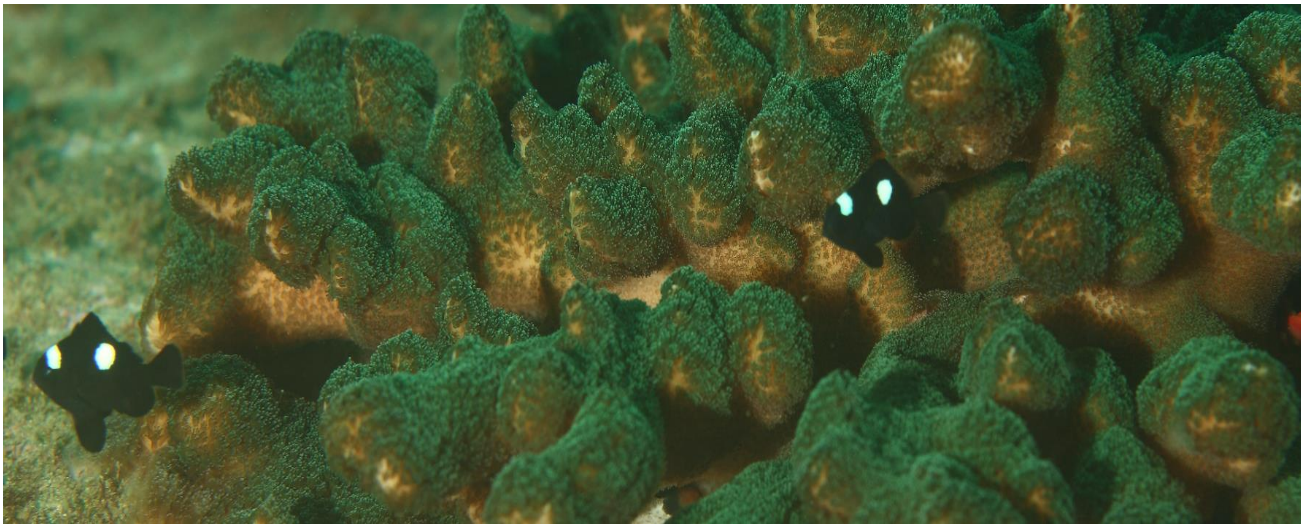
Effects on local and vagrant tropical fish assemblages of the range expanding coral *Pocillopora aliciae* into temperate SE Australia



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Thesis submitted in fulfilment of the requirements for the degree of

Masters of Science (Research)

under the supervision of Prof. David Booth and Dr. Ashley Fowler (NSW DPI)

University of Technology Sydney
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CERTIFICATE OF ORIGINAL AUTHORSHIP

I, Max James O’Connell declare that this thesis, is submitted in fulfilment of the requirements for the award of MSc (Research), in the School of Life Sciences (SoLS) at the University of Technology Sydney.

This thesis is wholly my own work unless otherwise referenced or acknowledged. In addition, I certify that all information sources and literature used are indicated in the thesis.

This document has not been submitted for qualifications at any other academic institution.

This research is supported by the Australian Government Research Training Program.

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Ethics approval and collection permit

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General Abstract

The increase in global sea surface temperatures and strengthening of poleward-moving western boundary currents has resulted in the expansion of tropical reef fish assemblages and habitat-forming corals into temperate ecosystems. These range-shifting species have already altered temperate ecosystems through competition of resources or alteration of habitat. Likely linked to these mechanisms, the Sydney Coral Gardens (SYCOGA) in Sydney, Australia, has seen a rapid proliferation of branching hard coral *Pocillopora aliciae* habitat and associated small tropical vagrant fish species since initially seen in 2013.

To address what mechanisms tropical vagrant recruits utilise when locating and settling on novel habitat I subjected humbug damselfish *Dascyllus trimaculatus* individuals to a four – way aquarium choice experiment, providing olfactory cues of *P. aliciae* and visual cues of conspecifics and congenerics (neon damselfish, *Pomacentrus coelestis*). *D. trimaculatus* individuals both selected and spent the most amount of time within quadrants that possessed the olfactory habitat cues and showed similar responses towards conspecific olfactory cues, outlining the importance of olfactory abilities of new recruits when locating and settling on novel habitat. To understand how range-shifting tropical and local temperate species spatially use coral habitat I observed behaviours of 14 fish species (tropical and temperate) associating with *P. aliciae* habitat, by mapping movement area and habitat partitioning. It was found that tropical individuals utilised different parts of coral heads to temperate species potentially allowing for reduced spatial competition within SYCOGA. Finally, I observed the seasonal changes in fish assemblages associated with the novel coral habitat, at locations in South-eastern Australia to study differences in fish assemblage composition between coral habitat and native temperate habitat located both adjacent to the coral in SYCOGA and at other sites in the Sydney region. Both tropical and temperate fish species were observed in far greater densities on the coral than surrounding habitat, showing this coral habitat facilitates dense assemblages of both tropical and temperate fish species, potentially aiding and accelerating the process of tropicalisation of temperate reef ecosystems within south-eastern Australia.

The results of this thesis show the ability, through olfactory and visual cues, of juvenile vagrant reef fish species to locate suitable but rare novel habitat and conspecifics. Furthermore, tropical and temperate fish species prefer different sections of individual coral heads, suggesting potential coexistence and a lack of space-use competition. Finally, this newly formed coral habitat, is providing preferred habitat for both tropical and temperate species seasonally compared to surrounding temperate habitat.

Contents

CERTIFICATE OF ORIGINAL AUTHORSHIP ii
Acknowledgements iii
Ethics approval and collection permit v
General Abstract vi
List of Figures 1
List of Tables 2
Chapter 1: General Introduction 3
  1.1 Global climate change in marine ecosystems 3
  1.2 The role of WBCs in species' poleward distributions 4
  1.3 Sensory mechanisms for settlement 5
  1.4 Impacts of tropicalisation on temperate ecosystems 6
  1.5 Thesis aims, hypotheses, and layout 7
Chapter 2: Recruiting a long way from home: Domino damselfish *Dascyllus trimaculatus* can detect new temperate coral habitat and conspecifics. 10
  Abstract 10
  2.1 Introduction 10
  2.2 Materials and Methods 12
  2.3 Results and Discussion 15
Chapter 3: Microhabitat use on novel coral habitat by coral-dwelling tropical vagrant and local temperate fish species in SE Australia 21
  Abstract 21
  3.1 Introduction 21
  3.2 Materials and Methods 24
  3.3 Results 26
  3.4 Discussion 29
Chapter 4: Range shifting coral attract high densities of both expatriated tropical and local temperate reef fish species in SE Australia 32
  Abstract 32
  4.1 Introduction 33
  4.2 Materials and Methods 37
    4.2.1 Study locations and species description 37
    4.2.2 Fish survey protocol 39
    4.2.3 Statistical analysis 40
  4.3 Results 41
    4.3.1 Species list and seasonal comparison of assemblage parameters on coral habitat within SYCOGA. 41

4.3.2 Comparison of assemblage parameters between coral habitat and directly adjacent rocky reef habitat within SYCOGA. 43

4.3.3 Comparison of assemblage parameters between SYCOGA and Northern Sydney rocky reef habitat 44

4.3.4 Comparison of assemblage parameters between SYCOGA and northern established *P. aliciae* habitat. 45

4.4 Discussion 45

Chapter 5: General Discussion 50

5.1 Key Findings 50

5.2 Future Research Directions 52

5.3 Implications of Tropicalisation 54

5.4 Concluding Remarks 55

References 57

List of Figures

Figure 1. a) Mean time spent (%) in coral odour quadrant during two trials (Trial 1: $n = 18$, Trial 2: $n = 17$). b) Mean time spent (%) in conspecific odour quadrant and conspecific visual quadrant ($n = 17$ for each experiment). Each bar indicates one experiment. One-sample t-test used average against null hypothesis of 25% (dashed line). Error bars indicate standard error c) Final selection of coral odour quadrant during two trials (± 95% CI) (Trial 1: $n = 18$, Trial 2: $n = 17$). d) Final selection for conspecific olfactory and conspecific visual cues (*D. trimaculatus* vs *P. coelestis*) ($n = 17$ in each) (± 95% CI). Binomial exact tests used against null hypothesis of 25% (horizontal line: Fig. 1a, 1b, 1c, 1d).

Figure 2. Example of simplified mud-map overlaid on observational area. Marked with maximum movement distance of *Dascyllus trimaculatus* individual exhibiting an occupation of 'centre' coral partitioning, *Parma microlepis* exhibiting occupation of 'boulder' habitat, and *Thalassoma lunare* exhibiting occupation of 'edge' habitat; MMD highlighted as orange line within range extent of *D. trimaculatus* individual (blue). For example, three habitat categories were edge (yellow circle), centre (red circle), and boulder (black circle). Light grey outlined coral heads on mud-map.

Figure 3. a) Mean proportional habitat use for observed species (% ± SE if $n > 1$). (S) indicates sub-adult individuals. b) Mean MMD (cm + SE if $n > 1$) of species recorded of similar body sizes. MMD compared to habitat position use (Edge, Centre, and Boulder). Tropical species boxed. Key study species categorised by sub-adult (S) and adult.

Figure 4. Photos indicating coral coverage increase within Cabbage Tree Aquatic Bay Reserve. Left image taken Jan 14th, 2019, Right image taken Aug 14th, 2021 (Photo cred. John Sear).

Figure 5. Location map showing location of study locations: Sydney Coral Gardens (SYCOGA) and Northern Sydney locations in Sydney and Broughton Island and Cabbage Tree Island in Port Stephens, NSW. And long-term monitoring locations (Booth et al., 2007b; Booth et al., 2018; Booth and Sear, 2018). Service Layer Credits: Esri, HERE, Garmin, © OpenStreetMap contributors, and the GIS user community.

Figure 6. a) Fish density (per 60 m^2 ± SE) of tropical (white) and temperate (black) fish species and b) species richness (± SE) within SYCOGA through sampling seasons Summer 2019, Autumn 2020, Winter 2020, Summer 2021, and Autumn 2021. Significance between seasons indicated with *. Errors bars indicate standard errors. $N = 9$.

Figure 7. Fish density (per 60 m^2 ± SE) of both tropical and temperate individuals combined on coral habitat vs adjacent (off) coral habitat over four sampling months within SYCOGA. * Indicates significance at $p < 0.05$.

Figure 8. Key tropical vagrant species densities across years (2019, 2020, and 2021) between Northern Beaches temperate rocky reef sites and SYCOGA. * Indicates significance between sites within years at $p < 0.05$.

List of Tables

Table 1. Results of linear mixed modelling of time spent in coral odour as a function of trial number, release direction and body size (mm, TL). Trial 1 was the reference category. Fish ID was included as a random effect. Bold indicates significance at $p < 0.05$. CI: confidence interval.

Table 2. Two-way ANOVA and subsequent post-hoc test observing proportional use of habitat comparing species category (Tropical vs Temperate) and Habitat position (Edge, Centre, Boulder). Significant results in bold.

Table 3. List of all species, number of observations, and habitat associations found at SYCOGA over the sampling period.

