fish (≦ 6 cm), over the entire study period (Days 1 - 50; low relief: 1.67 ± 1.22 species; high relief; 1.42 ± 1.12 species; $W = 9260.5$, $p = 0.06$; **Fig A3.2D, Table A3.2**).

Effects of habitat patch complexity and composition on fish recruitment

Attraction metric 1: relative recruitment rate

Relative recruitment rate in the early attraction phase (first 10 days of the experiment; **Fig 3.4A**) varied greatly between habitat patches differing in live coral composition and reefscape complexity (**Fig 3.4B**), and tended to show similar variation compared to ambient recruitment rate at control patches without added structure (**Table 3.2; Fig 3.4A**). There were no significant differences in relative recruitment rate within and between % living coral treatments nor between high and low relief areas (**Table 3.2; Appendix B**). However, in line with our hypothesis, relative recruitment rate in low relief areas tended to be lowest at 0% living coral treatments (-0.12 ± 1.81 fish m^2 d^{-1}), similar to one another at intermediate proportions of coral (30% [0.05 ± 1.41 fish m^2 d^{-1}], 50% [(0.05 ± 1 2.21 fish m^2 d^{-1}], 70% [0.01 ± 2.63 fish m^2 d^{-1}]) and highest at 100% living coral treatments (0.09 ± 2.27 fish m^2 d^{-1}), though these differences were not significant (Appendix B). In contrast, relative recruitment rate in high relief environments was more variable with no apparent trend along the gradient of increasing living coral (0% [-0.02 ± 1.95 fish m^2 d^{-1}], 30% [0.13 ± 1.89 fish m^2 d^{-1}], 50% [0.20 ± 2.11 fish m^2 d^{-1}], 70% [-0.04 ± 2.89 fish m^2 d^{-1}], 100% [0.08 ± 2.19 fish m^2 d^{-1}]; **Fig 3.4B**).

Attraction metric 2: relative recruit density

Counter to our hypothesis, the relative density of juvenile fishes observed throughout the experiment in the late attraction phase (i.e., days 10 - 50; **Fig 3.5A**) was significantly higher on habitat patches in low relief areas (1.65 ± 3.75 fish m^2) than in high relief areas (-0.61 ± 3.12 fish m^2; $t = 4.724$, $p = <.0001$), and tended to be greater than ambient densities at control patches without added structure (**Table 3.2; Fig 3.5B**). While post-hoc pairwise comparison revealed no significant differences between substrate composition treatments in low relief areas, relative juvenile density tended to show a concave shape; highest in treatments with homogenous substrate composition (i.e. 100% [2.45 ± 5.09 fish m^2] and 0% [1.80 ± 3.36 fish m^2] living coral), declining towards intermediate proportions of living substrate (70% [1.64 ± 3.69 fish m^2] and 30% live coral [1.48 ± 2.88 fish m^2]), and lowest at the 50% living coral (0.90 ± 3.16 fish m^2; **Fig 3.5B)**.

Counter to our hypothesis, in high relief areas relative juvenile fish density tended to be lower in patches with added habitat structure than ambient densities (i.e., at patches without added structure; mean values generally below zero), but showed the same concave shape; being significantly higher at 0% living coral (0.21 ± 3.72 fish m^2) than 50% living coral treatments (-1.25 ± 2.27 fish m^2). Post hoc pairwise comparison revealed significant differences between 0% and 50% treatments within high relief areas ($t = 3.67$, $p = 0.0024$; **Table 3.2**). Relative juvenile fish density at 30% (-0.68 ± 3.36 fish m^2), 70% (-0.61 ± 3.30 fish m^2) and 100% living coral patches (-0.74 ± 2.61 fish m^2) were comparable to ambient densities. Post-hoc pairwise comparison of substrate composition treatments between high and low relief areas showed juvenile fish densities were significantly different from each other for all % living coral treatments (0% [t = 2.41, p = 0.0162], 30% [t = 3.548, p = 0.0004], 50% [t = 3.786, p = 0.0002], 70% [t = 3.606, p = 0.0003], 100% [t = 4.758, p = <.0001]; **Appendix B**).

Retention metric 1: relative final density

Counter to our hypothesis, the relative density of grown fishes (4-6 cm TL) at the end of the experiment (Days 43-50; **Fig 3.6A**) was also significantly higher in low relief areas (1.43 ± 3.52 fish m^2) than in high relief areas (0.10 ± 3.65 fish m^2; z= = 3.06, $p = 0.002$; Table 3), and tended to be higher than ambient densities at control patches without added structure (**Fig 3.6B)**.

Also counter to our hypothesis, though not significantly different from one another (**Table 3.2**), relative final fish density again shows a concave shape across substrate composition treatments in low relief areas; tending to be highest on habitat patches with 100% living coral (1.75 ± 4.65 fish m^2), followed by 70% (1.58 ± 3.46 fish m^2), 0% (1.42 ± 3.47 fish m^2), 30% (1.41 ± 3.28 fish m^2) and lowest at 50% (0.96 ± 2.72 fish m^2; (**Fig 3.6B; Table 3.1**). In high relief areas, relative fish density of grown fishes on patches with added structure tended to be lower than ambient densities at the control patches, except at the 70% living coral treatment (1.71 ± 4.30 fish m^2), followed by the 100% treatment (0.42 ± 4.04 fish m^2). Again, fish density showed a concave shape, where the treatment with the lowest relative final densities was 50% living coral (-0.92 ± 2.57 fish m^2), followed by 0% living coral (-0.25 ± 3.01 fish m^2) and 30% (-0.46 ± 3.75 fish m^2). Surprisingly, 70% and 50% living coral treatments in high relief areas were significantly different from each other ($t = -2.78$, $p = 0.043$; **Fig 3.6B**), with 70% living coral treatments hosting nearly double the density of grown fishes than 50% living coral habitat patches. Post-hoc pairwise comparison of substrate composition treatments between high and low relief areas showed 30% ($z = 2.028$, $p = 0.0425$) and 50% ($z = 2.183$, $p = 0.029$) living coral treatments were significantly different from each other between background complexities (**Fig 3.6B; in Appendix B**).

Retention metric 2: relative species richness

Finally, again counter to our hypothesis, relative fish species richness of juvenile and grown fish over the entire study period (Days 1-50; **Fig 3.7A**) was also significantly higher in low relief areas (0.72 ± 1.40 species) than in high relief areas (0.16 ± 1.10 species; ($t = 8.24$, $p < 0.001$; **Fig 3.7B; Table 3.2**), and again tended to be greater than ambient richness at the control plots, except for 30% and 50% living coral treatments in high relief areas (**Fig 3.7B**). Also counter to our hypothesis, relative species richness in low relief areas again shows a concave shape; tending to be highest on habitat patches with 70% (1.39 ± 1.77 species), 100% (1.30 ± 1.90 species), and 0% living coral (1.25 ± 1.72 species) and lowest at patches with intermediate levels of coral (30% [0.79 ± 1.70 species], and 50% [0.77 ± 1.52 species]). Relative species richness in high relief areas follows the same concave shape but with a smaller magnitude, again tending to be highest on habitat patches with 70% (0.74 ± 1.70 species), 100% (0.48 ± 1.55 species) and 0% living coral (0.70 ± 1.39 species), and lowest on patches with intermediate levels of coral (30% [0.14 ± 1.46 species], and 50% [0.10 ± 1.35 species]). Post hoc pairwise comparisons revealed a significant difference between 70% and both 30% and 50% living coral treatments in low (30% [t = -2.815, p = 0.0396], 50% [t = -2.868, p = 0.0341]) and high (30% [t = -3.232, p = 0.011], 50% [t = -3.553, p = 0.0036]) relief areas (**Fig 3,7B; Appendix B**). In high relief areas, there were also significant differences between 0% and both 30% (t = 3.102, p = 0.0168) and 50% (t = 3.423, p = 0.0058) living coral treatments. Post-hoc pairwise comparison of substrate composition treatment between high and low relief areas showed all % living coral treatments were significantly different from each other between background complexities (0% [t = 2.654, p = 0.0081], 30% [t = 3.597, p = 0.0003], 50% [t = 3.862, p = 0.0001], 70% [t = 3.179, p = 0.0015], and 100% [t = 3.993, p = 0.001]; **Fig 3.7B**; **Appendix B**). Over the entire experiment we observed 43 fish species from 12 families, with a total of 39 species-identifiable, and 4 family-identifiable species (**Table 3.3**).

3.4 Discussion

Using coral reefs as model biogenic habitats, we examined the effects of modifying habitat patch-scale structural complexity and substrate composition on the attraction and retention of secondary organisms, and the role of structural context at larger scales (here, ambient structural complexity of the reefscape measured as "low" and "high" relief) in mediating these effects.

Monitoring fish recruitment patterns revealed that reefscape structural complexity (i.e., ~100m^2) mediates the attraction and retention of habitat-dependent organisms to biogenic habitat patches at local scales (i.e., ~1m^2). Regardless of substrate composition, adding structure to low relief reefscapes enhanced attraction (measured as relative recruitment rate and density of juvenile reef fish [≤ 3cm]) and retention (measured as final density of grown reef fish [4-6 cm] and species richness of juvenile and grown reef fish [≤ 6cm]) relative to ambient levels (i.e. in patches without augmented habitat), but this effect disappeared in more complex reefscapes—where added complexity tended to result in slightly lower average attraction and retention relative to ambient levels for most of our metrics. Our results align with studies that show species attraction and retention is highly influenced by ambient background complexity, potentially due preferential habitat patch use in varying environmental contexts. (Gratwicke and Speight 2005, Dominici et al. 2005, Yeager et al. 2017). Diverse coral traits and morphologies have been shown to support specific coral reef fish assemblages (Messmer et al. 2011, Darling et al. 2017). The technique provided here could be deployed in a cross-factor design to look at the effects of different coral growth forms (i.e., manipulating the type of structural complexity at a patch level) interacting with living habitat substrate.

We propose two main mechanisms may be driving the trend for enhanced attraction *and* retention in low relief areas: (1) "non-intuitive" cue use and/or (2) predator-prey dynamics. The first mechanism, non-intuitive cue use, suggests more secondary organisms may select for "low quality" habitats than predicted based on the relative abundance of those habitats in the landscape (Stamps and Krishnan 2005). Adding structurally complex habitat patches in low relief areas (i.e., low "quality") represents a greater proportion of the available habitat, resulting in strong visual cues for secondary organisms in the attraction phase compared to high relief areas. These findings align with other habitat selection studies on coral reefs and oyster reefs which suggest that in areas where habitat is non-limiting (i.e. high relief areas), adding structurally complex habitat patches may have similar attractiveness as surrounding options based on the dampened visual cues they provide in an already heterogeneous environmental context with high relief (Grabowski et al. 2005, Komyakova and Swearer 2019). The second mechanism of predator-prey interactions may be driven by high predator abundances in high relief reefscapes (Beukers and Jones 1998). Habitat augmentation in high complexity areas may result in overall similar recruits to habitat patches in low complexity areas, however constant consumption pressure by predators may result in high turnover from increased juvenile fish mortality, thus homogenizing density levels on habitat patches with ambient levels of attraction and retention in high complexity areas. Intensified predator abundances in high relief reefscapes may also drive non-consumptive effects by providing negative chemical cues to juvenile fishes, resulting in lower selection to any habitat patch (augmented or control) in the attraction phase (Benkwitt 2017). Finally, high relief reefscapes may contain features which limit the field of view of predators (e.g., sea fans and soft corals on reefs). This added cover may encourage risk-taking behaviours from small-bodied fishes, potentially increasing the frequency of their movement between habitat patches (Rilov et al. 2007), thus reducing both their late attraction and subsequent retention to specific habitat patch types.