Chapter 1: General Introduction

1.1 Global climate change in marine ecosystems

Anthropogenic climate change is rapidly altering the world's ecosystems on a scale which has previously been attributed to increased extinction rates and ecosystem collapses (Pachauri and Reisinger, 2007). The increase of atmospheric greenhouse gas concentrations has resulted in an increase in average global temperatures on land by ~ 0.2ºC globally per decade over the last three decades (Hansen *et al.*, 2006). In contrast, ocean temperatures have increased by 0.74°C during the 20th century (Hoegh-Guldberg *et al.*, 2007). However, rates of warming vary among different regions of the world, for instance coastlines that are impacted by poleward-flowing Western Boundary Currents (WBCs) are warming two to three times faster than the global mean surface ocean warming rate, termed 'Global hotspots' (Wu *et al.*, 2012).

One of these global hotspots is the south-eastern coast of Australia, with the intensification of the East Australian Current (EAC) transporting warmer tropical water poleward along the coast (Poloczanska *et al.*, 2007; Ridgway, 2007). Not only is the EAC warming at a faster rate than other regions around the world, but it is also strengthening and extending poleward by approximately 350 km as defined by increasing average trends of temperature and salinity in the south Tasman Sea (Southern Australia) over a 58-year period (1944-2002) (Ridgway and Hill, 2009). This increase in temperature and salinity is driven by the EAC extension, which is a poleward propagating eddy field formed as a result of the EAC jet turning eastward and joining the Tasman Front (Cetina-Heredia *et al.*, 2014). While the EAC main current is predicted to intensify by 0.7% between 1990 and 2060, the EAC extension is predicted to intensify by ~ 40% over the same period (Oliver and Holbrook, 2014), resulting in an increase of ocean warming three to four times the global average, which makes south east Australia one of the fastest warming regions in the southern hemisphere (Wu et al. 2012).

1.2 The role of WBCs in species' poleward distributions

Most marine organisms have a bipartite life cycle comprised of a highly motile larval phase followed by settlement prior to development of a sedentary adult phase (Leis, 2006). However, many tropical fish species only obtain their strongest swimming abilities towards the end of the pelagic phase (Fisher *et al.*, 2000), leaving them subject to variability of ocean currents. WBCs are primarily responsible for the dispersal of tropical larvae and plant and algae propagules into temperate latitudes, and there are numerous factors that determine settlement which may include: physical transport (currents), biological transport (swimming) and biotic factors (e.g., suitability of habitat, presence of conspecifics, absence of predators) (Booth *et al.*, 2007). Eddy fields produced by WBCs are important drivers of larval fish moving from the main current offshore to temperate nearshore areas that provide habitat [e.g., that observed in the North Atlantic's Gulf Stream (Hare *et al.*, 2002) and also along the eastern coast of Australia (Suthers *et al.,* 2011)]. The survival and growth of tropical larval fish during this pelagic translocation phase is dependent on food availability, water temperature, predation, and the length of the pelagic larval phase. Pelagic larval duration (PLD) may be a useful predictor for poleward distributions, for example Booth *et al.* (2007) observed that tropical vagrant species with a longer PLD (*Chaetodon auriga* and *C. flavirostris*; ~ 45 days) were found further south than species with a shorter PLD (*Abudefduf vagiensis* and *A. sexfasciatus*; ~ 20 days) in temperate south-eastern Australia.

The transport of tropical fish larvae along the western and eastern coast of Australia has been well documented as far as Rottnest Island (32° S) by the Leeuwin current in the west (Hutchins and Pearce, 1994) and Merimbula (37° S) in the east (Hutchins *et al.*, 1991) during the austral summer. The WBC that is responsible for movement of pelagic tropical larvae on the eastern coast of Australia is the East Australian Current (EAC), flowing from the southern tip of the Coral Sea down along the coast of northern NSW.

1.3 Sensory mechanisms for settlement

Reef fish larvae have strong sensory capabilities, particularly during time of settlement onto reef habitat (Leis *et al.*, 2002; Lecchini *et al.*, 2005). This ability to detect local environmental factors plays a vital role in the locating and selecting viable habitat when transitioning from a pelagic and motile larval phase to a benthic settlement phase. Larval fishes are known to employ a range of sensory modalities. For example, Kingsford *et al.* (2002) observed that multiple cues, whether they be olfactory (0-10 km range), auditory (0-100 km range), or visual 0-0.1 km range), are employed simultaneously or in sequence, dependent on intensity of gradients and distance from the source. Reef fish larvae have been shown to exhibit highly developed olfactory systems during the settlement stage (Arvedlund *et al.*, 2007; Lara, 2008), indicating an evolutionary advantage to develop this system prior to benthic settlement. As settlement mostly occurs at night for tropical coral reef fish (Booth 1992), the olfactory response to chemical cues is thought to be the most important process for locating settlement habitat (Sweatman, 1988).

When testing olfactory cues of fish, lab experiments are useful to isolate individual cue as these cues can be isolated and many laboratory preference experiments use two or four chamber flume setups (Gerlach *et al.*, 2007; Munday *et al.*, 2009; Coppock *et al.*, 2013; Lecchini and Nakamura, 2013). While the apparatus reduces the issues with release direction, it may be considerably more artificial than experiments in the field, because marine larvae do not encounter such laminar flows in their natural environment (Arvedlund and Kavanagh, 2009).

1.4 Impacts of tropicalisation on temperate ecosystems

The introduction of novel tropical assemblages brings with it many challenges for the local temperate fauna, which may include tropical habitat-forming species. Novel interactions between species, alterations of temperate habitat, and niche competition increase as more tropical species shift poleward and establish reproductive populations (Nagelkerken and Simpson, 2013; Coni *et al.*, 2021). As marine communities are regulated by top-down forces, to a greater extent than terrestrial ecosystems (Shurin *et al.*, 2006), the negative effects that poleward migrating herbivorous tropical fish cause on temperate habitat is one of the main consequences of poleward-shifting species (Vergés *et al.*, 2016). Grazing by tropical herbivorous fishes has been a key driver in the removal of temperate kelp habitat in Japan, Australia, America, South America, and the Mediterranean, which is intensified as warmer ocean temperatures increase grazing rates of tropical fishes (Smith, 2008) and maybe lead to corals replacing these.

For example, the rabbitfish, *Siganus fuscescens* and parrotfish *Calotomus japonicus* are two herbivorous tropical species that are responsible for the overgrazing of *Ecklonia cava* beds and the creation of barren substrate, termed '*isoyake*' in southern Japan (Fujita, 2010; Yamaguchi, 2010). The creation of *isoyake* within southern Japan has led to the infilling of tropical and sub-tropical reef building corals (primarily *Acropora muricata* and *A. latistella*) (Mezaki and Kubota, 2012). This poleward expansion of reef-building corals as a response to increasing coastal ocean temperatures and tropical fish herbivory has led to a dominance of tropical species in abundance, diversity, and size class compared to the local temperate population

(Nakamura *et al.*, 2013). Similarly, the eastern coast of Australia has also observed processes leading to the tropicalisation of temperate marine communities. Over a 10-year period (2002-2011), Vergés *et al.* (2016) observed complete loss of kelp coverage in combination with increasing tropical fish assemblages and tropical fish herbivory as ocean temperatures increased.

Key tropical habitat-forming organisms, such as corals, have not kept pace with fish in respect to poleward expansion, as seen in other regions around the world (e.g., Japan) (Baird *et al.*, 2012). However, within the last several years, colonies of the subtropical branching hard coral *Pocillopora aliciae* (Pocilloporidae) (Schmidt-Roach *et al.*, 2013a) have been observed infilling urchin barrens within Sydney's Cabbage Tree Aquatic Bay Reserve, in New South Wales, Australia. Presently, it is the only scleractinian branching coral species within Sydney. Observations have been made of tropical vagrant fish species settling on this this novel coral habitat, such as Humbug damselfish *Dascyllus trimaculatus*, *D. reticulatus* and *Plectroglyphidodon dickii* (Booth and Sear, 2018).

1.5 Thesis aims, hypotheses, and layout

The conceptual basis for this thesis was to understand the dynamics of arrival of tropical vagrant fish larvae as they settle and integrate into a novel environment (subtropical hard coral) in south-eastern Australia and how the local fish assemblages might be influenced by this expatriating habitat. The overall aim is to understand how expatriate tropical fish detect rare suitable habitat outside their natal range, how they and local temperate species utilise that habitat, and whether this novel and rare temperate coral habitat might facilitate or hinder assemblages of tropical and temperate fish species. With these rare habitats potentially supporting tropical assemblages and continuing to expand within temperate Australia, this may facilitate the tropicalisation of temperate coasts.

In Chapter 2, a series of laboratory experiments were used to test whether juvenile tropical damselfish *D. trimaculatus* could detect rare coral habitat (*P. aliciae*) through olfactory senses alone, and conspecifics, using isolated olfactory and visual cues. Based on tropical damselfish's strong olfactory abilities, it was expected that *D. trimaculatus* individuals would be able to detect both coral habitat and conspecifics through olfactory and visual cues.

In Chapter 3, *in-situ* observations of the habitat use and movement ranges of both tropical vagrant and temperate species on *P. aliciae* were analysed to understand whether this assemblage is experiencing overlap or partitioning of habitat between tropical and temperate species. It was anticipated that there would be significant overlap in habitat use by tropical and temperate species, creating competition that has been observed elsewhere around the world (see Nakamura *etal.,* 2013).

Finally, in Chapter 4 I tested whether this novel range-expanding coral (*P. aliciae*) is facilitating both tropical and temperate fish assemblages by comparing assemblages against surrounding temperate habitat. It was hypothesised that due to the increase structural complexity provided by *P. aliciae*, higher densities of both tropical and temperate reef species than surrounding barren rock and kelp habitat, would be observed, enhancing tropicalisation as a consequence.

Three data chapters (Chapters 2, 3, and 4) are presented and structured as a progression of independent but complementary studies, followed by a general discussion (Chapter 5). These data chapters form the foundation of stand-alone manuscripts that are intended to be submitted for publication in peer-reviewed scientific journals, and therefore have been formatted for the specific journals. As such, there is some unavoidable repetition.

Chapter 2: Recruiting a long way from home: Domino damselfish *Dascyllus trimaculatus* can detect new temperate coral habitat and conspecifics.

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Abstract

Climate change is driving tropicalisation of temperate reefs, yet it is unclear how range-shifting tropical fishes locate suitable habitat. I tested whether juvenile tropical damsels *Dascyllus trimaculatus* could detect rare coral habitat (*Pocillopora aliciae)* and conspecifics on temperate rocky reefs using olfactory and visual preference experiments. For all cues, individuals selected and spent more time than expected in a testing arena quadrant with the cue present, which included coral odour and conspecific odour and visual cues. This indicates that vagrant coral-reef fish can detect rare suitable habitat outside of their natal range.

2.1 Introduction

Strengthening and poleward penetration of Western Boundary Currents under climate change facilitates the movement of tropical propagules such as reef fish larvae into temperate areas (Stobutzki and Bellwood, 1994; Stobutzki and Bellwood, 1997). In eastern Australia, the strengthening East Australian Current (EAC) (Ridgway and Hill, 2009; Suthers *et al.*, 2011), in conjunction with warming ocean temperatures, has facilitated an increase in "vagrant" coral reef fish arrivals into temperate reefs (Booth *et al.*, 2007; Fowler *et al.*, 2018). However, other factors such as habitat and local species interactions in the receiving environment (Harriott and

Banks, 2002; Nakamura *et al.*, 2013) can limit the establishment and expansion of invading tropical populations.

Reef fish larvae have strong sensory capacity (Leis *et al.*, 2002), which can play an important role in location and selection of suitable habitat during the transitioning from a pelagic to benthic life stage. The use of olfactory and visual cues at various stages, to orientate and discern predators has been demonstrated within and around natal reefs (Kingsford *et al.*, 2002; Lecchini *et al.*, 2014). However, the ability of tropical reef fish to locate suitable habitat outside their natal range has received little attention. Here, we examine the use of visual and olfactory sensory mechanisms to understand how such tropical vagrant fishes could locate suitable habitat in novel temperate ecosystems, where suitable habitat may be considerably scarcer and limiting than in natal regions.

Based on previous tropical studies, coral reef fish settle at night (Sweatman, 1988 and Booth 1991), suggesting that visual cues may be less effective and olfactory cues may play the key role in habitat detection. As a result of the differences in habitat structure and environmental factors compared to their natal locations, olfactory settlement cues may be atypical, and the normal settlement process for these individuals may be affected.

The three-spot damselfish, *Dascyllus trimaculatus,* is a coral reef fish that is transported poleward as larvae on Australia's east coast and has previously been observed in Sydney's temperate rocky reefs (Fowler *et al.*, 2018). *D. trimaculatus* individuals have been shown to occupy anemones often cohabiting with heterospecific Pomacentrids but can often be out competed for resources (Schmitt *et al.,* 1999). While occupying anemones (which are not present within Sydney's temperate ecosystems) in its natal range (Schmitt and Holbrook, 2000), in temperate rocky reefs *D. trimaculatus* utilise a sub-tropical branching coral species, *Pocillopora aliciae* (Schmidt-Roach *et al.*, 2013b) which was first observed in Sydney in 2013 (Booth and Sear, 2018). It is the region's only known branching scleractinian coral and may also be expanding its range poleward, thereby facilitating range expansions of tropical fauna that use the species as habitat.

This study examined habitat and conspecific preferences, and their sensory mechanisms, in juvenile *D. trimaculatus*. Specifically, I asked: 1) Can *D. trimaculatus* differentiate and select *P. aliciae* through olfactory chemical cues alone? 2) Can *D. trimaculatus* differentiate and select for conspecific olfactory cues? 3) Do *D. trimaculatus* select conspecifics over heterospecifics using visual cues? Understanding the specific senses and preferences involved with habitat selection can help explain how tropical reef fish find suitable habitat, and the role of conspecifics in extra-natal environments, which will assist prediction of range shifts due to climate change.

2.2 Materials and Methods

Due to research diving prohibition resulting from the COVID-19 pandemic, and a poor recruitment year for *D. trimaculatus* in south-eastern Australia, all fish used in experiments were sourced from an aquarium supplier (Cairns Marine Pty. Ltd.) that collected wild juveniles from coral reef located off Cairns, Australia. I sourced the smallest individual fish available, ranging from 27-49 mm in total length (TL) (mean of 37.05±1.5 mm). These represented young recruits, although they were larger than new settlers (~15 mm TL).

An opaque circular aquarium (hereafter "arena") (110 cm d x 45 cm h) was used to test selection of different olfactory and visual cues by *D. trimaculatus*. The arena was divided equally into four quadrants with an open centre area (30 cm diam.) for individuals to view quadrants prior to selection. An acclimation tube with a pulley system was used to release individuals without researcher interference. No circulation or aeration mechanisms were used within the arena to limit mixing of testing cues. A video camera (GoPro Hero 7®) was positioned above the arena in a 'birds-eye' field of view. Water height was 9 cm and water temperature was 23°C. Artificial lights illuminated the arena on a diel cycle.

Several fragments of *Pocillopora aliciae* were collected from Sydney's Shelley Beach Headland Intertidal Protection Area (DPI Scientific Collection Permit No. P15/0042-2.0). Water quality in holding tanks (66 L) was maintained during the experiment through aeration, water flow, use of cultured live rock, and daily water changes (75%). Water from a coral tank (hereafter "coral odour") was used to introduce a coral cue into the choice arena. Coral fragments were placed into a smaller holding tank (12 L) without live rock for 12 hours prior to experimentation to isolate the coral cue [*sensu* Wright *et al.* (2005)].

Three experiments were used to test preferences of *D. trimaculatus* involving olfactory and visual cues: 1) a choice between coral odour (1 quadrant) and seawater (3 quadrants), 2) a choice between conspecific odour (1 quadrant) and no conspecific odour (3 quadrants), and 3) a choice between visual cues of conspecifics (1 quadrant) and visual cues of heterospecific groups (3 quadrants. confamilial *Pomacentrus coelestis*) (n = 18 *D. trimaculatus*). Experiments were completed in succession and given 3 days between experiments. Olfactory cues were eliminated in the latter experiment by restricting treatment fish to plastic bags (1 L). Two trials of Experiment 1 were conducted to examine repeatability and were separated by three days.

For coral odour trial 1, 18 individuals were individually tested. For all remaining experiments 17 individuals were tested as one individual died between experiments. Each individual was placed into the acclimation tube for 1 min. The odour cue (coral or conspecific) was then released into a randomly selected quadrant at a rate of 2.5 mLs^{-1} for 10 s. Spread of the cues was estimated by dispersal trials using coloured dye that indicated the water containing the cues would remain in the quadrant for up to 20 min. The individual was then released into the arena for 20 mins and filmed, after which they were caught, measured for identification, then fed. The arena was rinsed and refilled between trials to remove trace odours.

The conspecific odour cue was obtained from tank water with conspecifics present for 12 hours. Using the same arena configuration, two conspecific individuals were placed into a transparent sealed bag (1 L) with aerated seawater and placed into a randomly selected quadrant. The other three quadrants each contained a bag with two similarly-sized confamilial individuals (*Pomacentrus coelestis*), to provide a non-conspecific cue. The test individual was then acclimated and released into the arena. No ill effects of confinement were observed.

Preference for cues was examined from video using two response variables: 1) selection of the quadrant with a cue (e.g., coral odour) following a period of initial exploration ("final selection") and 2) the proportion (%) of time spent in that quadrant during the experiment ("time spent"). The two metrics were used due to initial observations of fish roaming throughout the array prior to cueing toward a stimulus, along with an initial flight response that was unlikely related to cueing.

Linear mixed effect modelling was initially used to explore the effects of successive trials on the same individuals, release direction and body size (total length [TL], cm) on time spent in coral odour. Results were used to inform subsequent analyses (see below) and assist in interpretation. Fixed effects were selected based on the significance of their *t*-value at the 0.05 level (Zuur *et al*., 2009). The random factor for the model was defined as each individual fish to account for individual variability (Fish ID). Model validity was examined through comparison of residuals to fitted values and comparison of standardised residuals to theoretical quantiles (Zuur *et al.*, 2009). Modelling was run using the 'lme4' package (Bates *et al.*, 2014) in the R software environment (vers. 4.0.3).

Following initial model exploration, a one-sample *t*-test was used to examine whether time spent in the coral odour quadrant was greater than chance alone (expected 25% of the experimental duration). The values from Trials 1 and 2 for each individual were averaged [*sensu* Kroon and Housefield (2003), James *et al.* (2008)], an approach supported by the lack of a trial effect in initial modelling.

Binomial exact tests were used to test the significance of final quadrant selection at 20 minutes in all experiments relative to that expected by chance alone (expected: 25%). Results were considered significant if $p < 0.05$. One-sample t-tests were conducted using SigmaPlot 14.0 (Systat Software Inc, 2020), and binomial exact tests were conducted in the R software environment (RStudio Team, 2020).

2.3 Results and Discussion

Mixed modelling indicated that individuals released towards the coral odour quadrant spent significantly greater time in that quadrant compared to individuals not released towards it (Table 1). The result suggests that releases directed at the cue of interest must be balanced with releases not directed at the cue, even when direction of release is randomised. No difference in time spent in coral odour was found between Trials 1 and 2, supporting combination of values from both trials into a single average for subsequent comparison (Table 1). Body size also did not affect time spent (Table 1).

Table 1 Results of linear mixed modelling of time spent in coral odour as a function of trial number, release direction and body size (mm, TL). Trial 1 was the reference category. Fish ID was included as a random effect. Bold indicates significance at $p < 0.05$. CI: confidence interval.

Predictors	*Estimates*	*CI*	*p*	*df*
Intercept	13.92	1.47 – 26.36	**0.030**	17.73
Trial 2	0.77	-2.88 – 4.43	0.659	15.58
Release	8.00	2.25 – 13.75	**0.008**	26.87
Size	-0.22	-0.54 – 0.10	0.169	15.80
Fish ID				
σ^2	23.11			
$\tau_{00\ \mathrm{ID}}$	4.33			
ICC	0.16			
N_{ID}	17			

The combined results from the three experiments suggest *D. trimaculatus* can employ olfactory and visual cues to select coral habitat and conspecific groups. Fish spent significantly more time in quadrants with coral olfactory cues present than the null-hypothesised average of 25% of the experimental duration (mean % of time: 37.24 ± 4.79 (Fig. 1a); one-sample *t*-test; $t = 2.558$, $df = 16$, $p = 0.011$). Final selection of the coral odour quadrant occurred significantly more often than the null-hypothesised proportion of 25% in Trial 2 (binomial exact test; 59%, $p = 0.003$) (Fig. 1c), but not in Trial 1 (binomial exact test; 44%, $p = 0.057$). The non-significant result during Trial 1 may have been caused by variability in behaviour over a timescale of days, or insufficient acclimation prior to the first trial. However, as shown by the confidence intervals, there is a strong suggestion of the *D. trimaculatus* individuals selecting the coral odour. The preference for coral odour observed in the current study has also been observed for fish on coral reefs (Feary *et al.*, 2007; McCormick *et al.*, 2010; Coppock *et al.*, 2020), suggesting general importance of olfactory mechanisms for locating coral habitat during early life.