We also found that substrate composition (i.e., the proportion of live coral tissue) affected both the attraction and retention of reef fishes to added habitat structures relative patches without habitat augmentation (i.e., ambient levels), however the direction and magnitude of effects were not as we anticipated (**Table 3.1**). In particular, a concave pattern emerged moving across substrate composition treatments from 0% to 100% living coral, with the magnitude of both attraction and retention metrics lowest at sites with the most heterogenous composition (50% coral). While the magnitude of the response varied depending on the response metric and background complexity, this pattern was remarkably consistent; The concave pattern was of greater magnitude in low relief areas, however we also see similar (if, dampened) trends in high relief areas, where lowest densities were consistently observed at 50% treatments and tended to be highest at 0% and 100% living coral treatments. These results suggest that juvenile fish are attracted and retained to habitat augmented patches, but to a lesser extent at 50% coral treatments, regardless of environmental reefscape complexity, a trend we did not expect. Our results suggest that larger-bodied (i.e., grown) fishes are relatively equally retained at habitat patches that provide high levels of resources from living substrate and complex structure (100% living coral) *and* habitat patches with just structural resources (0%living coral,) compared with intermediate levels (30%, 50%, and 70%) of living substrate. We propose three potential mechanisms that may explain the non-linear relationship we observed between substrate composition and fish recruitment: (1) density-dependent effects, (2) indirect cue use, and (3) taxa or trait specific selection.

The first mechanism, density-dependent effects may be at play if fish association with habitats are a result of habitat limitation from enhanced competition rather than behavioural preference (Bohnsack 1989). Our results suggest that recruits may be selecting for habitats with higher proportions of living corals during the initial attraction phase **Fig 3.4A**; means increase with % coral, though not significantly different), but then as habitats with both substrate composition *and* structural complexity cues (30-100% living coral treatments) are filled to saturation (i.e., a maximum threshold density at which the microhabitat is considered “filled”; Huntington et al. 2017), they may then be forced to occupy lower ”quality” habitats with lower proportions of living coral substrate during the late attraction phase (**Fig 3.5B**). However, high rates of late attraction and retention to patches with 0% living coral might suggest that either: a) having intermediate levels of living substrate is indicative of “lower” quality habitats to juvenile fish compared to 0% living substrate, and/or b) another mechanism other than or in addition to density-dependent effects is driving this trend.

The second mechanism, indirect cue use, is a density independent process where cues other than visual cues from structurally complex habitat patches and olfactory cues from living coral tissue may be influencing late attraction and retention to habitats (Muller et al. 1997, Stamps and Swaisgood 2007, Fobert and Swearer 2017). Typically, these indirect cues may be biochemical, visual or auditory and come from either positive conspecific attraction cues/heterospecific repellant cues (Sweatman 1983, Lecchini et al. 2005a, Salas et al. 2018), native predator cues that repel prey species (Benkwitt 2017), or top-predator cues that dissuade recruit-feeding mesopredators (Palacios and McCormick 2020). Conspecific cue attraction (also called priority effects) has been well-studied in juvenile reef fish and suggests either the presence of adult or juvenile conspecifics may attract conspecific juveniles (Sale 1991, Almany 2004, Coppock et al. 2016). Since the order in which species colonize habitat patches in the attraction phase may determine which species are retained (Vannette and Fukami 2014), the concave pattern observed during the late attraction and retention phases may be driven by a) initial recruitment to 0% and 100% living substrate treatments by specific taxa/trait assemblages, subsequently encouraging conspecific attraction and retention (as seen by the persistence of the u-shape in both retention metrics (Green et al. 2015, Macura et al. 2019, Coppock et al. 2020, Thompson et al. 2021).

Finally, for the third mechanism, we suggest two trait-based species assemblages which vary in their associations with substrate composition: a) species with high site fidelity (potentially more likely to rely on living coral resources), and b) species with varying aggregating behaviour (potentially less likely to rely on living coral resources). We expect species with high site fidelity will respond to augmented habitat structural complexity and substrate composition more strongly than other taxa as they are likely more closely dependent on micro-habitat patches for shelter, feeding, and reproduction resources (Brandl et al. 2019). For example, damselfish (genera *Stegastes* and *Microspathodon*) are often used as a model organism in experimental studies due to their predictably territorial behaviour (Holbrook et al. 2000, Pratchett et al. 2020) and strong response to habitat patch changes (Schopmeyer and Lirman 2015). They would also be ideal contenders to study the interactive effects of indirect cue and habitat feature cue processes as their aggressive behaviour may include conspecifics and exclude heterospecifics (Robertson 1996, Bay et al. 2001), and loss of living substrate has been shown to alter their behaviour (Di Santo et al. 2020). Cryptobenthic species (family *Gobiidae* and *Blenniidae*; typically ≤ 5cm TL) are also species with high site-fidelity that account for a large proportion of consumed recruit biomass on reefs that show strong homing to living substrate habitat through olfactory cues and rely heavily on habitat patch structural complexity for shelter from predation (Brandl et al. 2019). Lab-based evidence shows coral-dwelling fishes with high site fidelity provide added resilience to coral hosts against coral bleaching (Chase et al. 2018); one could expand upon this study to examine how habitat composition and environmental complexity interact to enhance species with high site-fidelity to bolster against the effects of coral bleaching *in situ*. Species with different schooling behaviours may also be impacted by habitat structural complexity, substrate composition and environmental context. Namely, species that form social aggregations (conspecific or heterospecific assemblages) may be less reliant on habitat for immediate shelter from predation due to their predator deterrence behaviour (Vulinec and Miller 1989, Johannesen et al. 2014).

Thus, we may expect to see the mechanisms presented in our original hypotheses (**Table 3.1**) be more important for solitary fishes that do not benefit from the social protection of aggregating behaviour, thus rely less on substrate composition and more on sheltering resources. One could extend this study by incorporating biochemical assays to detect and isolate chemical compounds emitted by living habitat substrate or con/heterospecific species (Lecchini et al. 2005a).

3.4.1 Implications

Information on structural and compositional characteristics of biogenic habitats that encourage habitat selection by secondary species is important for conservation and restoration planning, particularly as restoration monitoring programs increasingly suggest including secondary species colonization as a measure of ecosystem function. Results from this study indicate habitat composition affects fish recruitment, but that environmental context mediates the direction and magnitude of that response. Regardless of the mechanism, our results support the notion that restoring structural complexity via habitat augmentation, particularly in low structural complexity environments, will likely enhance density and diversity of reef-dependent organisms. This recommendation aligns with other results which suggest the direction and magnitude of response to adding structure via augmenting local habitat patches greatly depend on ambient environmental contexts (Macura et al. 2019, Gilby et al. 2019). Efforts to better quantify ambient structural complexity are in early stages of development and may elucidate more nuanced relationships between secondary organism associations to structurally complex habitat characteristics across multiple spatial scales, particularly on coral reefs (Helder and Green; in press). One of the emerging methods to better quantify metrics of structural complexity at the scale of <100m^2 across terrestrial and aquatic ecosystems is structure-from-motion 3D photogrammetry, a process wherein multiple 2D images are spatially referenced against each other to generate a 3D model of structural characteristics (Burns et al. 2015, Woodget et al. 2017, Iglhaut et al. 2019, Mohamed et al. 2020). More established techniques in remote sensing may be used to discern structural complexity characteristics at larger scales (>100m^2; Mumby et al. 1997, Osborne et al. 2001, Nagendra et al. 2013).

Although metrics of attraction and retention were high to 0% living coral substrates relative to background levels (although, they did not exceed 100% living coral treatments), we concur with other researchers that artificial structures should not be used to replace vital biogenic habitats in wide-scale restoration (Shaver et al 2020; Robertson and Hutto 2006) lest they become ecological traps (pull organisms away from "high quality" habitat; Battin 2004) rather in pilot studies or manipulative studies such as the one presented here. We suggest that species or trait specific responses are likely driving the trend of high attraction and retention to 0% and 100% living coral treatments, indicative of resource partitioning strategies among diverse fish communities. We recommend further investigation is needed to determine differences in fish community habitat selection processes, and that longer-term studies may elucidate adult fish assemblages affected during the recruitment habitat selection phase.

3.4.2 Future Directions

We suggest three considerations for future studies aiming to understand key characteristics of biogenic habitats for restoration purposes: (1) spatial considerations, (2) temporal considerations, and (3) target restoration species. As seen in this study, the interaction of structural complexity and substrate composition may differ across spatial scales, from structural complexity at the habitat patch level (1 -10m^2) to reefscape structural complexity (10 – 100m^2).

Considering that recruitment processes may show site-specific differences (or inter-regional differences; Hein et al. 2020) in response to benthic (i.e. seafloor) habitat features (Opel et al. 2017), we recommend more studies like this on different reefs to understand how these interactions may differ site-to-site or region-to-region. For example, dominant currents or larval life-histories may affect larval fish dispersal strength, affecting their detection and navigation towards biogenic habitats (Swearer and Shima 2010). Additionally, the spatial placement of habitat patches within a site may influence search effort and search costs for secondary organisms (i.e. edge effects; McCollin 1998). We randomized and equally distributed the placement of substrate composition treatments (including control plots where no corals were added) within our study site to avoid edge effects, but suggest future studies may specifically focus on disentangling how connectivity, isolation, and placement of habitat patches may also influence habitat selection.

Habitat selection is a highly variable process which may vary over temporal scales or show inter-annual variation (Becker et al. 2017, Richter et al. 2020), We measured recruitment over only part of the season in which larval fish are moving from the water column on to reefs (i.e. capturing dynamics from May-June, while recruitment occurs from May-early September), and note that longer-term studies may reveal alternate patterns of attraction and retention to habitats by different juvenile fish assemblages. This has implications when identifying how structural complexity and compositional features may retain mature fishes through multiple seasons and years, an important consideration for restoration monitoring and evaluating long-term restoration success. Recruitment “failure” (where juveniles of a given species do not recruit to biogenic habitats in a given year) may also only be detected over a time lag in adult populations (Lin et al. 2021), therefore longer-term studies of habitat selection may further our understanding of the implications for habitat selection to biogenic habitats. Some evidence indicates that ocean acidification may hinder the olfactory sensory systems of fish larvae (Munday et al. 2009), thus longer-term studies looking at reef degradation (through dissolution of their calcium carbonate skeletons from acidification) may provide insights into how this would affect habitat detection and selection processes.

Finally, tracking target restoration species' (i.e., key secondary species that may disproportionately be affected through habitat augmentation from restoration activities and/or species which confer key benefits to restored habitats) response to structural and compositional features may elucidate important habitat features driving their attraction and retention (Arias-Godínez et al. 2021). On coral reef ecosystems, herbivorous fishes have been associated with enhanced ecosystem functioning as they graze on fleshy macroalgae that compete with corals for space on reefs (Topor et al. 2019, Ladd and Shantz 2020) and may be an important source of fish-derived nutrients (Shantz et al. 2015). Herbivores have been documented to show sensitivity to habitat characteristics within reefscapes (Pombo-Ayora et al. 2020, Eggertsen et al. 2020), thus gaining an understanding of habitat characteristics that attract and retain herbivores may leverage their positive trophic facilitations to bolster restoration success. (For further discussion on other factors affecting coral reef fish recruitment and future avenues of research please see **Supporting Information B**)

3.4.3 Conclusion

The results from this study indicate that biogenic substrate composition, structural complexity, and the local environmental context (ambient structural complexity) mediate secondary organism attraction and retention to biogenic habitats. We found that ambient structural complexity strongly affected the attraction and retention of secondary organisms, and mediated the effect of adding structurally complex habitat patches to reefscapes. In the context of global habitat restoration, our results suggest that 1) habitat augmentation increases both the attraction and retention of juvenile reef fish, particularly when habitat patches are placed in low complexity environments, 2) intermediate levels (%) of living coral cover at the patch-level lower the attraction and retention of secondary species, regardless of reefscape environmental context, likely driven by species and trait specific responses, and that 3) ultimately, habitat selection behaviour (attraction and retention) represents trade-offs in present and future fitness costs that affect animals across life-stages and evolutionary time-scales (Morris 2003), we recommend further study to disentangle the complex patterns driving habitat selection. Understanding the complex processes that drive habitat selection to biogenic habitats allows us to better understand what factors are driving key ecosystem processes, incorporate this knowledge into conservation and restoration initiatives, and helps answer one of the fundamental questions in ecology.

Table 3.1: Alternative hypotheses associated with each recruitment pattern response (rows, A = recruitment rate, B = juvenile fish density, C = grown-fish density, D = species richness) and research questions (columns, 1 = ambient relief, 2 = structural complexity. References are noted the first time a mechanism is proposed in a given column.

	1.Ambient Relief (High vs Low)	**2a. Structural Complexity** (Structure vs. no Structure)	**2b. Structural Complexity and Ambient Relief**	**3a. Substrate Composition** (0-100% living biogenic substrate)	**3b. Substrate Composition and Ambient Relief**
Ecological Process: Inferred early Attraction **Response Metric A:** juvenile fish recruitment rate(≲ 3cm)	Ha: ↑ in high relief areas due to strong association between reef-scape structural complexity and juvenile fish colonization from visual cues (Caley and St John 1996; Darling et al 2017; Gratwicke and Speight 2004)	Hb: ↑ to areas with added structure due to the increased visual cues (Ladd et al 2019)	Ha: ↑ to structures in low complexity areas due to added habitat representing a greater proportion of available habitat (strong visual cues) vs. ↕ to structures in high complexity areas due to broader micro-habitat availability and choice (less effect of visual cues; Stamps and Krishnan 2005) Hb: ↑ to added structure in high complexity areas, as they would be the most structurally complex combination, augmenting visual cues	Ha: ↑ to habitats with greater proportions of living biogenic substrate due to presence of both visual and biochemical cues (Hadfield and Paul 2002; Coker et al 2012)	Ha: ↑ to habitats with greater proportions of living biogenic substrate in high relief areas as they contain strong visual and biogenic cues (Beukers and Jones 1998) Hb: ↕ to habitats with greater proportions of living biogenic substrate in low relief areas due to limited options in the environment (i.e. cost from increased predation risk outweighs attraction cues and selectivity behaviours; Stamps et al 2005) Hc: ↕ to habitats (regardless of composition) in high relief areas as there are diverse visual and biochemical cues in the local environment
Ecological Process: Inferred late Attraction **Response Metric B:** juvenile fish density (≲ 3cm)	Ha: ↑ in high relief areas due to strong association between reef-scape structural complexity and juvenile fish colonization from visual cues	Ha: ↑ to areas with added structure due to the increase visual cues	Ha: ↑ to structures in low complexity areas due to added habitat representing a greater proportion of available habitat (strong visual cues) vs. ↕ to structures in high complexity areas due to broader micro-habitat availability and choice (less effect of visual cues) Hb: ↑ to added structure in high complexity areas, as they would be the most structurally complex combination, augmenting visual cues	Ha: ↑ to habitats with greater proportions of living biogenic substrate due to presence of both structural and biochemical cues Hb: ↑ to habitats with lower proportion of living biogenic substrate if they were filled quickly in the early recruitment phase (i.e. reached early saturation)	Ha: ↑ to habitats with greater proportions of living biogenic substrate in low relief areas due to limited selection of high "quality" habitats after early attraction phase vs. ↕ in high relief areas due to diverse visual and biochemical cues in the entire environment Hb: ↕ to habitats with living biogenic substrate in low relief areas due limited options in the environment (i.e. cost of being selective outweighs attraction cues) vs. ↑ in to habitats with living biogenic substrate in high relief areas over time for greater access to diverse resources

Table 3.1: continued

Ecological Process: Inferred Retention **Response Metric C:** Grown-fish final density (4-6cm)	Ha: ↑ in high relief areas due to strong evidence of reef fish association to structural complexity and broad ecological resources they provide	Ha: ↑ to areas with added structure due to continued resources of shelter from predation as recruits grow (Urbina-Barreto 2020; Aguodo-Adriani et al 2016)	Ha: ↑ to areas with added structure in high relief areas due to cumulative interaction of shelter availability and wide suite of resources available in high complexity areas (Graham and Nash 2013)	Ha: ↑ to habitats with greater proportions of living biogenic substrate due to presence of both structural and compositional resources as recruits grow	Ha: ↑ to habitats with living biogenic substate in low relief areas due to selection of higher "quality" resources in the given environment vs. ↕ to habitats with living biogenic substrate in high relief areas due to broader availability of resources in the environment relative to the added habitat patch Hb: ↕ to habitats with living biogenic substrate in low relief areas due limited options in the environment (i.e. can't afford to select habitat with compositional and structural resources if structural resourced more important) vs. ↑ to habitats with living biogenic substrate in high relief areas over time for specifically enhanced structural and biogenic resources (Lagdsgaard and Johnson 2001)
Ecological Process: Retention of Biodiversity **Response Metric D:** Species Richness (1-6 cm)	Ha: ↑ in high relief areas due to diverse reef fish association to structural complexity and diverse ecological resources they provide (Messmer et al 2011; Komyakova et al 2018)	Hb: ↑ in areas with added structure as the habitat-patch diversifies available habitat space and resources	Ha: ↑ in areas with added structure in high relief areas due to diversifying resource availability in an already structurally diverse and complex environmental context (Darling et al 2017)	Ha: ↑ in habitats with greater proportions of living biogenic substrate due to the wider availability of resources supporting diverse species assemblages Hb: ↕, may be taxa or trait specific (i.e. species-specific response to heterogeneous living coral substrates; Bonin 2012)	H1: ↑ to living biogenic habitats in high relief areas due to presence of both structural and biochemical cues and resources that may support diverse species assemblages H2: ↑ to living biogenic habitats in low relief areas due to presence of both structural and biochemical cues and resources in a habitat "desert" (i.e. otherwise structurally homogeneous) H3: ↑ to intermediate levels of living biogenic habitats (regardless of ambient relief) as heterogeneous habitat composition may promote diverse fish assemblages

Table 3.2 Model results for each recruitment metric. Values are model coefficients (± SE).

	Dependent variables:			
	Relative Recruitment Rate	Relative Saturation Density	Relative Final Density	Relative Species Richness
	Linear mixed effects	*Generalized linear mixed effects*	*Generalized linear*	*Generalized linear mixed effects*
	(1)	(2)	(3)	(4)
Low, 0% (intercept)	-0.117	2.056^{***}	0.156^{***}	$< 2e\text{-}16^{***}$
	(0.314)	(0.090)	(0.020)	(0.0467)
Low, 30%	0.160	-0.041	0.000	0.031^{*}
	(0.381)	(0.071)	(0.028)	(0.054)
Low, 50%	0.156	-0.125^{*}	0.012	0.027^{*}
	(0.376)	(0.071)	(0.029)	(0.0536)
Low, 70%	0.146	-0.029	-0.004	0.511
	(0.378)	(0.071)	(0.028)	(0.054)
Low, 100%	0.205	0.068	-0.008	0.837
	(0.377)	(0.071)	(0.028)	(0.054)
High, 0%	0.103	-0.243^{**}	0.055	0.008^{***}
	(0.380)	(0.114)	(0.034)	(0.054)
High, 30%	-0.027	-0.114	0.010	0.504
	(0.533)	(0.100)	(0.048)	(0.076)
High, 50%	0.057	-0.136	0.022	0.392
	(0.528)	(0.100)	(0.051)	(0.076)
High, 70%	-0.172	-0.118	-0.058	0.709
	(0.530)	(0.100)	(0.043)	(0.078)
High, 100%	-0.106	-0.231^{**}	-0.018	0.343
	(0.527)	(0.100)	(0.045)	(0.076)
Observations	640	800	240	1280
Akaike Inf. Crit.	2,814.742	3,880.456	1,247.508	3940.7
R^2	0.0570	0.1377	0.0686	0.0958
Note:				$^{*}p^{**}p^{***}p<0.01$

Table 3.3 List of all fish species (juvenile and grown fish, ≤ 6cm total length), their common name and their Family over the study period. Listed alphabetically by Family.

Family	**Species name**	**Common name**
Acanthuridae	Acanthurus coeruleus	Blue Tang
Acanthuridae	Acanthurus bahianus	Ocean Surgeonfish
Blenniidae	Blenniidae	Blenny Family
Blenniidae	Parablennius marmoreus	Seaweed Blenny
Chaenopsidae	Acanthemblemaria spinosa	Spinyhead Blenny
Chaenopsidae	Acanthemblemaria chaplini	Papillose Blenny
Chaenopsidae	Acanthemblemaria maria	Secretary Blenny
Chaetodontidae	Chaetodon capistratus	Foureye Butterflyfish
Gobiidae	Coryphopterus dicrus	Colon Goby
Gobiidae	Coryphopterus glaucofraenum	Bridled Goby
Gobiidae	Gnatholepis thompsoni	Goldspot Goby
Gobiidae	Coryphopterus personatus	Masked Goby
Gobiidae	Coryphopterus eidolon	Pallid Goby
Gobiidae	Goby sp.	Goby sp. unid.
Haemulidae	Haemulon sp.	Grunt unid. Species
Labridae	Thalassoma bifasciatum	Bluehead Wrasse
Labridae	Halichoeres maculipinna	Clown Wrasse
Labridae	Halichoeres garnoti	Yellowhead Wrasse
Labridae	Halichoeres radiatus	Puddingwife
Labridae	Halichoeres bivittatus	Slippery Dick
Labridae	Halichoeres poeyi	Blackear Wrasse
Labrisomidae	Malacoctenus triangulatus	Saddled Blenny
Labrisomidae	Malacoctenus macropus	Rosy Blenny
Pomacentridae	Stegastes partitus	Bicolor Damselfish
Pomacentridae	Stegastes diencaeus	Longfin Damselfish
Pomacentridae	Stegastes planifrons	Threespot Damselfish
Pomacentridae	Stegastes dorsopunicans	Dusky Damselfish
Pomacentridae	Chromis cyanea	Blue Chromis
Pomacentridae	Microspathodon chrysurus	Yellowtail Damselfish
Pomacentridae	Stegastes variabilis	Cocoa Damselfish
Pomacentridae	Stegastes leucostictus	Beaugregory
Scaridae	Sparisoma aurofrenatum	Redband Parrotfish
Scaridae	Scarus iserti	Striped Parrotfish
Scaridae	Sparisoma viride	Stoplight Parrotfish
Scaridae	Scarus taeniopterus	Princess Parrotfish
Scaridae	Sparisoma atomarium	Greenblotch Parrotfish
Scaridae	Scarus vetula	Queen Parrotfish
Scaridae	Scarid sp.	Scarid - unidentified
Scaridae	Sparisoma rubripinne	Yellowtail Parrotfish
Serranidae	Hypoplectrus sp.	Hamlet species
Serranidae	Hypoplectrus unicolor	Butter Hamlet
Tetraodontidae	Canthigaster rostrata	Sharpnose Puffer
Tripterygiidae	Enneanectes boehlkei	Roughead Blenny