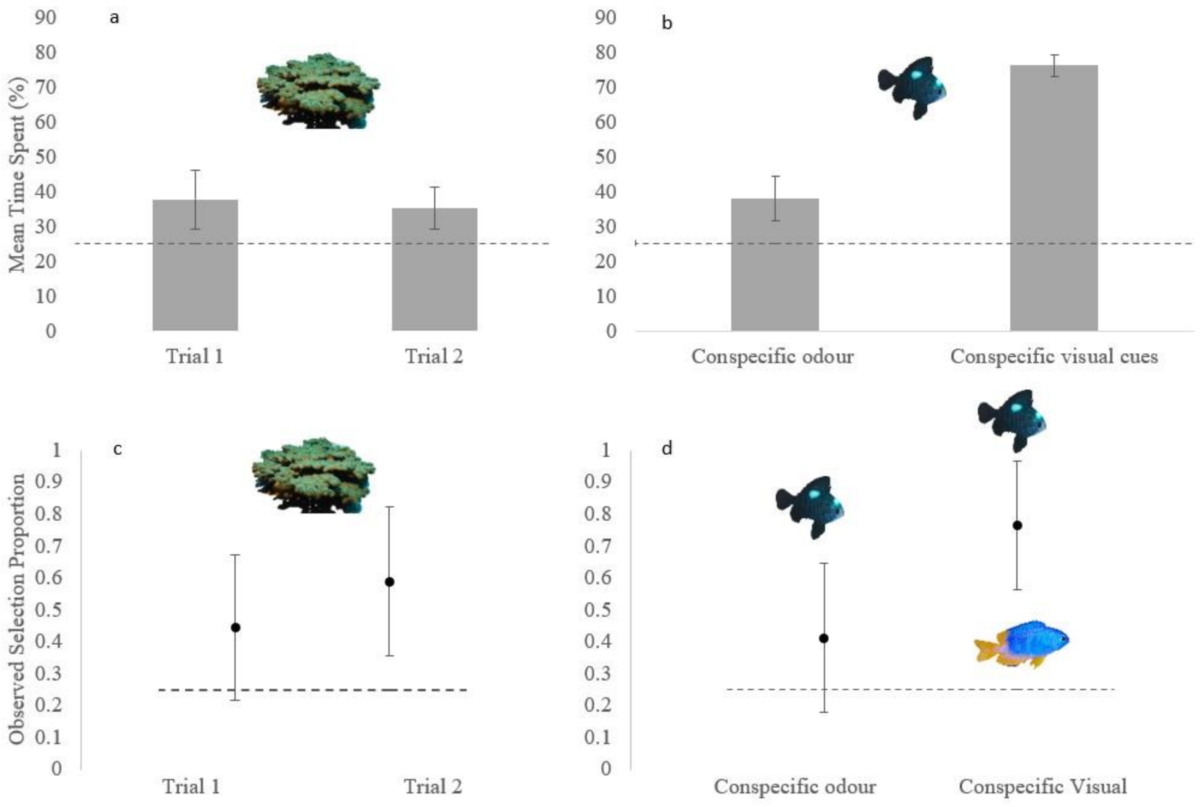


Figure 1 a) Mean time spent (%) in coral odour quadrant during two trials (Trial 1: n = 18, Trial 2: n = 17). b) Mean time spent (%) in conspecific odour quadrant and conspecific visual quadrant (n = 17 for each experiment). Each bar indicates one experiment. One-sample t-test used average against null hypothesis of 25% (dashed line). Error bars indicate standard error c) Final selection of coral odour quadrant during two trials (± 95% CI) (Trial 1: n = 18, Trial 2: n = 17). d) Final selection for conspecific olfactory and conspecific visual cues (D. trimaculatus vs P. coelestis) (n = 17 in each) (± 95% CI). Binomial exact tests used against null hypothesis of 25% (horizontal line: Fig. 1a, 1b, 1c, 1d).

Time spent by *D. trimaculatus* in the conspecific odour quadrant was greater than the null-hypothesised average of 25% of the experimental duration (mean % of time = 37.963 ± 6.43 one-sample *t*-test (Fig. 1b); $t = 2.017$, $df = 16$, $p = 0.03$). The same preference was not demonstrated with final quadrant selection [binomial exact test, 41%, $p = 0.107$ (Fig. 1d)], however, as shown by the confidence intervals, there is a strong suggestion of the *D. trimaculatus* individuals selecting the conspecific odour.

Time spent by *D. trimaculatus* in the conspecific quadrant (vs the confamilial *P. coelestis* quadrants) was three times greater than the null-hypothesised average of 25% of the experimental duration (mean % of time: 76.23 ± 3.139 (Fig. 1b); one-sample *t*-test; $t = 16.320$, $df = 16$, $p < 0.001$). Final selection of the conspecific quadrants also occurred three times more often than the null-hypothesised proportion of 25% [binomial exact test; 76%, $p = <0.001$ (Fig. 1d)].

Once fish approach a reef within sufficient distance for both visual and olfactory cues, the focus on habitat selection may change to visual cues for conspecifics (Lecchini and Nakamura, 2013). Both olfactory and visual cues (much stronger in the current study) of conspecifics could be key indicators for new recruits on whether or not a habitat is considered suitable, as it infers adequate shelter, food, and/or an absence of predators (Booth, 1992; Vail and McCormick, 2011). The lack of conspecifics in temperate ecosystems may result in fewer available olfactory and visual cues for tropical vagrants, at least during the early stages of colonisation and extra-natal population establishment. Potential future studies could combine conspecific and coral olfactory cues and determine how one may enhance the other for individuals finding new habitat.

The individuals used for this experiment were not pre-settlement larvae, but young post-settlement individuals acquired through the aquarium trade. Olfactory abilities may change ontogenetically, as the size of the olfactory organ and its amount of lamellae increase with age in certain fish (Zeiske *et al.*, 1992). However, Wright *et al.* (2005) observed that pre- and post-settlement confamilials (*Pomacentrus nagasakiensis*) displayed similar olfactory responses, suggesting that our results may be applicable to new settlers. Furthermore, Kavanagh and Alford (2003) found that olfactory development in *D. trimaculatus* began later and developed at a slower rate than other damselfish species that exhibit an affinity for specialist live habitat. Therefore, despite not using pre-settlement individuals, the results obtained from the current study still provide insights into the ability of *D. trimaculatus* to use chemical and conspecific cues to find habitat. The lack of a size effect on time spent in coral cues from the mixed modelling further suggests that larger individuals used can provide insights into the sensory abilities of smaller individuals, closer to settlement size. Nevertheless, conclusions regarding settlement abilities of *D. trimaculatus* are made cautiously here, and research on settlement-stage larvae is ultimately required to verify our results here. In practice, research on settlement cues of late-stage larvae is rarely feasible, due to the difficulty of locating such individuals in sufficient abundance and the challenge of observing larvae while they make settlement choices in the field (Leis *et al.*, 2002; Lecchini *et al.*, 2005).

Conspecific olfactory and visual cues are likely to become a more integral part of the recruitment process for tropical vagrant species migrating to temperate SE Australia. As vagrant coral-reef fish species are able to overcome the bottleneck of overwintering (Figueira and Booth, 2010), the establishment of conspecific and congeneric communities which will provide a greater source of olfactory and visual cues to assist in recruitment than currently exists during the initial colonisation. The isolation of the various cues outlined in this study would be impractical *in-situ*, and the use of laboratory techniques allows for the study of individual sensory cues to be measured and to determine which were involved in habitat selection. This study has demonstrated the potential for poleward migrating coral reef fishes to detect scarce stands of hard branching corals that are expanding throughout south-eastern Australia as water temperature increases. The findings of this study note a wider relevance of general olfactory abilities in novel environments, as a result of active (e.g. movement of juveniles between habitats after settlement) or reactive (e.g. storm displacement) movement.

Booth and Sear (2018) have recorded several vagrant reef fish species only found on the coral bed, suggesting further understanding of sensory cues and mechanisms specifically in relation to coral detection is an important part of revealing the processes behind tropicalisation of temperate ecosystems.

Chapter 3: Microhabitat use on novel coral habitat by coral-dwelling tropical vagrant and local temperate fish species in SE Australia

This chapter is currently being prepared for submission to a peer-reviewed journal:
O'Connell, M.J., Allan, S.J., Fowler, A.M., Beretta, G. A., Booth., D.J. "Microhabitat use on novel coral habitat by coral-dwelling tropical vagrant fish and local temperate species in SE Australia". *Current Target Journal: Journal of Fish Biology*

Abstract

Poleward range expansions of tropical reef fish are generating novel interactions with local temperate species and habitats. We asked how expatriating tropical fishes and local temperate fishes utilise novel and scarce coral habitat (*Pocillopora aliciae*), which is expanding in temperate Australia. By directly observing behaviours of 14 fish species, we show that tropical species occupy the centre of coral expanses while temperate species occupy edges or adjacent boulder habitat and exhibit ontogenetic shifts /differences in habitat use which may facilitate coexistence. Also, there was no differences in individual movement distance for tropical or temperate individuals of similar sizes. This study identified spatial separation as a mechanism for coexistence of expatriating tropical fishes and temperate species on new coral habitat, allowing high densities of fish on the corals compared to nearby temperate reefs and enhancing tropicalisation.

3.1 Introduction

The ranges of many marine fishes are shifting poleward in response to increased sea-surface temperatures and strengthening boundary currents (Wu *et al.*, 2012). South-east Australia is a global hotspot for ocean warming (Hobday and Pecl, 2014), with a measurable increase of the temperature and flow rate of the East Australia Current (Ridgway, 2007). These oceanographic changes are associated with poleward expatriation of marine fishes, and the increase and persistence of "vagrant" coral reef fish ("tropical vagrants" hereafter) in SE Australia's temperate ecosystems have already been well documented (Booth *et al.*, 2007; Figueira and Booth, 2010; Fowler *et al.*, 2018; Monaco *et al.*, 2021). Hard coral habitat is also expanding its range poleward in eastern Australia, also as a result of strengthening boundary currents and rising sea surface temperatures, including the coral Families Acroporidae (e.g., *A. intermedia, A. microclados* , and Pocilloporidae (sub-tropical, branching scleractinian coral, *Pocillopora aliciae*) (Schmidt-Roach *et al.*, 2013). *P. aliciae* was first observed in the Sydney Coral Gardens ("SYCOGA" hereafter) in 2013 (Booth and Sear, 2018) and has been proliferating and infilling surrounding urchin barrens since then (*pers. obs.*).

This expansion of branching corals into temperate environments may increase overall hard structure complexity, often infilling the bare substrate ("urchin barrens") left by poleward-expanding tropical sea urchins (Steneck *et al.*, 2002; Vergés *et al.*, 2014). How such increases in habitat complexity may drive changes in fish assemblages and facilitate higher fish densities is poorly understood. Increased structural complexity mediates density-dependent competition (Holbrook and Schmitt, 2002), provides refuges from predators (Steele, 1999), and reduces juvenile fish mortality (Connell and Jones, 1991). Many studies on coral reefs focus on coral-dwelling fishes' responses to loss of live coral habitat and/or degradation. These responses may include relocation (Wismer *et al.*, 2019) or changes in behaviour ([e.g. loss of predation avoidance behaviour (McCormick *et al.*, 2017; Boström-Einarsson *et al.*, 2018)]. However, in temperate regions where habitat-forming species like hard corals are expanding their range, we may observe different adaptation behaviours, with a proliferation of tropical species that require complex coral habitat. As poleward range shifts of marine fishes continue (Sorte *et al.*, 2010), focuses on interactions between arriving tropical vagrants and the habitats available to them within the receiving environment are becoming more crucial.