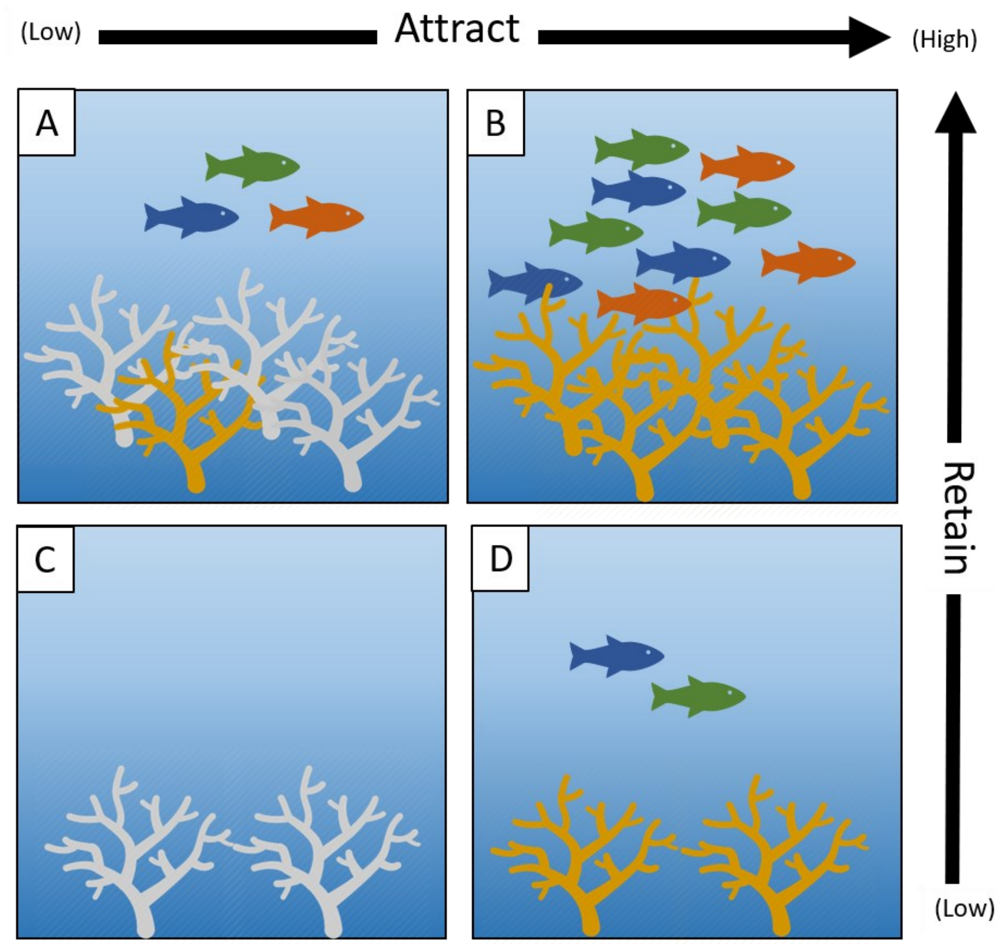

Fig 3.1: The structural complexity and substrate composition of biogenic habitats (e.g., coral reef, *Acropora cervicornis*) mediate a range of visual, auditory, and chemosensory cues affecting the selection (attraction) and use (retention) of secondary species (e.g., juvenile reef fish). For example, secondary species sense biochemical features of high-value (e.g., high proportion living tissue) substrate via olfactory cues, and are subsequently retained via enhanced foraging resources the substrate provides. Secondary species detect high-value three-dimensional features (e.g., high structural complexity) via visual cues, and are retained at habitats by shelter resources provided by the structure. We predict that when habitats contain: (A) high complexity structure but low-proportion live substrate composition, resident organisms will be attracted at low rates, but retained once they are attracted due to sheltering resources, (B) high complexity structure and high proportion live substrate, highly available cues and resources attract and retain species at high rates, (C) low complexity structure and live substrate composition, species attraction and retention is low, and (D) low complexity structure but high-proportion live substrate compositional, organisms are attracted at high rates via cue stimulation, but few are retained due to low overall resource availability. This experiment tests hypotheses of attraction and retention as exemplified in (A) and (B) by manipulating substrate composition (living tissue) and holding structural complexity constant.

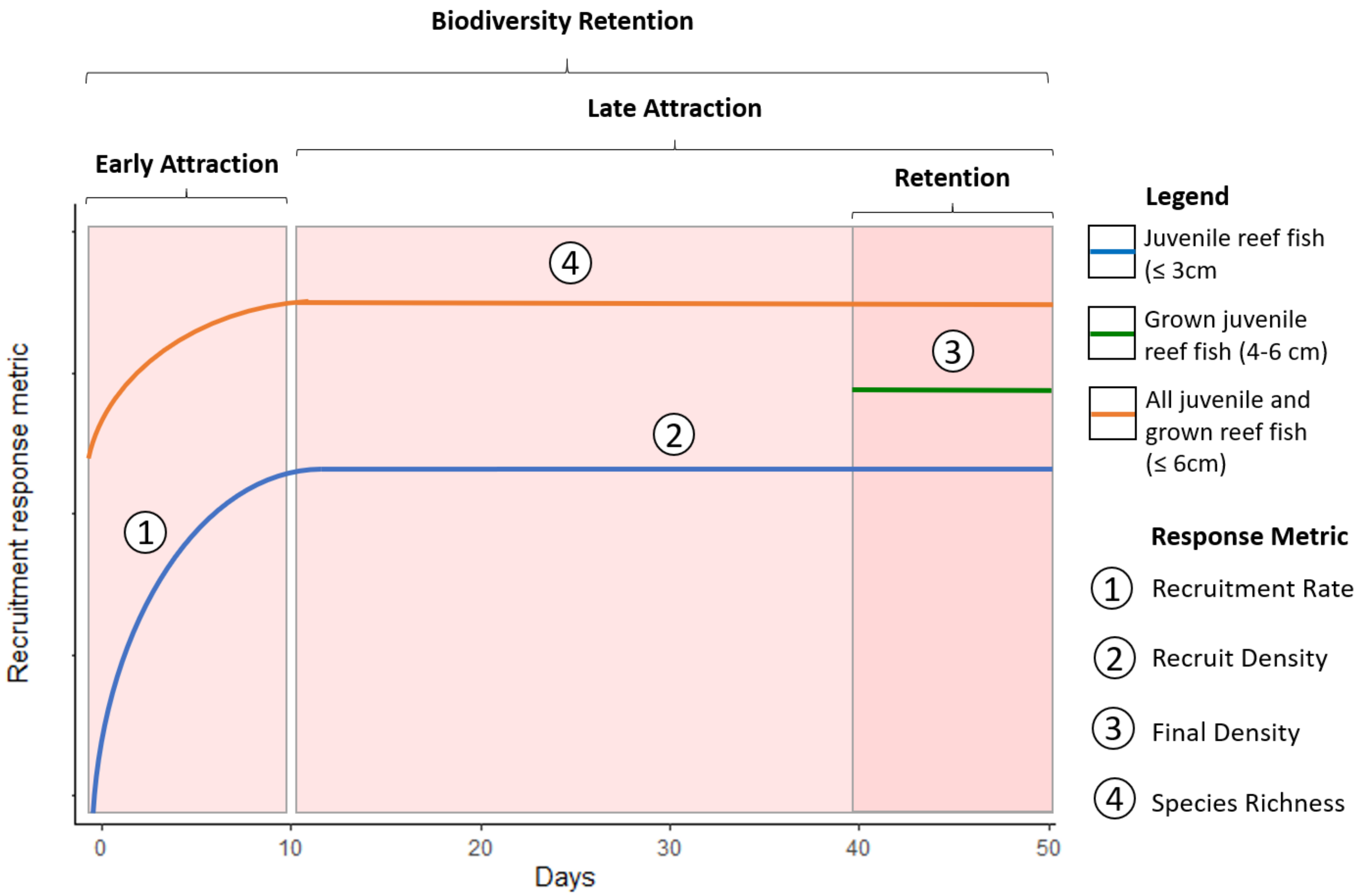

Fig. 3.2: Illustration of our approach to calculating metrics that capture fish attraction and retention to reef patches (i.e. 'recruitment') over the 50-day habitat augmentation experiment. 1) Recruitment rate of juvenile fish (i.e. "recruit" ≤ 3cm) is measured in the first 10 days and captures initial habitat selection in the early attraction phase, 2) Recruit density of juvenile fish (i.e. "recruit" ≤ 3cm) is measured from days 10-50 and captures filling of habitat patches in the late attraction phase, 3) Final density of grown fish (4-6cm) is measured in the last three visits of the experiment (after day 37) and captures juvenile fish that grow and use the resources available at that habitat patch in the retention phase, 4) Species richness of juvenile and grown fish (≤ 6cm) is measured over the entire study period and captures biodiversity at each habitat patch that is retained over the experiment.

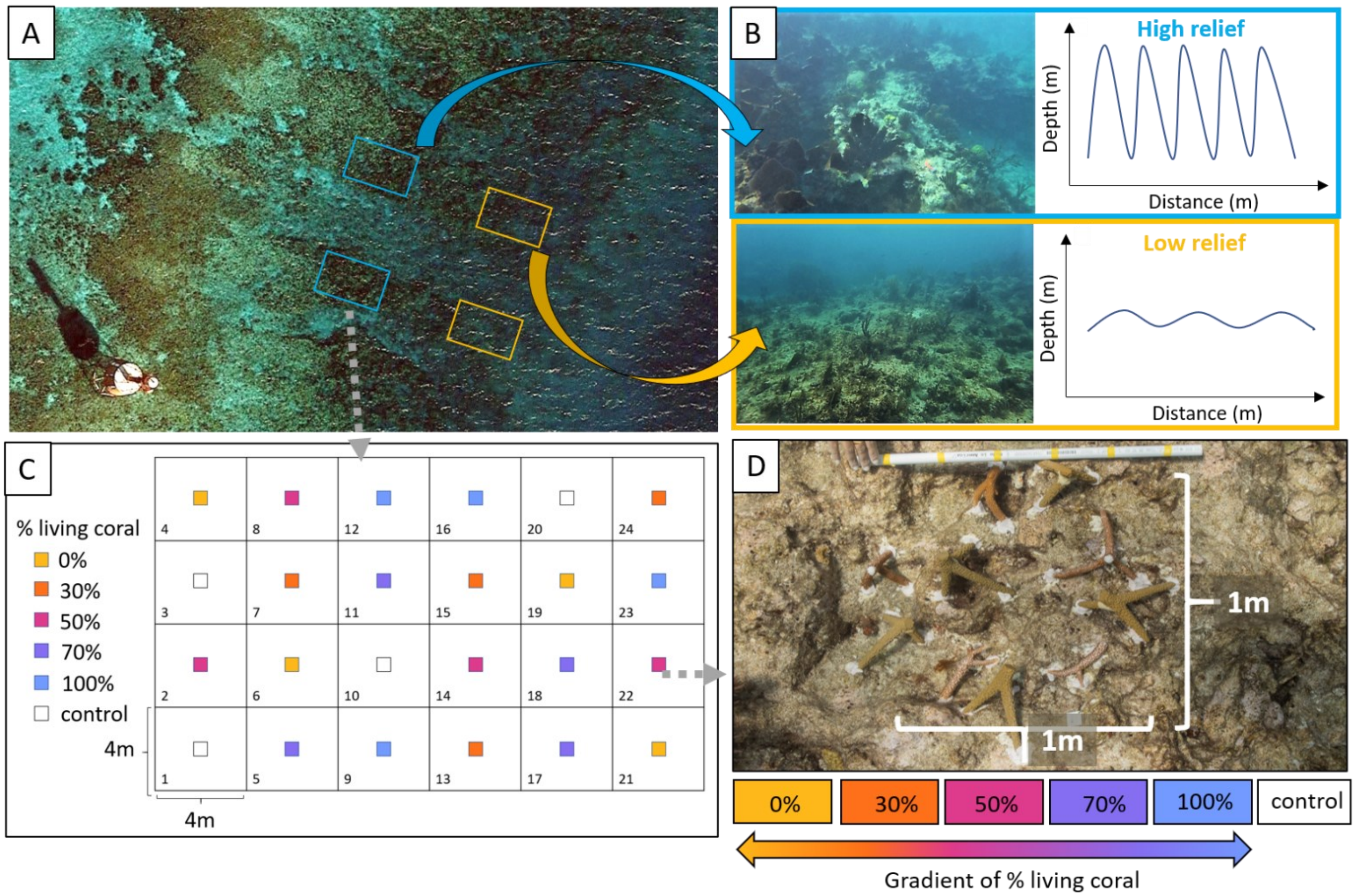

Fig. 3.3 (A) Carysfort Reef in the Florida Keys National Marine Sanctuary (USA), where our study took place in four 24x16m^2 experimental plots spaced at 22m distances from each other. Two plots outlined in blue are in high background complexity environments and the two plots outlined in yellow are in low background complexity environments. (B) Top image (outlined in blue) depicts high background complexity areas at this reef site, with a diagram depicting a high relief reefscape (mean relief of the reef framework ≈ 3m); bottom image (outlined in yellow) depicts low background complexity areas at this reef site, with adjacent diagram depicting a low relief reefscape (mean relief of the reef framework ≈ 0.5m). (C) Each 24x16m^2 experimental plot was divided into 24 4x4m^2 grid cells and habitat patches were placed at the centre of each grid cell in tight 1m^2 cluster. (D) Each 1m^2 habitat patch contained a tight cluster of ten corals at different ratios living: artificial coral fragments representing a categorical gradient of substrate composition treatments: 0% (0 living corals, 10 artificial corals), 30% (3 living corals, 7 artificial corals), 50% (5 living corals, 5 artificial corals), 70% (7 living corals, 3 artificial corals), and 100% (10 living corals, 0 artificial corals)

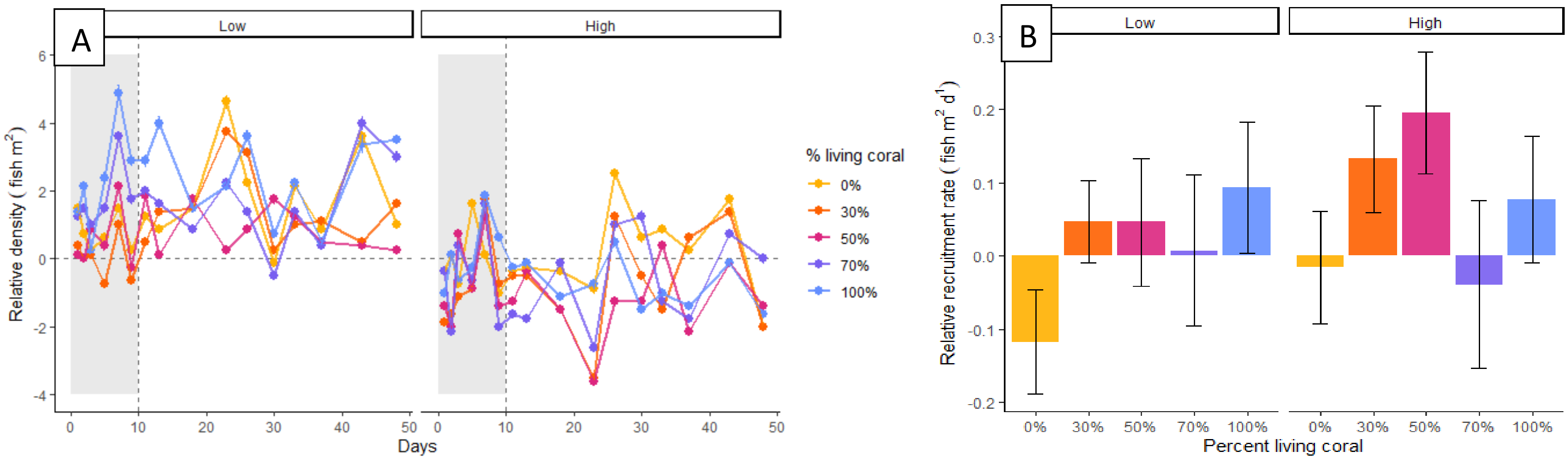

Fig. 3.4 (A) Density (mean ± S.E.) of recruit-sized fishes (≲ 3cm) on experimental habitat patches relative to control plots (i.e. no added habitat) in low and high relief reef environments over the course of the study. Habitat patches were structurally identical but varied in percent live coral cover. Day is relative to the date on which habitat patches were added to the environment (i.e. Day 0). Greyed area represents the initial attraction phase of the experiment (i.e. the first 10 days since structure was added) where rapid colonization to structures is occurring and from which relative recruitment rate was calculated. (B) Mean daily recruitment rate for each substrate composition treatment (mean ± S.E.; 0% [0 living corals, 10 artificial corals], 30% [3 living corals, 7 artificial corals], 50% [5 living corals, 5 artificial corals], 70% [7 living corals, 3 artificial corals], and 100% [10 living corals, 0 artificial corals]) over the initial phase of the experiment (Days 1-10). Recruitment rate was calculated by taking the difference in density between consecutive visits divided by number of days between those visits.

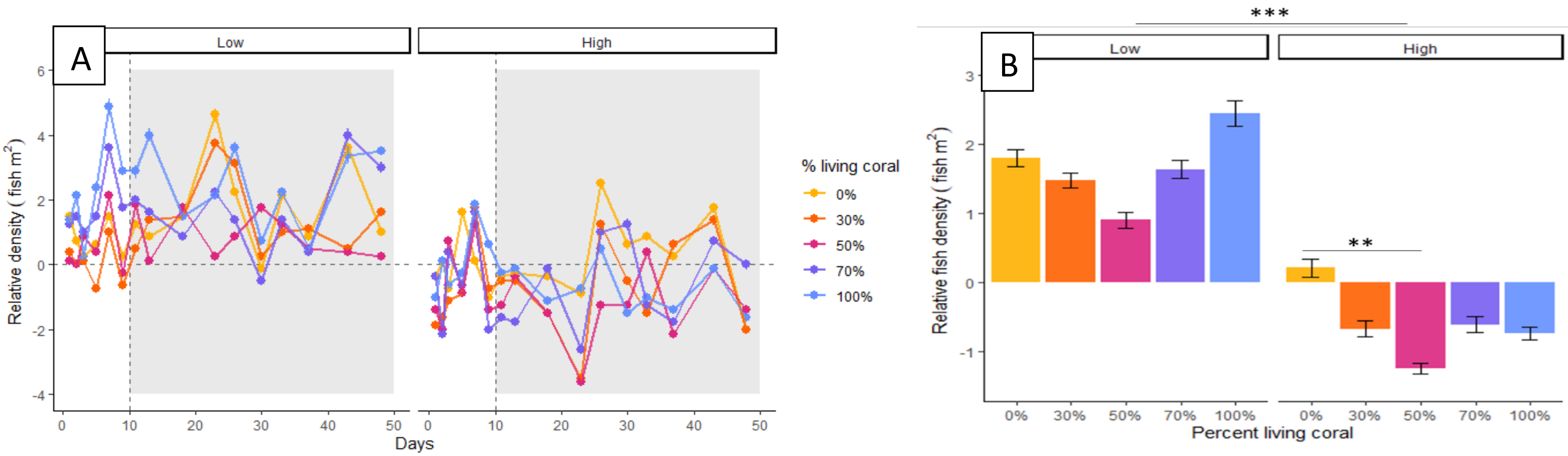

Fig 3.5. (A) Density (mean ± S.E.) of recruit sized fishes (≲ 3cm) on experimental habitat patches relative to control plots (i.e. no added habitat) in low and high complexity reef environments over the course of the study. Habitat patches were structurally identical but varied in percent live coral cover. Day is relative to the date on which habitat patches were added to the environment (i.e. Day 0). Greyed area represents the late attraction phase of the experiment (i.e. from day 10 - 50 since structure was added) where fish recruits are finished rapidly colonizing structures and are settling to specific habitat patches, and from which relative density was calculated. (B) Mean recruit density for each substrate composition treatment (mean ± S.E.; 0% [0 living corals, 10 artificial corals], 30% [3 living corals, 7 artificial corals], 50% [5 living corals, 5 artificial corals], 70% [7 living corals, 3 artificial corals], and 100% [10 living corals, 0 artificial corals]) over the settlement phase of the experiment (Days 10-50).

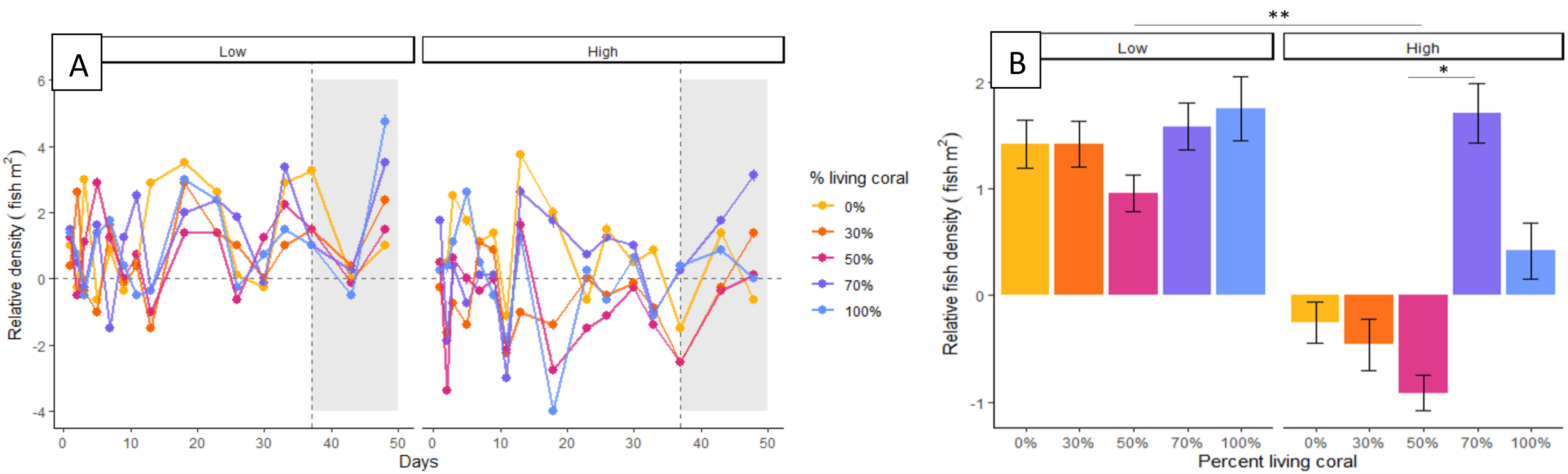

Fig 3.6. (A) Density (mean ± S.E.) of larger fishes (4-6cm) on experimental habitat patches relative to control plots (i.e., no added habitat) in low and high complexity reef environment over the course of the study. Habitat patches were structurally identical but varied in percent live coral cover. Day is relative to the date on which habitat patches were added to the environment (i.e., Day 0). Greyed area represents the retention phase of the experiment (i.e., the last 3 survey visits) where a portion of juvenile fish have settled and grown into larger fishes (4-6cm) and from which relative final density was calculated. (B) Mean final density for each substrate composition treatment (mean ± S.E.; 0% [0 living corals, 10 artificial corals], 30% [3 living corals, 7 artificial corals], 50% [5 living corals, 5 artificial corals], 70% [7 living corals, 3 artificial corals], and 100% [10 living corals, 0 artificial corals]) over the final 3 days of the experiment (Days 37, 43, and 48).