Competition for resource availability, including habitat space, as well as other inter-species interactions are key determinants of population establishment of expatriating tropical species in temperate environments. It has been well documented that competition for resources increases as suitable habitat declines (Polis and McCormick, 1987; Boström-Einarsson *et al.*, 2014). In SE Australia, winter sea surface temperature is a key limiting factor for many tropical species to establish reproductive populations within temperate environments, yet overwintering has becoming more common as ocean temperatures increase (Figueira and Booth, 2010; Hirata *et al.*, 2011), therefore habitat availability will become more of an important factor for persistence of tropical fish communities. In addition, local temperate species can be displaced by range shifting tropical fauna in not only range-shifting tropical habitat but also in traditionally temperate habitats such as barrens, and macroalgal species [e.g., in Western Japan, Nakamura *et al.,* (2013)]. Historically, the local temperate fish species within SE Australia have been associated with the previously mentioned temperate habitats such as urchin barrens, algal beds, and macroalgal species, and the inclusion of range-expanding branching corals have introduced structure that has deterred temperate species in other parts of the world (see Nakamura *et al.,* 2013). Yet, within SYCOGA these temperate fishes have been observed to congregate around this habitat to a higher propensity than surrounding temperate habitats (*O'Connell et., al., in press*) possibly for increased shelter or resource availability, however, this is not fully known yet. However, the capacity for existence may be dependent on competition for resources, that is minimising overlap of trophic niche space and food resource [e.g., (Kingsbury *et al.*, 2020)]. Range-extending tropical vagrants may also exhibit novel interactions within their new temperate ecosystem, such as changes in prey-predator interactions and trophic competition (Wernberg *et al.*, 2011; Alexander *et al.*, 2016).

Individual movement distances is a fundamental metric used to assess a species' ecology and it can be influenced by environmental drivers within an ecosystem, including distribution of shelter, territorial behaviours, and prey-predator interactions (Börger *et al.*, 2008). As vagrant species find themselves within a novel, temperate environment, food resources may be less available, and of lesser quality than what is found in their natal environment (Chapman, 1981), requiring increasing movement from shelter. For small expatriating tropical vagrant recruits, the risk of predation is high (Booth and Beretta, 2004), limiting movement away from shelter. Here we ask how novel coral habitat in Sydney is utilised by both incoming tropical vagrants and the local temperate fishes. The goal of this study was to observe how habitat use differed between tropical and temperate species, for both adult and sub-adult individuals, and to compare spatial overlap and movement distances between those groups. Novel coral habitats may act as a facilitator for both tropical and temperate fishes, with minimal overlap of resource use, this may enhance tropicalisation by supporting high fish densities.

3.2 Materials and Methods

Sampling was conducted within the *Pocillopora aliciae* gardens in SYCOGA, Manly, NSW (33.80S, 151.30E) over the course of six dives within three expeditions in March 2021 – May 2021, within the summer recruitment season (January – May) (Booth et al., 2007). Two areas in the coral gardens, which contained the highest coral cover ('Section 1' = ~ 32.73% coral cover; 'Section 2' = ~ 33.38% coral cover), and the highest species richness and density of fishes, were selected for observation. Each section was divided into two adjacent 3 m x 4 m sub-sections which were each observed by an individual diver.

Small-scale habitat uses and movement distances of vagrant and local species were assessed by *in-situ* observations and visual tracking of both vagrant and local fish individuals for 15-

minute periods. Following the methodology of Streit *et al.* (2021), images of the four sub-sections in SYCOGA (Fig. 2 – cartoonised image overlay of sub-section) were taken prior to the dives and a 'mud-map' of all coral expanses and important geographic markers was transcribed onto water-proof paper. Data were pooled across all four sub-sections.

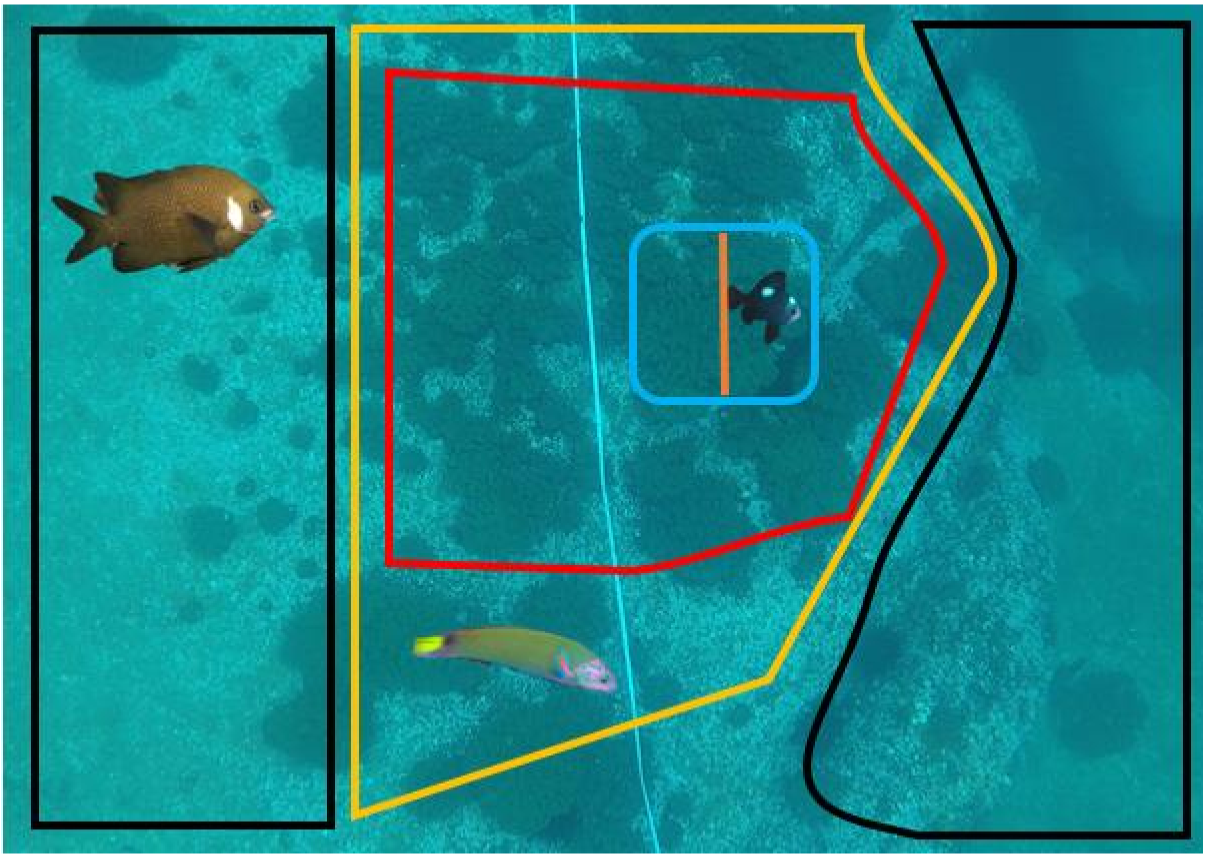


Figure 2 Example of simplified mud-map overlaid on observational area. Marked with maximum movement distance (MMD) of Dascyllus trimaculatus individual exhibiting an occupation of 'centre' coral partitioning, Parma microlepis exhibiting occupation of 'boulder' habitat, and Thalassoma lunare exhibiting occupation of 'edge' habitat; MMD highlighted as orange line within range extent of D. trimaculatus individual (blue). For example, three habitat categories were edge (yellow circle), centre (red circle), and boulder (black circle). Light grey outlined coral heads on mud-map.

Four divers simultaneously remained stationary, approximately 1 m away from their respective sub-sections with the 'mud-map' for 15 minutes observing all individuals, noting their locations in relation to an individual coral expanse they were associated with, and categorising the location as either 'coral edge' or 'coral centre' habitat. This 15-minute observation period was repeated twice per dive expedition across the three sampling months. Each diver only mapped their allocated sub-section. The area where individuals moved in this time was also recorded, noting landmarks at extreme edges of the movement range then measuring distance between these, to provide an indication of movement range which was later checked against a known scale to get maximum movement distance (MMD; Fig. 1). Individuals that were primarily observed in areas between the four coral sections but not using the corals were classed as using 'boulder' habitat, which consisted of granitic boulders with minimal complexity and little algal growth.

The proportions of individuals observed on each habitat section (coral edge, coral centre, or boulder) was compared between tropical vagrant and temperate species groups using a two-factor analysis of variance (ANOVA) on square-root transformed data. Tukey's *post-hoc* tests were used to compare habitat categories between species groups. Differences in MMD between habitat position and species type (tropical vs temperate) were analysed by way of two-factor PERMANOVA, following Harasti (2016) using the PRIMER V6 software (www.primer-e.com/). A PERMANOVA was used for comparisons of MMD between habitat position and species origin as equal variances were violated within an ANOVA. The analysis was performed on the Bray-Curtis similarity matrix, with species origin analysed as a fixed factor with two levels (temperate and tropical) and habitat position analysed as a fixed factor with three levels (edge, centre, and boulder). Significance was determined from n = 999 permutations. Adult *P. microlepis* and *P. unifasciata* were excluded from this analysis to keep body sizes relatively similar among individuals and species (see results).

3.3 Results

Over the course of the study, 130 individuals from 14 species were observed, with five of those species categorised as tropical vagrants. The most abundant species were the vagrant tropical wrasse *Thalassoma lunare* (sub categorised as sub-adult or adult), and the temperate damselfishes *Chromis hypsilepis*, *Parma unifasciata*, and *Parma microlepis* [categorised as sub-adult (25 to 55 mm TL) or adult (80 + mm TL)]. Some species we observed were uncommon, predominantly tropical species e.g., *Chaetodon guentheri* (n = 1). The proportion of individuals observed on each habitat position (coral edge, coral centre, and boulder) differed between species origins (tropical vagrant vs temperate) (two-factor ANOVA, $F_{2,48} = 3.640$, $p = 0.034$, Table 2).

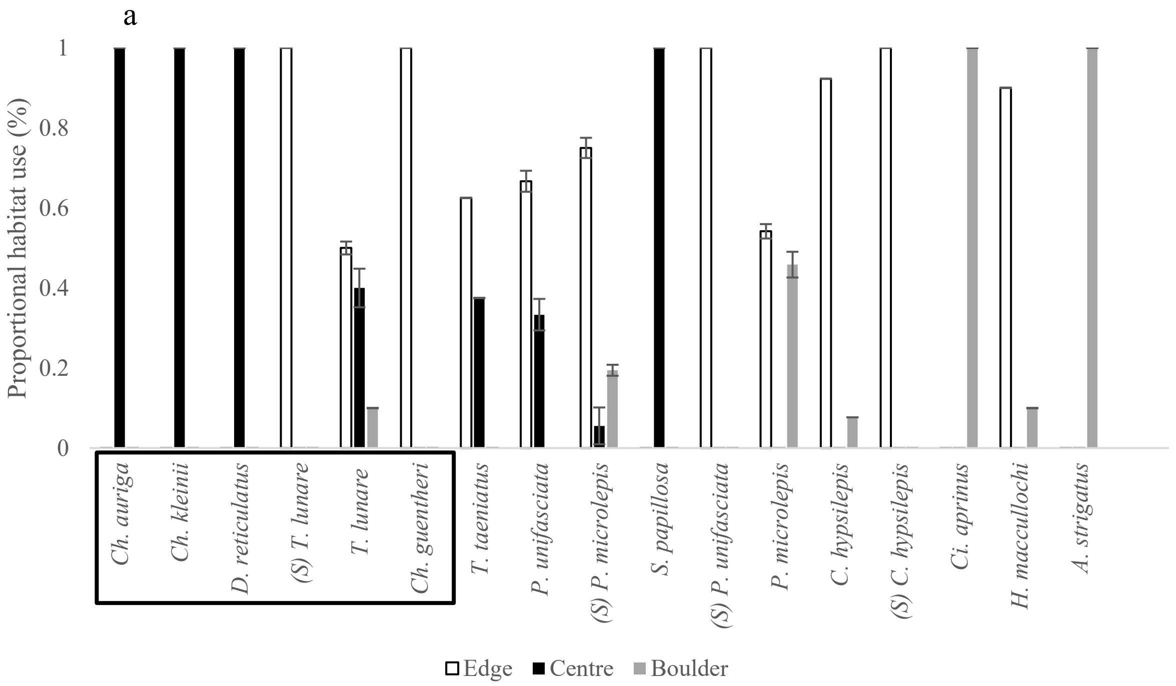
Table 2 Two-factor ANOVA and subsequent post-hoc test observing proportional use of habitat comparing species origin (Tropical vs Temperate) and Habitat position (Edge, Centre, Boulder). Significant results in bold.