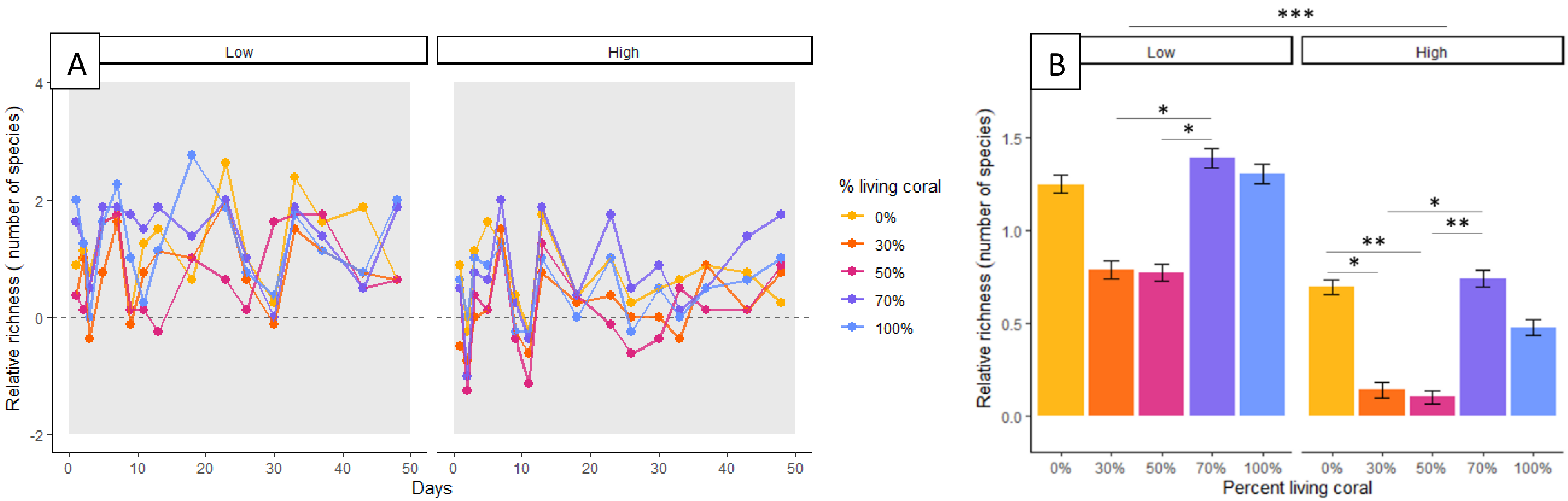

Fig 3.7. (A) Number of species (mean ± S.E.) of juvenile and grown fishes (≾ 6cm) on experimental habitat patches relative to control plots (i.e. no added habitat) in low and high complexity reef environments over the course of the study. Habitat patches were structurally identical but varied in percent live coral cover. Day is relative to the date on which habitat patches were added to the environment (i.e. Day 0). Greyed area represents the entire experiment phase where all juvenile (≾ 6cm) and grown (4-6 cm) fishes were pooled to give total species richness (B) Mean number of species for each substrate composition treatment (mean ± S.E.; 0% [0 living corals, 10 artificial corals], 30% [3 living corals, 7 artificial corals], 50% [5 living corals, 5 artificial corals], 70% [7 living corals, 3 artificial corals], and 100% [10 living corals, 0 artificial corals]) over the entire experimental period (Days 1-50).

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3.6 Supporting Information B

Cues and resources driving juvenile reef fish attraction and retention

Like other biogenic habitats, both the structural complexity and substrate composition of *A. cervicornis* features are hypothesized to provide cues that attract fishes, and their respective resources may then retain fishes. It has been well documented in lab and field studies that visual cues from structurally complex habitats drive non-linear increases in fish biomass, abundance, and densities and is therefore a strong predictor of coral reef fish recruitment (Caley and St John 1996, Friedlander and Parrish 1998, Kawasaki et al. 2003, Rogers et al. 2014, Agudo-Adriani et al. 2016). Complex structures also provide important resources that may retain fishes such as shelter from predators, shelter from physical stress, and nesting sites (Robertson et al. 1981, González-Rivero et al. 2017). At the spatial scale of a small habitat patch (i.e. a cluster of coral fragments in a $1m^2$ area), advances in 3D photogrammetry and 3D printing have quantified structural complexity metrics and shown how increased habitat complexity is associated with higher reef fish abundances (Pérez Pagán and Mercado-Molina 2018, Urbina-Barreto et al. 2020). The main factors degrading the visual cues and sheltering resources provided by coral structural complexity are three-dimensional degradation from coral bleaching (Alvarez-Filip Lorenzo et al. 2009, Magel et al. 2019), acidification weakening the calcium carbonate skeleton of corals (Foster et al. 2016), and physical destruction from increased storm frequency (Gardner et al. 2005).

Rapid decline of coral dwelling fish within days after a bleaching event (and before structural degradation) indicates that substrate composition from living coral tissue is also an important feature driving reef fish attraction and retention (Booth and Beretta 2002, Bonin et al. 2009). Chemical cues associated with coral reef habitats can play a strong role during the summer fish recruitment season by attracting larval fish to reef habitats (Tolimieri et al. 2000, Svane and Petersen 2001, Booth and Beretta 2002, Gerlach et al. 2007, Brooker and Dixson 2016). The biochemical compounds released by living coral reefs may be detected via olfactory cues by fish anywhere from 1-1000m range (Kingsford et al. 2002), and lab trials studying biochemical cues found that larval fish recognize and orient towards water from areas with high coral-cover compared to algae-dominated low coral cover areas (Atema et al. 2002, Bonin et al. 2009, Lecchini and Nakamura 2013, Dixson et al. 2014). Living substrate composition is also important to recruit retention by providing enhanced foraging resources to reef fish (Brandl et al. 2015).

Other characteristics of coral reef fish recruitment

Other complex and interacting factors affect habitat selection processes, particularly for coral reef fish recruitment to coral reefs. Some of these factors include: recruitment pulses (Leis et al. 2014), season (Cook et al. 2021), connectivity (Rilov and Benayahu 2002, Gilby et al. 2019), protected areas and associated adult fish biomass (Knowlton and Jackson 2008), and lunar cycle recruitment cues (Robertson 1992). Since our study took place in the middle of the 2019 summer recruitment season, on one reef site, in a marine protected area, and no spikes in recruitment were observed following new-moon periods, we have further confidence that the results we see here are due to the manipulated variables in the study. We acknowledge that the metrics measured here are inferred measurements based on counts and sizing of fishes (as done in other studies; Pratchett et al. 2020), so recommend future studies may tag individual fish for a true recruitment metric. Growing evidence suggests that recruits may have higher plasticity thresholds to habitat requirements than previously expected (Pastor et al. 2013, Mercader et al. 2019), thus continued studies like this may provide further understanding of habitat selection mechanisms (Gaillard et al. 2008).

Future research

In this case study we chose to look at coral reef fish recruits as secondary organisms colonizing to biogenic coral habitats. One could also examine the effect of habitat structural complexity and living substrate composition on other important reef invertebrates. For example, newly added coral patches on reefs are particularly susceptible to mortality by corallivorous animals during the initial out-planting phase (Shaver et al. 2020); Is there an optimal combination of artificial and living coral proportions that allow fish recruitment, while also providing negative cues towards corallivores? One may also look at other important invertebrate herbivores on reefs like crabs, lobsters and urchins may provide ecological benefits at the habitat patch-level and are increasingly being incorporated into restoration planning (Francis et al. 2019).

Longer-term studies may evaluate the risk of biofouling algae to artificial habitat modules either by manipulating the casting material or surface texture complexity, also an important consideration to avoid competitive macro-algae abundance (Svane and Petersen 2001). One could even combine studying coral larval recruitment to artificial structures to enhance both biogenic species and secondary organism recruitment (Yanovski and Abelson 2019). Multiple species recruitment could be studied by altering casting material type, manipulating module surface texture, or manipulating structural complexity to simulate a diverse structural complexity options, thus supporting diverse species assemblages.

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3.7 Appendix A

<u>Data cleaning:</u>

removed roving shoals or large schools of fish that were in transit during the survey period. (based on surveyor notes or those that had 15-50 schools of fish like bluehead wrasse [*Thalassoma bifasciatum*] not closely associated to habitat). Removed survey data from one survey (the Northern High complexity plot) on June 9th, as a dangerous boater in the protected area could have influenced recruitment patterns and posed dangerous for divers. *don't need to include this in text, keep in code notes*

<u>Heteroscedasticity of recruitment rate over time:</u>

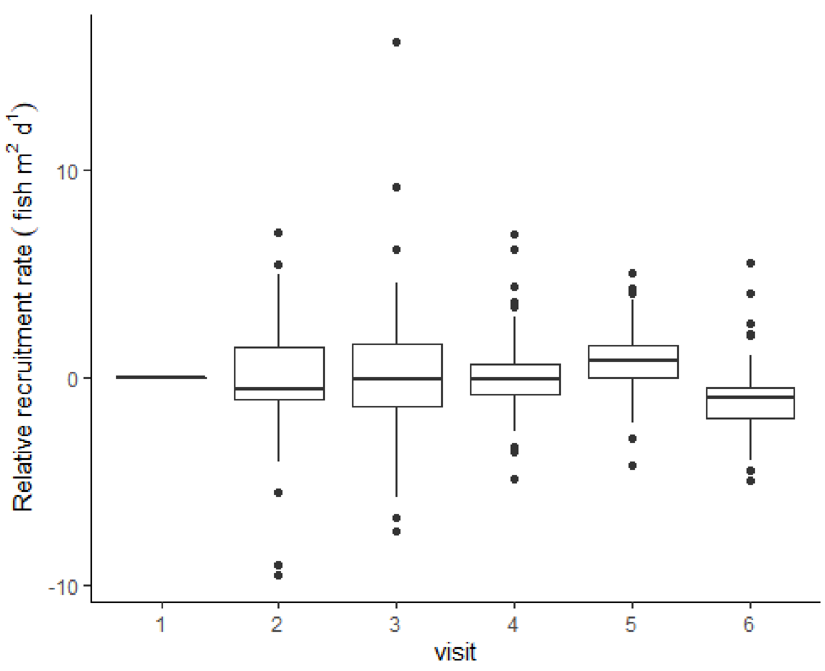

Fig A3.1: Visual examination of relative recruitment rate heteroscedasticity over time.

Table A3.1: Top model structure for each recruitment response metric.