	df	*SS*	*MS*	*F*	*P*
Model Terms					
Species Origin	*1*	0	0	0	1
Habitat Position	*2,48*	0.769	0.385	2.488	0.094
Species Origin x Habitat Position	***2,48***	**1.125**	**0.563**	**3.64**	**0.034**
Residuals	*48,53*	7.420	0.155		

Tukey Pairwise tests

	Diff. of Means	*q*	*P*
Temperate species			
Edge vs Centre	0.387	3.409	0.051
Edge vs Boulder	0.215	1.893	0.381
Centre vs Boulder	0.172	1.516	0.536
Tropical species			
Edge vs Centre	0.15	0.935	0.787
Edge vs Boulder	0.4	2.492	0.193
Centre vs Boulder	0.55	3.427	0.05
Species Origin within Edge Use			
Temperate vs Tropical	0.117	0.843	0.554
Species Origin within Centre Use			
Temperate vs Tropical	**0.42**	**3.019**	**0.038**
Species Origin within Boulder Use			
Temperate vs Tropical	0.302	2.176	0.131

Tropical individuals appeared eight times more likely to be found within the centre of a coral expanse than over boulder habitat, although this was not significant due to the high degree of variability among individuals (*p* = 0.050, Table 2; Fig. 3a). Temperate individuals were generally observed more often (but not significantly so) on the edge of coral expanses compared to the centre of coral expanses (*p = 0.051*; 69.6% edge, 7.1% centre, Fig. 3a), however, possibly with higher power this result would lead to significance. Also, tropical individuals were found more often (44% observed) within the centre of a coral expanse than temperate individuals (7% observed) (*p* = 0.038, Fig. 3a).



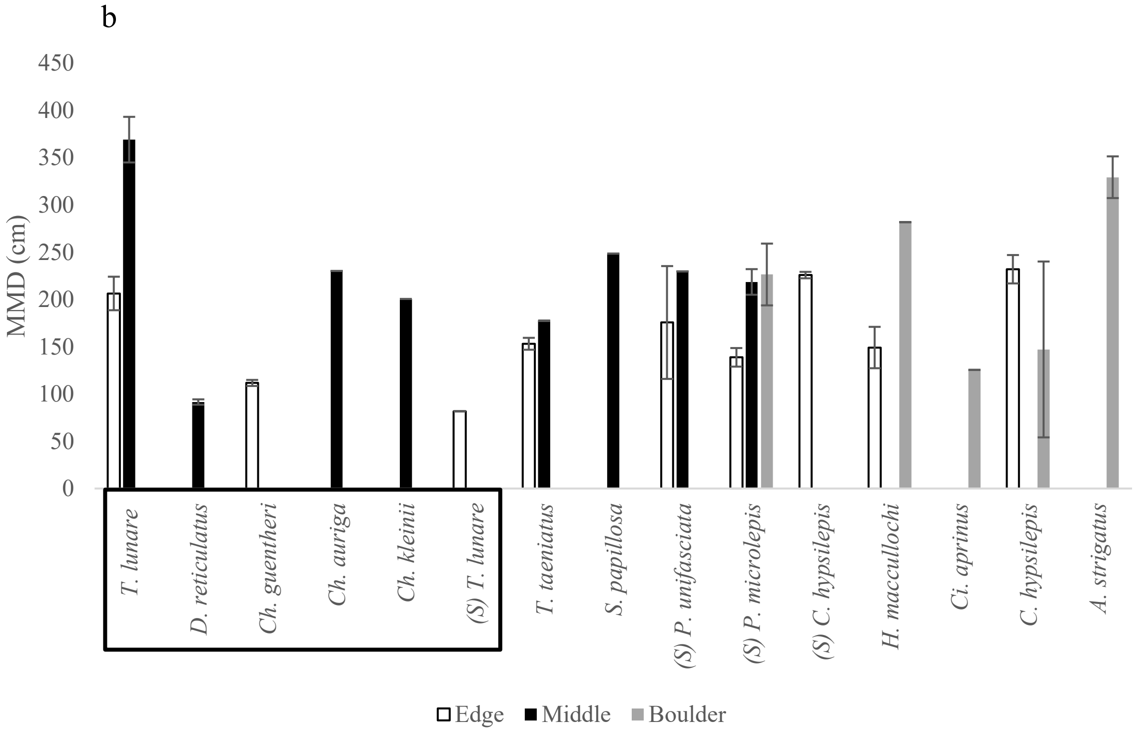


Figure 3 a) Mean proportional habitat use for observed species (% ± SE if n > 1). (S) indicates sub-adult individuals. b) Mean MMD (cm + SE if n > 1) of species recorded of similar body sizes. MMD compared to habitat position use (Edge, Centre, and Boulder). Tropical species boxed. Key study species categorised by sub-adult (S) and adult.

There was no significant effect of species category or habitat position on average MMD (two-Factor PERMANOVA, $F_{1,99} = 0.76$, p = 0.407, Fig. 3b).

3.4 Discussion

Here, we showed that fish of different origins (tropical vagrant, local temperate) use space differently on novel coral habit, which would reduce competition and, in turn, facilitate coexistence. Tropical species were observed approximately 6 times residing within the centre of coral habitat than temperate species than at edges or adjacent rocky boulder habitat, while temperate species are 3 times more likely to be observed on the edge of coral expanses than the centre, suggesting spatial separation may enhance coexistence of the two groups and allow overall increased fish densities as a result. Our findings suggest spatial separation, with regards to habitat use, between poleward-expanding vagrant fish and the local temperate population in SE Australia, in contrast to a study of western Japan's Tosa Bay (Nakamura *et al.,* 2013), providing insight into variation in the domination of tropical fish species in temperate regions. It must be stated that as a result of small sample sizes of particular species (e.g., *Chaetodon guentheri*)*,* results may not account for among-individual variation in behavioural preferences. The incursion of poleward shifting *P. aliciae* habitat would benefit tropical vagrant fishes which are highly associated with live coral and to date have exhibited far less success in establishment on temperate substrates (Booth *et al.*, 2007). In addition, temperate species exhibited higher densities on this habitat compared to adjacent temperate rocky reefs (Chapter 4). Within novel temperate ranges, tropical vagrant fish have been shown to modify behavioural niches and increase their behavioural niche breadth, as has been observed in altered shoaling and feeding behaviours (Coni *et al.*, 2021).

The use of the centre portion of a coral bed by tropical species, and in particular all *D. trimaculatus* individuals, is also observed within tropical coral reefs. *D. trimaculatus* is often found within the central portion of a host anemone's oral disk and are rarely attacked by predatorial species compared to individuals on the edges of the oral disk or within the water column (Holbrook and Schmitt, 2002). *D. trimaculatus* have been observed within the natal tropical habitat to coexist with anemonefish within a single anemone (Schmitt *et al.*, 1999), which are not found within Sydney's temperate ecosystems. This coexistence exhibited a direct negative effect on *D. trimaculatus* density as the anemonefish (*Amphiprion chrysopterus*) was a superior competitor (Schmitt and Holbrook, 2003). Coexistence between the vagrant damselfish *D. trimaculatus* and the local common *P. microlepis,* in SE Australia, in contrast, may be facilitated by such habitat separation, as *P. microlepis* is highly aggressive and territorial (Buckle and Booth, 2009).

We observed no differences in MMD, between tropical and temperate individuals of similar sizes. Streit *et al.* (2021) noted that the relationship of home ranges (likely related to MMD) and body size is dictated by coral cover. This is due to higher coral cover reducing space use for larger fish, causing focus around a smaller area, as *P. aliciae* coral cover increases due to the brooding nature of the species. Movement distances may potentially decrease for all individuals leading to increased inter-species interactions and competition for resources. The *P. aliciae* paratype found in SYCOGA are flat plate-like coral expanses with small gaps and thick branches (see morphotypes described in Schmidt-Roach *et al.*, 2013, Fig. 4) which smaller fish species prefer [e.g., *Dascyllus aruanus* (Holbrook *et al.*, 2000)]. This occupation of edge habitat by temperate species may be a sufficient compromise between protection from predation while also having greater access to resources. However, an area of future study regarding this small-scale habitat uses and overlapping of individuals, may be what processes are driving this difference of habitat use, is it merely preference of habitat coverage? Or possibly individuals keeping tropical vagrant species within the centre of the coral habitat.

In this study, we identified spatial separation as a mechanism that may facilitate coexistence of tropical and temperate species utilising novel and sparse range-expanding coral habitat within SE Australia. We observed range-expanding tropical vagrant fish to utilising the centre of coral habitat in greater proportion to temperate species where they could shelter within the structural complexity of *P. aliciae* expanses from predators.

Chapter 4: Range shifting coral attracts high densities of both expatriated tropical and local temperate reef fish species in SE Australia

This chapter is currently being prepared for submission to a peer-reviewed journal:
O'Connell, M.J., Allan, S.J., Fowler, A.M., Beretta, G. A., Booth., D.J. "Range shifting coral beds attract high densities of both invading tropical and local temperate reef fish species in SE Australia". *Current Target Journal: Climactic Change or Coral Reefs*

Abstract

The strengthening of western boundary currents and the consequent increase in water temperatures under climate change has resulted in greater poleward movement of tropical reef fish and the establishment of novel habitats in temperate marine ecosystems. We censused coastal reef fish assemblages seasonally in and adjacent to a newly established temperate coral bed (*Pocillopora aliciae*) in the Sydney Coral Gardens (SYCOGA), NSW, Australia, to understand if novel coral habitat is facilitating assemblages of tropical and temperate fishes. This study presents the first comprehensive assessment of species associating with this novel coral habitat within a temperate environment. Twenty fish species were identified associating with the coral bed (8 tropical, 12 temperate), with cooler winter temperatures correlating with decreasing abundance and density of both tropical and temperate species. Both temperate and tropical species were observed at much greater (66% greater on average) densities on the coral than on directly adjacent non-coral rocky substrate, suggesting that the corals concentrate fish assemblages, and may aid in tropicalisation for those species that use tropical coral as habitat. SYCOGA had similar, and on occasion higher, densities of reef fishes than surrounding temperate rocky reef locations within Sydney.

4.1 Introduction

The world's oceans have significantly warmed over the past several decades as a result of anthropogenic climate change (IPCC, 2014). However, rates of warming vary among regions of the world, with a number of coastlines with poleward-flowing Western Boundary Currents (WBCs) exhibiting water warming two to three times faster than the global average (Wu *et al.*, 2012) - termed 'global hotspots'. These hotspots include eastern Japan (Nakamura *et al.*, 2013), eastern USA (Fodrie *et al.*, 2010), Brazil (Barneche *et al.*, 2009), South-eastern Africa (Lloyd *et al.*, 2012), and the Mediterranean (Sala *et al.*, 2011), all of which have WBCs that have significantly changed the natal marine assemblages (Hughes *et al.*, 2005; Vergés *et al.*, 2014). One of these global hotspots is South Eastern Australia, with the intensification of the East Australian Current (EAC) transporting warm tropical water from the Coral Sea further poleward along the temperate coast (Poloczanska *et al.*, 2007; Ridgway, 2007).

Tropicalisation has been a well-studied phenomenon over the last several years and refers to poleward migration of marine species (Pecl *et al.*, 2017). It has been loosely defined as assemblages within sub-tropical or temperate environments' changing in composition as tropical species move poleward as a result of increasing water temperatures (Figueira and Booth, 2010) and strengthening WBCs, increasing intensity of both tropical larval and large mobile species dispersal (Coleman *et al.*, 2011). This is then coupled with a poleward expansion of tropical habitat-forming species such as scleractinian corals (Yamano *et al.*, 2011). Tropicalisation can lead to differing outcomes in temperate ecosystems. "Simplification", as described by Agostini *et al.* (2021), is a recently identified phenomenon which, in contrast to tropicalisation, is that a lack of infilling tropical habitat (leading to full tropicalisation) is observed, leaving bare substrate exposed. The consequence of this is a loss in temperate habitat without replacement as opposed to the maintenance of habitat complexity, with different species.

While abiotic effects associated with climate change have significant impacts on the range expansions of marine organisms, there are also indirect biotic drivers such as changes to habitat. The habitat modification in temperate ecosystems, brought upon by expatriating tropical fauna, has resulted in loss of macroalgal communities (Steneck *et al.*, 2002). This has then led to replacement by tropical and sub-tropical coral species (Mezaki and Kubota, 2012) or simple turf-dominated ecosystems (Agostini *et al.*, 2021). For instance, Tosa Bay in the south of Japan has seen a dramatic decline in temperate kelp (*Ecklonia spp.*) and fucoids (*Sargassum spp.*) throughout the last two decades as the substantial movement of warmer tropical water and tropical herbivorous fishes moved poleward (Serisawa *et al.*, 2004). Overgrazing of poleward shifting tropical fishes, such as the rabbitfish *Siganus fuscescens* and parrotfish *Calotomus japonicus*, has led to the creation of bare or crustose-algae covered rock which thereby increases in intensity with warming ocean temperatures (Smith, 2008). Within Australia, the alteration of temperate habitat through the immigration of tropical herbivorous fish and the sea urchin *Centrostephanus rodgersii* (Diadematidae) has facilitated poleward range shifts (Ling *et al.*, 2008). Kelp has historically exhibited high resilience in the face of environmental stressors (Filbee-Dexter and Scheibling, 2014), however recent recovery from disturbance has decreased in Western Australia (Wernberg *et al.*, 2010) resulting in infilling by reef-building corals (Mezaki and Kubota, 2012). Barren ecosystems significantly impact local fauna and flora communities. The new space available for other habitat forming species has the potential to both alter local communities, while also facilitating range-shifts for those tropical species with specific non-macroalgal habitat requirements (Precht and Aronson, 2004; Yamano *et al.*, 2011; Coni *et al.*, 2021).

Most marine fish have pelagic larvae which facilitates transport and dispersal of tropical fishes over large distances into temperate ecosystem (Leis, 1991). The dispersal of expatriating tropical reef fish into temperate ecosystems has been well documented both in Australia (Hutchins *et al.*, 1991; Hutchins and Pearce, 1994; Fowler *et al.*, 2018) and elsewhere, such as Japan (Nakamura *et al.*, 2013), the US (McBride and Able, 1998), and the Mediterranean (Rilov and Galil, 2009). Settlement of these expatriating species employs a variety of senses, including smell, hearing, and sight. These are used for detecting and selecting suitable habitat (Lecchini *et al.,* 2005), discerning conspecifics and predators, and foraging (Figueira and Booth, 2010), which together determines settlement success. Once settled, overwintering has been identified as a key bottleneck for the establishment of these range-shifting populations (Figueira and Booth, 2010), however, as ocean temperatures continue to rise we expect to see greater numbers of overwintering species and the establishment of reproductive populations as habitat suitability may become more important.

Coral reef fish species are shifting poleward, (Booth *et al.*, 2018; Fowler *et al.*, 2018), yet the key habitats, such as corals, have not kept pace (Baird *et al.*, 2012). In SE Australia, colonies of *Pocillopora aliciae* (Pocilloporidae) (Schmidt-Roach *et al.*, 2013), have recently been observed in Cabbage Tree Bay Aquatic Reserve, Sydney, New South Wales (NSW) (Sydney Coral Gardens, from here on “SYCOGA”, Fig. 4) (Booth and Sear, 2018). *P. aliciae* is particularly abundant in the Solitary Islands in eastern Australia (-30.205, 153.267) and occurs frequently on rocky reef habitats between 2-32 m deep (Smith and Simpson, 2010). Reproduction is frequent and exhibits both brooding and broadcasting distribution processes (Harriott and Banks, 1995). Due to the recency of coral establishment, the fish assemblages associate with this novel habitat have not been comprehensively investigated (e.g., within the bay of Cabbage Tree Aquatic Reserve, Little Manly, Shelley Beach). Currently, it is Sydney’s only scleractinian branching coral species and has been observed proliferating and infilling urchin barrens and nearby kelp (*Ecklonia spp.*) habitat. This establishment has provided habitat for some coral-reef fishes (e.g. humbug damselfish *Dascyllus trimaculatus* and *D. reticulatus* (Booth and Sear, 2018). *D. trimaculatus* and *D. reticulatus* are known to inhabit anemones in their natal range (Schmitt and Holbrook, 2000), but have been observed to utilise branching Acroporidae and Pocilloporidae coral species throughout tropical (Wilson *et al.*, 2008; Coker *et al.*, 2014) and now temperate environments (Booth and Sear, 2018).

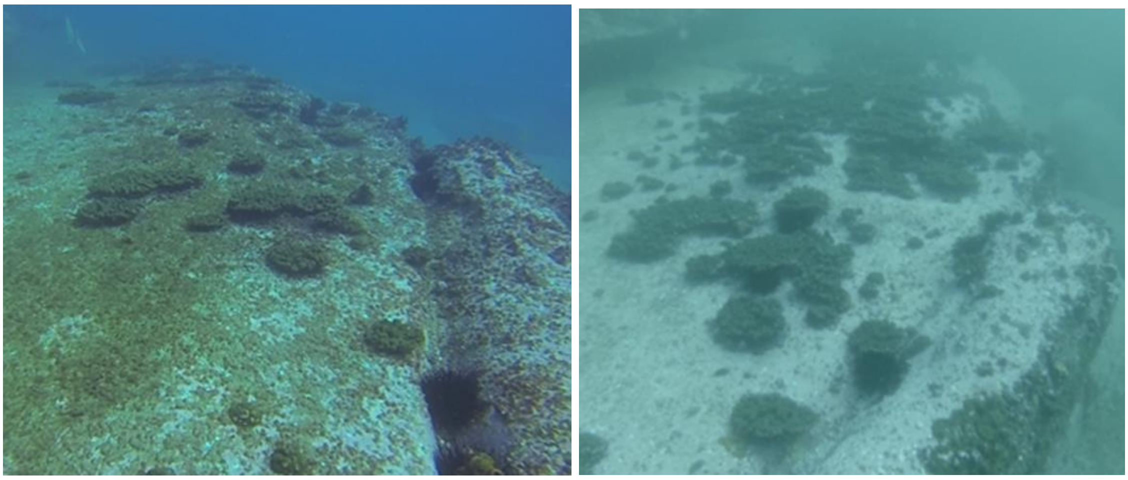


Figure 4 Photos indicating coral coverage increase within Cabbage Tree Aquatic Bay Reserve. Left image taken Jan 14th, 2019, Right image taken Aug 14th, 2021 (Photo cred. John Sear).

The aim of this study was to investigate the SYCOGA fish assemblage, specifically to 1) identify fish species (both tropical and temperate) utilising novel *P. aliciae* habitat and observe changes in these communities seasonally, 2) assess the potential importance of coral habitat for temperate and tropical species by comparing fish densities on coral to the surrounding kelp and urchin barren habitats, 3) estimate the future habitat utility of SYCOGA following further establishment by comparing fish assemblages with those in locations where both the coral and fish assemblages are well established on islands 215 km north, and 4) understand whether SYCOGA enhances tropicalisation or leads to simplification via changes to fish assemblages.

Findings provide insights into the role of novel coral habitat as habitat for both local temperate and exotic tropical fish species.

4.2 Materials and Methods

4.2.1 Study locations and species description

The study was undertaken at SYCOGA, Manly, NSW, Australia (33.800 S, 151.300 E), and Broughton Island (32.615 S, 152.323 E) and Cabbage Tree Island (32.695 S, 152.223 E), Port Stephens, NSW, Australia (Fig. 5). All sites are dominated by the seasonal western boundary current (EAC) and the associated eddies that form off of the EAC extension (Cetina-Heredia *et al.*, 2014). Similar to coastal Sydney, underwater benthos on both islands have been affected by *C. rodgersii* urchin barrens which have given way to the infilling of *P. aliciae* colonies (Beger *et al.*, 2014). The Sydney coral garden, is at 12-15 m depth on bare rock substrate and the proliferation via local propagule release of *P. aliciae* has resulted in approximately 540 m^2 of novel coral habitat (*pers. obs.*). Surrounding habitat westward towards shore is dominated by kelp *E. radiata*, whereas the eastern, northern, and southern habitat is predominantly urchin barren and encrusting algae.

The second location for this study was within the Port Stephens Great Lakes Marine Park (PSGLMP). Cabbage Tree Island and Broughton Island are two islands within the park located on the mid-north coast of NSW, Australia (Fig. 5). They are approximately 1.5 km east and 14 km northeast, respectively, from the entrance of Port Stephens. Broughton Island coral heads are interspersed between algae and macrophyte habitat (*pers. obs.*) and there is less delineation between habitat types.