Response metric	Top model (structure)
Attraction 1: Relative recruitment rate (lmm with AR1)	relative recruitment rate ~ % living coral treatment*background complexity, random effect= visit, correlation = corAR1(form = 1|visit)
Attraction 2: Relative density (glmm with visit and plot as random effects)	Relative density~ % living coral treatment*background complexity, random effect = visit + plot, Family = Gamma (log link function)
Retention 1: Relative final density (glm)	Relative final density ~ % living coral treatment*background complexity, Family = Gamma (log link function)
Retention 2: Relative species richness (glmm with visit as random effect)	Relative species richness~ % living coral treatment*background complexity, random effect = visit, Family = Gamma (log link function)

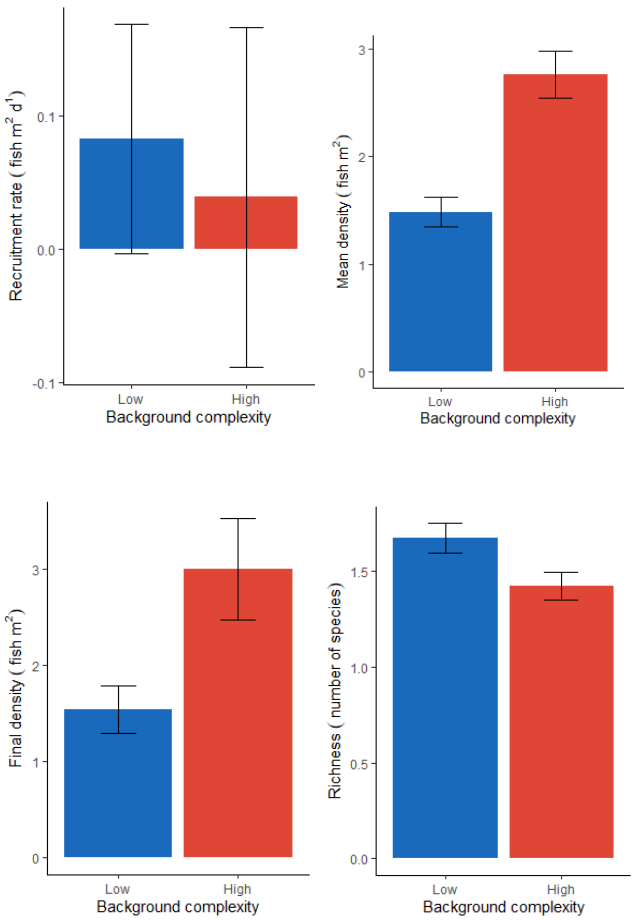

Fig A3.2: (A) Mean daily recruitment rate (mean ± S.E.) of recruit sized fishes (≲ 3cm) on control plots (i.e. no added habitat) for low and high background complexity areas over the initial phase of the experiment (Days 1-10). (B) Density (mean ± S.E.) of recruit sized fishes (≲ 3cm) on control plots (i.e. no added habitat) for low and high background complexity areas over the settlement phase of the experiment (Days 10-50). (C) Density (mean ± S.E.) of larger fishes (4-6cm) on control plots (i.e. no added habitat) for low and high background complexity areas over the final 3 days of the experiment (Days 37, 43, and 48). (D) Number of species (mean ± S.E.) of recruit-sized fishes (≲ 3cm) on control plots (i.e. no added habitat) for low and high background complexity areas over the entire experimental period (Days 1-50).

Table A3.2 Summary statistics and model results for each recruitment metric for control plots (i.e. no added habitat patches)

Recruitment metric	Statistical test	Background complexity	Mean (± SD)	Test value	df	p-value
Recruitment rate	Welch's two-sample t-test	Low	0.14 ±1.80 fish m^2 d^{-1}	t = 0.08	94	0.9396
		High	0.10 ± 2.21 fish m^2 d^{-1}			
Recruit density	Wilcoxon test	Low	1.68 ± 2.05 fish m^2	W = 2460	158	0.01001
		High	3.08 ± 3.81 fish m^2			
Final Density	Wilcoxon test	Low	1.54 ± 1.74 fish m^2	W = 228	46	0.2094
		High	3.00 ± 3.62 fish m^2			
Species Richness	Wilcoxon test	Low	1.67 ± 1.22 species	W = 9260.5	254	0.06091
		High	1.42 ± 1.12 species			

3.8 Appendix B

Pairwise comparison contrast tables

Attraction metric 1: relative juvenile fish recruitment rate

Table B3.1: Pairwise comparison of relative recruitment rate between low and high complexity areas.

contrast	estimate	SE	df	t.ratio	p.value
low - high	-0.114	0.22	465	-0.518	0.605

Table B3.2: Pairwise comparisons of relative recruitment rate between substrate composition treatments (% living coral)

contrast	estimate	SE	df	t.ratio	p.value
0% - 30%	-0.1704	0.323	465	-0.528	0.9844
0% - 50%	-0.2421	0.317	465	-0.763	0.941
0% - 70%	-0.1276	0.319	465	-0.4	0.9946
0% - 100%	-0.255	0.317	465	-0.805	0.929
30% - 50%	-0.0718	0.321	465	-0.223	0.9994
30% - 70%	0.0427	0.313	465	0.137	0.9999
30% - 100%	-0.0847	0.319	465	-0.265	0.9989
50% - 70%	0.1145	0.316	465	0.362	0.9963
50% - 100%	-0.0129	0.32	465	-0.04	1
70% - 100%	-0.1274	0.315	465	-0.404	0.9944

Table B3.3: Pairwise comparisons of relative recruitment rate between substrate composition treatments (% living coral), between respective background complexities (low and high)

treatment	contrast	estimate	SE	df	t.ratio	p.value
0%	Low - High	-0.125	0.461	465	-0.272	0.7859
30%	Low - High	-0.242	0.46	465	-0.525	0.6
50%	Low - High	-0.151	0.46	465	-0.328	0.7432
70%	Low - High	0.101	0.454	465	0.224	0.8232
100%	Low - High	-0.154	0.458	465	-0.336	0.7369

Table B3.4: Pairwise comparisons of relative recruitment rate between substrate composition treatments (% living coral), within respective background complexities (low and high)

complexity	contrast	estimate	SE	df	t.ratio	p.value
low	0% - 30%	-0.11217	0.462	465	-0.243	0.9992
low	0% - 50%	-0.22926	0.454	465	-0.504	0.9869
low	0% - 70%	-0.24098	0.457	465	-0.527	0.9846
low	0% - 100%	-0.24061	0.455	465	-0.529	0.9844
low	30% - 50%	-0.11709	0.454	465	-0.258	0.999
low	30% - 70%	-0.12881	0.445	465	-0.289	0.9985
low	30% - 100%	-0.12844	0.452	465	-0.284	0.9986
low	50% - 70%	-0.01172	0.45	465	-0.026	1
low	50% - 100%	-0.01135	0.454	465	-0.025	1
low	70% - 100%	0.000368	0.441	465	0.001	1
high	0% - 30%	-0.22854	0.45	465	-0.508	0.9866
high	0% - 50%	-0.25501	0.443	465	-0.576	0.9786
high	0% - 70%	-0.01432	0.445	465	-0.032	1
high	0% - 100%	-0.26941	0.441	465	-0.611	0.9733
high	30% - 50%	-0.02647	0.454	465	-0.058	1
high	30% - 70%	0.214225	0.441	465	0.486	0.9886
high	30% - 100%	-0.04087	0.45	465	-0.091	1
high	50% - 70%	0.240691	0.443	465	0.543	0.9827
high	50% - 100%	-0.0144	0.45	465	-0.032	1
high	70% - 100%	-0.2551	0.45	465	-0.567	0.9797

Attraction metric 2: relative juvenile fish density

Table B3.5: Pairwise comparison of relative densities in the late recruitment phase between low and high complexity areas. Bolded values indicate a significant difference between comparisons.

contrast	estimate	SE	df	t.ratio	p.value
Low - High	**0.36**	**0.0761**	**787**	**4.724**	**<.0001**

Table B3.6: Pairwise comparisons of relative densities in the late recruitment phase between substrate composition treatments (% living coral). Bolded values indicate a significant difference between comparisons.

contrast	estimate	SE	df	t.ratio	p.value
0% - 30%	0.11552	0.0578	627	1.998	0.2681
0% - 50%	**0.22647**	**0.0579**	**627**	**3.912**	**0.001**
0% - 70%	0.09059	0.0579	627	1.564	0.5212
0% - 100%	0.09604	0.0578	627	1.661	0.4593
30% - 50%	0.11095	0.0579	627	1.917	0.3091
30% - 70%	-0.02493	0.0579	627	-0.431	0.9928
30% - 100%	-0.01947	0.0578	627	-0.337	0.9972
50% - 70%	-0.13589	0.058	627	-2.344	0.1325
50% - 100%	-0.13043	0.0579	627	-2.253	0.1618
70% - 100%	0.00546	0.0578	627	0.094	1

Table B3.7: Pairwise comparisons of relative densities in the late recruitment phase between substrate composition treatments (% living coral), between respective background complexities (low and high)

treatment	contrast	ratio	SE	df	t.ratio	p.value
0%	**Low / High**	**1.27**	**0.126**	**787**	**2.411**	**0.0162**
30%	**Low / High**	**1.42**	**0.141**	**787**	**3.548**	**0.0004**
50%	**Low / High**	**1.46**	**0.145**	**787**	**3.786**	**0.0002**
70%	**Low / High**	**1.43**	**0.142**	**787**	**3.606**	**0.0003**
100%	**Low / High**	**1.6**	**0.159**	**787**	**4.758**	**<.0001**

Table B3.8: Pairwise comparisons of relative densities in the late recruitment phase between substrate composition treatments (% living coral), within respective background complexities (low and high)

complexity	contrast	estimate	SE	df	t.ratio	p.value
low	0% - 30%	0.04145	0.0712	787	0.582	0.9777
low	0% - 50%	0.12513	0.0713	787	1.755	0.4007
low	0% - 70%	0.02858	0.0713	787	0.401	0.9945
low	0% - 100%	-0.06896	0.0713	787	-0.967	0.8699
low	30% - 50%	0.08368	0.0712	787	1.174	0.766
low	30% - 70%	-0.01288	0.0713	787	-0.181	0.9998
low	30% - 100%	-0.11041	0.0713	787	-1.549	0.5308
low	50% - 70%	-0.09655	0.0712	787	-1.355	0.6566
low	50% - 100%	-0.19409	0.0713	787	-2.724	0.0514
low	70% - 100%	-0.09754	0.0712	787	-1.37	0.6473
high	0% - 30%	0.15458	0.0712	787	2.17	0.1922
high	**0% - 50%**	**0.26163**	**0.0713**	**787**	**3.671**	**0.0024**
high	0% - 70%	0.14739	0.0713	787	2.068	0.2353
high	0% - 100%	0.16386	0.0712	787	2.301	0.1457
high	30% - 50%	0.10706	0.0713	787	1.502	0.5616
high	30% - 70%	-0.00719	0.0713	787	-0.101	1
high	30% - 100%	0.00928	0.0713	787	0.13	0.9999
high	50% - 70%	-0.11424	0.0714	787	-1.6	0.4975
high	50% - 100%	-0.09778	0.0713	787	-1.371	0.6462
high	70% - 100%	0.01647	0.0713	787	0.231	0.9994

Retention metric 1: relative grown fish final density:

Table B3.9: Pairwise comparison of final relative density between low and high complexity areas. Bolded values indicate a significant difference between comparisons.

Contrast	estimate	SE	df	z.ratio	p.value
Low- High	**0.249**	**1.0813**	**Inf**	**3.063**	**0.0022**

Table B3.10: Pairwise comparisons of final relative density between substrate composition treatments (% living coral). Bolded values indicate a significant difference between comparisons.

contrast	estimate	SE	df	z.ratio	p.value
0% - 30%	0.0437	0.128	Inf	0.341	0.9971
0% - 50%	0.1275	0.128	Inf	0.998	0.8563
0% - 70%	-0.1667	0.128	Inf	-1.304	0.6888
0% - 100%	-0.0773	0.128	Inf	-0.605	0.9744
30% - 50%	0.0838	0.128	Inf	0.657	0.9653
30% - 70%	-0.2104	0.128	Inf	-1.65	0.4655
30% - 100%	-0.1209	0.128	Inf	-0.948	0.8782
50% - 70%	-0.2942	0.128	Inf	-2.307	0.1425
50% - 100%	-0.2048	0.128	Inf	-1.605	0.4939
70% - 100%	0.0895	0.128	Inf	0.701	0.9562

Table B3.11: Pairwise comparisons of final relative density between substrate composition treatments (% living coral), between respective background complexities (low and high)

treatment	contrast	estimate	SE	df	z.ratio	p.value
0%	Low - High	0.3103	0.181	Inf	1.713	0.0867
30%	**Low - High**	**0.3669**	**0.181**	**Inf**	**2.028**	**0.0425**
50%	**Low - High**	**0.3949**	**0.181**	**Inf**	**2.183**	**0.029**
70%	Low - High	-0.0203	0.18	Inf	-0.112	0.9105
100%	Low - High	0.1928	0.181	Inf	1.065	0.2868

Table B3.12: Pairwise comparisons of final relative density between substrate composition treatments (% living coral), within respective background complexities (low and high)

complexity	**contrast**	**estimate**	**SE**	**df**	**z.ratio**	**p.value**
low	0% - 30%	0.01539	0.181	Inf	0.085	1
low	0% - 50%	0.08521	0.18	Inf	0.472	0.9898
low	0% - 70%	-0.00143	0.181	Inf	-0.008	1
low	0% - 100%	-0.01849	0.181	Inf	-0.102	1
low	30% - 50%	0.06982	0.18	Inf	0.387	0.9953
low	30% - 70%	-0.01682	0.18	Inf	-0.093	1
low	30% - 100%	-0.03388	0.181	Inf	-0.188	0.9997
low	50% - 70%	-0.08664	0.18	Inf	-0.48	0.9892
low	50% - 100%	-0.1037	0.181	Inf	-0.574	0.9789
low	70% - 100%	-0.01706	0.18	Inf	-0.095	1
high	0% - 30%	0.07194	0.181	Inf	0.398	0.9947
high	0% - 50%	0.16981	0.181	Inf	0.94	0.8812
high	0% - 70%	-0.33201	0.181	Inf	-1.839	0.3513
high	0% - 100%	-0.13603	0.181	Inf	-0.754	0.9436
high	30% - 50%	0.09787	0.18	Inf	0.543	0.9829
high	30% - 70%	-0.40395	0.181	Inf	-2.238	0.1658
high	30% - 100%	-0.20797	0.181	Inf	-1.148	0.7806
high	**50% - 70%**	**-0.50182**	**0.18**	**Inf**	**-2.782**	**0.0431**
high	50% - 100%	-0.30584	0.181	Inf	-1.692	0.439
high	70% - 100%	0.19599	0.181	Inf	1.085	0.8142

Retention metric 2: relative species richness of juvenile and grown fish (≤ 6cm)

Table B3.13: Pairwise comparison of relative species richness between low and high complexity areas. Bolded values indicate a significant difference between comparisons.

contrast	estimate	SE	df	t.ratio	p.value
Low - High	**0.185**	**0.024**	**1268**	**7.715**	**<.0001**

Table B3.14: Pairwise comparisons of relative species richness between substrate composition treatments (% living coral). Bolded values indicate a significant difference between comparisons.

contrast	estimate	SE	df	t.ratio	p.value
0% - 30%	**0.1409**	**0.0379**	**1268**	**3.719**	**0.0019**
0% - 50%	**0.1509**	**0.0379**	**1268**	**3.983**	**0.0007**
0% - 70%	-0.0211	0.0379	1268	-0.556	0.9811
0% - 100%	0.0248	0.0379	1268	0.656	0.9656
30% - 50%	0.0101	0.0379	1268	0.265	0.9989
30% - 70%	**-0.162**	**0.0379**	**1268**	**-4.276**	**0.0002**
30% - 100%	**-0.116**	**0.0379**	**1268**	**-3.064**	**0.0189**
50% - 70%	**-0.172**	**0.0379**	**1268**	**-4.54**	**0.0001**
50% - 100%	**-0.1261**	**0.0379**	**1268**	**-3.329**	**0.008**
70% - 100%	0.0459	0.0379	1268	1.212	0.7443

Table B3.15: Pairwise comparisons of relative species richness between substrate composition treatments (% living coral), between respective background complexities (low and high)

treatment	contrast	estimate	SE	df	z.ratio	p.value
0%	**Low - High**	**0.142**	**0.0536**	**1268**	**2.654**	**0.0081**
30%	**Low - High**	**0.193**	**0.0536**	**1268**	**3.597**	**0.0003**
50%	**Low - High**	**0.207**	**0.0536**	**1268**	**3.862**	**0.0001**
70%	**Low - High**	**0.17**	**0.0536**	**1268**	**3.179**	**0.0015**
100%	**Low - High**	**0.214**	**0.0536**	**1268**	**3.993**	**0.0001**

Table B3.16: Pairwise comparisons of relative species richness between substrate composition treatments (% living coral), within respective background complexities (low and high)

complexity	**contrast**	**estimate**	**SE**	**df**	**t.ratio**	**p.value**
low	0% - 30%	0.1156	0.0536	1268	2.159	0.1963
low	0% - 50%	0.11851	0.0536	1268	2.211	0.1761
low	0% - 70%	-0.03521	0.0536	1268	-0.657	0.9653
low	0% - 100%	-0.01105	0.0536	1268	-0.206	0.9996
low	30% - 50%	0.0029	0.0536	1268	0.054	1
low	**30% - 70%**	**-0.15081**	**0.0536**	**1268**	**-2.815**	**0.0396**
low	30% - 100%	-0.12665	0.0536	1268	-2.364	0.1259
low	**50% - 70%**	**-0.15371**	**0.0536**	**1268**	**-2.868**	**0.0341**
low	50% - 100%	-0.12956	0.0536	1268	-2.417	0.1113
low	70% - 100%	0.02416	0.0536	1268	0.451	0.9915
high	**0% - 30%**	**0.16616**	**0.0536**	**1268**	**3.102**	**0.0168**
high	**0% - 50%**	**0.18338**	**0.0536**	**1268**	**3.423**	**0.0058**
high	0% - 70%	-0.00695	0.0536	1268	-0.13	0.9999
high	0% - 100%	0.06072	0.0536	1268	1.134	0.7886
high	30% - 50%	0.01721	0.0536	1268	0.321	0.9977
high	**30% - 70%**	**-0.17312**	**0.0536**	**1268**	**-3.232**	**0.011**
high	30% - 100%	-0.10545	0.0536	1268	-1.969	0.282
high	**50% - 70%**	**-0.19033**	**0.0536**	**1268**	**-3.553**	**0.0036**
high	50% - 100%	-0.12266	0.0536	1268	-2.289	0.1489
high	70% - 100%	0.06767	0.0536	1268	1.263	0.7138

Chapter 4: Conclusion

4.1 Study Objectives

We integrated techniques from across disciplines (engineering, paleontology and art) to design a method of creating artificial habitats modules that considers ecology, scalability, and accessibility in the design and deployment of artificial habitat modules that can be used to for habitat selection studies (Chapter 1). We then employed this method to study the effects of substrate composition and structural complexity (at two spatial scales: habitat patch [1m^2] and seascape background structural complexity [100m^2]) on habitat selection processes (Chapter 2). This research allowed us to address major gaps in the biogenic habitat selection field by creating artificial habitat modules that are highly realistic (to fully disentangle structural complexity vs substrate composition features of biogenic habitats) and designing a manipulative field study to test two different habitat selection processes that occur over time: the attraction *and* retention of dependent organism to biogenic habitats.

4.2 Main Findings

We used coral foundational species as a model biogenic habitat, and monitored patterns of juvenile reef fish attraction and retention to structurally complex habitat patches with varying proportions of living substrate composition placed in two kinds of environmental contexts: high and low background complexity environments. As expected, we found that ambient structural complexity (i.e., local environmental context) played a major role in mediating the attraction and retention of juvenile reef fishes to habitat patches; adding structurally complex habitat patches to low structural complexity environments enhanced attraction *and* retention of juvenile fish to habitat patches relative to ambient levels, compared to a dampened effect in high background complexity environment. Counter to what we expected, we found that habitat patches with the lowest (0%) and highest (100%) proportions of living coral substrate had higher attraction and retention compared to habitat patches with intermediate (50%) proportions of living biogenic substrate.

The attraction of dependent organisms to biogenic habitats is driven by visual cues from structural complexity, and olfactory cues from the biochemical composition of living tissue, while the retention of species is driven by patch-level resources after the attraction phase. It is unsurprising to see high species attraction and retention to habitat patches in low structural complexity areas (low relief), as new habitat patches represent a greater proportion of the available habitat relative to ambient environmental availability of structure to shelter in, what we suggest are non-intuitive selection cues driving this trend. Comparatively, when no habitat patches are added to the reefscape, attraction and retention of juvenile reef fish was higher in high structural complexity areas, indicating that adding structurally complex habitat patches in low relief areas exerts strong selective preference in juvenile reef fish.

Substrate composition influenced juvenile fish attraction and retention unexpectedly; for both attraction and retention metrics a u-shape pattern emerged when increasing living substrate treatments (i.e., increasing from 0% to 100% living coral). We suggest the potential mechanisms driving this trend could be density-dependent effects driving patch-level competition for living substrate patches, indirect cues from con/heterospecific reef fishes, taxa or trait specific habitat selection, and scale-dependent habitat heterogeneity. We recommend further study to understand other cumulative mechanisms driving habitat selection to biogenic habitats.

4.3 Contribution to informing habitat restoration design

Results from this study have implications for habitat restoration ecology and restoration planning. In the context of global habitat decline, gaining a better understanding of ecological features that enhance species abundance and biodiversity to restored habitats may bolster habitat restoration success and leverage positive ecological facilitations between foundational and secondary species. Results from this study confirm that identical habitat patches are functionally distinct from each other when placed in different local environmental contexts (high vs low relief areas with distinct ambient structural complexity), and that habitat composition is an important driver of these trends.

We suggest: (1) habitat augmentation increases both the attraction and retention of juvenile fish, particularly when habitat patches are placed in low complexity environments, and that (2) intermediate levels of % living coral at the habitat-patch scale lower the attraction and retention of secondary species (regardless of reefscape environment), a pattern likely driven by species and trait-specific assemblages.

We recommend: (1) continued habitat augmentation via coral restoration activities to diverse reefscapes, particularly low complexity reefscapes, to attract and retain diverse fish assemblages, and (2) longer-term studies may elucidate inter-annual retention to habitats with varying levels of biogenic substrate composition, with implications for retaining healthy adult reef fish populations.

4.4 Contribution to informing habitat selection processes

The method and results presented here also have implications to the broader ecological field, specifically to key questions in habitat selection on biogenic habitats. Both the structural complexity and substrate composition of biogenic habitats are hypothesized to influence attraction and retention to habitats, and this study confirms that the context in which habitat patches are placed mediate these responses. This was the first study done using this method; we recommend future studies may employ this method to test other related processes driving habitat selection including indirect cues from conspecifics, heterospecifics and predators, incorporating or quantifying biochemical compounds in biogenic habitats and casting material, or looking at asynchronous attraction and retention of foundational species to artificial habitat modules. Through direct mediation, indirect ecological effects and trophic facilitations, protecting and restoring coral reef fish populations along with corals can contribute to coral reef restoration, recovery, and future resilience.

4.5 Concluding remarks

Biogenic habitats and the foundational species of which they are composed are threatened by multiple chronic and acute disturbances, namely widespread habitat destruction, degradation due to the cumulative effects of climate change, and the exploitation of secondary organisms that contribute vital ecosystem services. Understanding biogenic habitat features may help us approach applied and theoretical ecological questions, so we may contribute towards enhancing their survival and longevity. This is especially important as we now face a key period of opportunity to rectify the potentially irreversible damage of habitat destruction via habitat restoration, and to simultaneously restore the diverse and interdependent assemblages within them.

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