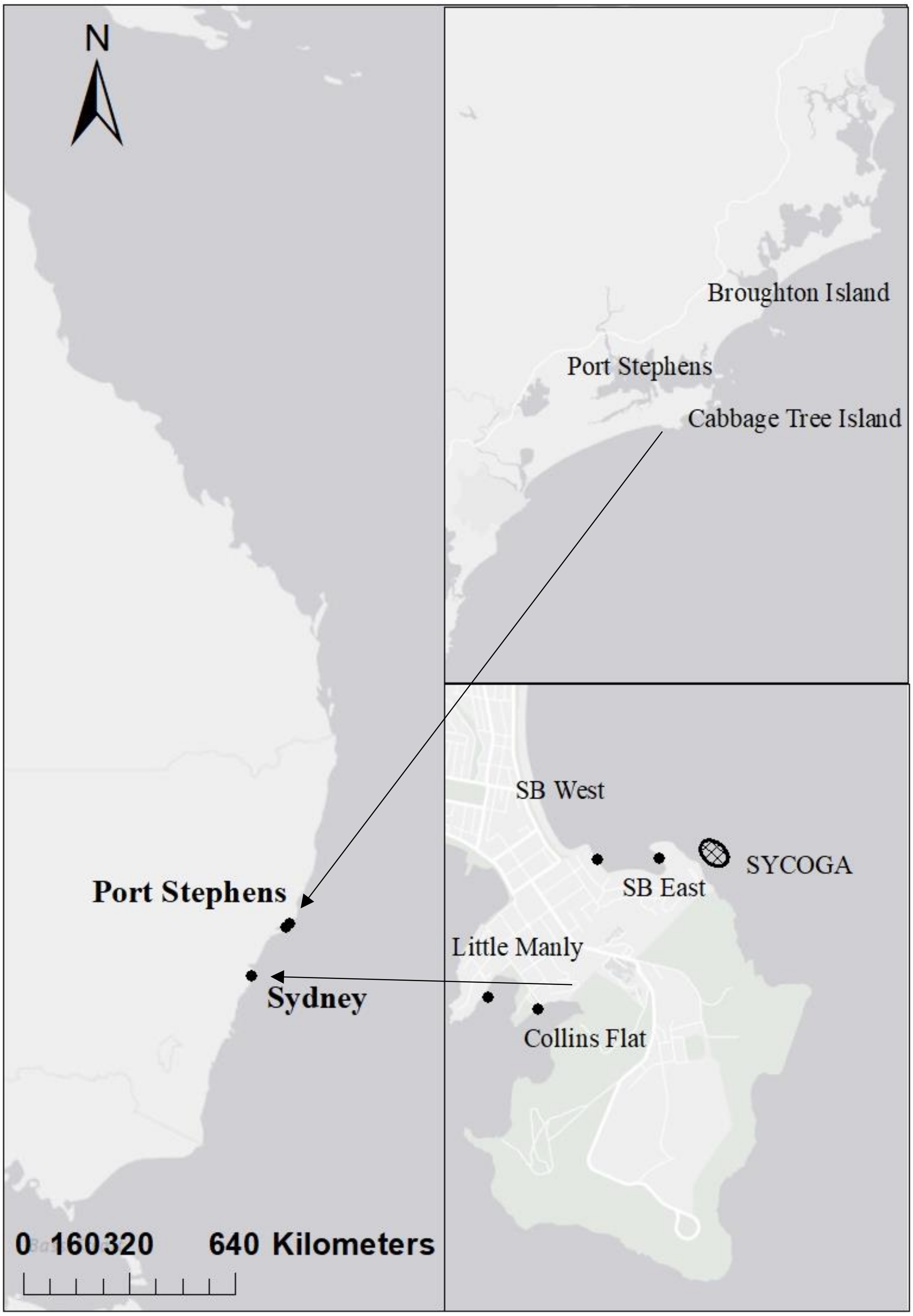


Figure 5 Map showing study locations: Sydney Coral Gardens (SYCOGA) and Northern Sydney locations in Sydney and Broughton Island and Cabbage Tree Island in Port Stephens, NSW. And long-term monitoring locations (Booth et al., 2007; Booth et al., 2018; Booth and Sear, 2018). Service Layer Credits: Esri, HERE, Garmin, © OpenStreetMap contributors, and the GIS user community.

4.2.2 Fish survey protocol

Sydney sampling was conducted opportunistically from November 2019 - May 2021 due to the exposed nature of the location and impact on suitable diving conditions. Each season was comprised of 2-3 sampling expeditions except for Summer 2019-2020 (n =1) and Winter 2020 (n = 1). Following Booth (2000), permanent transects of 10 m x 6 m that encompassed the entirety of the coral garden were surveyed. Consistent with the coral habitat census protocol, a diver would slowly traverse the transect recording all fish found within a 10 m x 6 m section.

Surveys were also recorded adjacent to the coral habitat at the SYCOGA, within typical temperate rocky reef habitat which included kelp (predominantly *Ecklonia radiata*), rock, turfing algae and sponges. Over the course of 4 months (1 expedition per month; Feb, March, April, May 2021), a total of twenty 10 m x 6 m transects were haphazardly placed in habitat adjacent to the coral gardens.

To further compare tropical assemblages on SYCOGA coral habitat to those on temperate rocky reefs, data on species density and species richness of tropical species from other sites in Sydney (*D.J. Booth unpub. data*) were also used from a long-term study. However, assemblage parameters such as focal species densities were collected using the roaming transect method as described in Beck *et al.* (2014). These locations were Shelley Beach west (1.4 km^2), Shelley Beach east (1.0 km^2), Little Manly (1.4 km^2), and Collins Beach (1.4 km^2) all located within northern Sydney, as is SYCOGA (Fig. 2). To compare with assemblages from transects surveyed in the current study, the area of each roaming transect was calculated through Google Maps and measured as length surveyed (m) x 6 m transect width. Fish were surveyed in the same seasons at SYCOGA and other locations within Sydney.

4.2.3 Statistical analysis

Density (individuals per 60 m²) and species richness were used as assemblage parameters within this study, as described by Fowler and Booth (2013).

4.2.3.1 Seasonal comparison of assemblage parameters on coral habitat within SYCOGA.

Data were grouped into southern-hemisphere seasons: Summer 2019 (December – February), Autumn 2020 (March – May), Winter 2020 (June – August), Summer 2020, and Autumn 2021. Density of tropical and temperate species separately, and species richness were compared among seasons using separate one-way Analyses of Variance (ANOVA) with a Holm-Sidak *post-hoc* (on arcsine square root transformed data) test using IBM SPSS software (IBM Corp, 2019).

4.2.3.2 Comparison of assemblage parameters between coral habitat and rocky reef habitat within SYCOGA.

Assemblage parameters within SYCOGA coral habitat were compared to adjacent rocky reef habitat (2 Levels: coral habitat vs rocky reef; Fixed) across the four sampling expedition during summer/autumn 2021 (4 Levels: Feb-May; Random), through a two-way ANOVA utilising IBM SPSS software (on arcsine square root transformed data) (IBM Corp, 2019). Species richness was not utilised and density of tropical and temperate species within this test were pooled since no tropical species were observed in the adjacent temperate habitat.

4.2.3.3 Comparison of assemblage parameters between SYCOGA coral habitat and rocky reef habitat at other locations in Northern Sydney.

To further test tropical vagrant assemblage parameters of most abundant tropical species densities between SYCOGA coral and temperate rocky reef habitat; total tropical vagrant species densities (individuals per 60 m^2) were pooled and compared across years (2019-2021) and habitat (Northern Sydney reefs vs SYCOGA coral). The key vagrant species were: *Dascyllus trimaculatus, D. reticulatus, Chaetodon auriga, C. flavirostris, C. kleinii, C. guentheri, Acanthurus nigrofuscus,* and *Thalassoma lunare.* Key tropical species were defined as the most abundant throughout the locations. A two-factor analysis of variance (two-way ANOVA, on arcsine square root transformed data) was used utilising the same factors as the previous test. Since new fish would be observed each year, due to mortality in winter, years were considered independent. However, some individuals of *T. lunare* may persist through winter into the following years, as previously observed with other tropical vagrant species (Figueira and Booth, 2010).

4.2.3.4 Comparison of assemblage parameters between SYCOGA coral and northern P. aliciae habitat.

Fish density of both tropical and temperate fish (individuals per 60 m^2) on coral habitat was compared between the three locations through a two-way ANOVA (factor Habitat; 3 levels: SYCOGA, Broughton Island, Cabbage Tree Island and species category [factor Species Origin; 2 levels: tropical or temperate)]. These locations could not be included in the seasonal analysis as the sites could only be sampled during much more limited time period. Data were square-root transformed to satisfy normality assumptions and a two-way ANOVA with a Tukey *post-hoc* test was executed to observe differences between established and novel coral habitat.

4.3 Results

4.3.1 Species list and seasonal comparison of assemblage parameters on coral habitat within SYCOGA.

Overall, 8 tropical and 12 temperate fish species were recorded from 11 families on the coral gardens (Table 3). Tropical species were sub-adult except for *T. lunare*. which was present in both sub-adult and adult life stages.

Table 3 List of all species, number of observations, and habitat associations (as observed) found at SYCOGA over the sampling period.

Species name	**Origin**	**Family**	**# Observed**	**Habitat**
Acanthurus dussumieri	Tropical	Acanthuridae	2	Coral/Rocky Reef
Acanthurus nigrofuscus	Tropical	Acanthuridae	1	Coral/Rocky Reef
Chaetodon auriga	Tropical	Chaetodontidae	4	Coral/Rocky Reef
Chaetodon kleinii	Tropical	Chaetodontidae	2	Coral/Rocky Reef
Chaetodon guentheri	Tropical	Chaetodontidae	3	Coral/Rocky Reef
Thalassoma lunare	Tropical	Labridae	118	Coral/Rocky Reef
Dascyllus trimaculatus	Tropical	Pomacentridae	9	Coral
Dascyllus reticulatus	Tropical	Pomacentridae	4	Coral
Aulopus purpurissatus	Temperate	Aulopidae	6	Rocky Reef
Notolabrus gymnogenis	Temperate	Labridae	10	Rocky Reef
Ophthalmolepis lineolata	Temperate	Labridae	16	Rocky Reef
Cheilodactylus vestitus	Temperate	Latridae	4	Coral/Rocky Reef
Atypichthys strigatus	Temperate	Microcanthidae	135	Coral/Kelp/Rocky Reef
Pempheris affinis	Temperate	Pempheridae	10	Coral/Rocky Reef
Trachinops taeniatus	Temperate	Plesiopidae	424	Coral/Rocky Reef
Parma microlepis	Temperate	Pomacentridae	241	Coral/Rocky Reef
Parma unifasciatus	Temperate	Pomacentridae	39	Coral/Rocky Reef
Chromis hypsilepis	Temperate	Pomacentridae	113	Rocky Reef
Scorpis lineolata	Temperate	Scorpididae	16	Rocky Reef
Hypoplectrodes maccullochi	Temperate	Serranidae	24	Coral/Rocky Reef

There were significant differences in fish density among seasons for both tropical fishes (One-way ANOVA, $F_{4,81} = 3.036$, p = 0.022, Fig. 6a) and temperate fishes (One-way ANOVA, $F_{4,80} = 2.88$, p = 0.028, Fig. 6a). Summer 2019 had 7 times higher tropical fish densities than Winter 2020 (Holm-Sidak, $t = 3.094$, p = 0.027, Fig. 6a). Holm-Sidak *post-hoc* tests indicated no significant differences in temperate densities between individual seasons. There were no significant differences in species richness among seasons (One-way ANOVA, $F_{4,76} = 1.064$ p = 0.079, Fig. 6b).

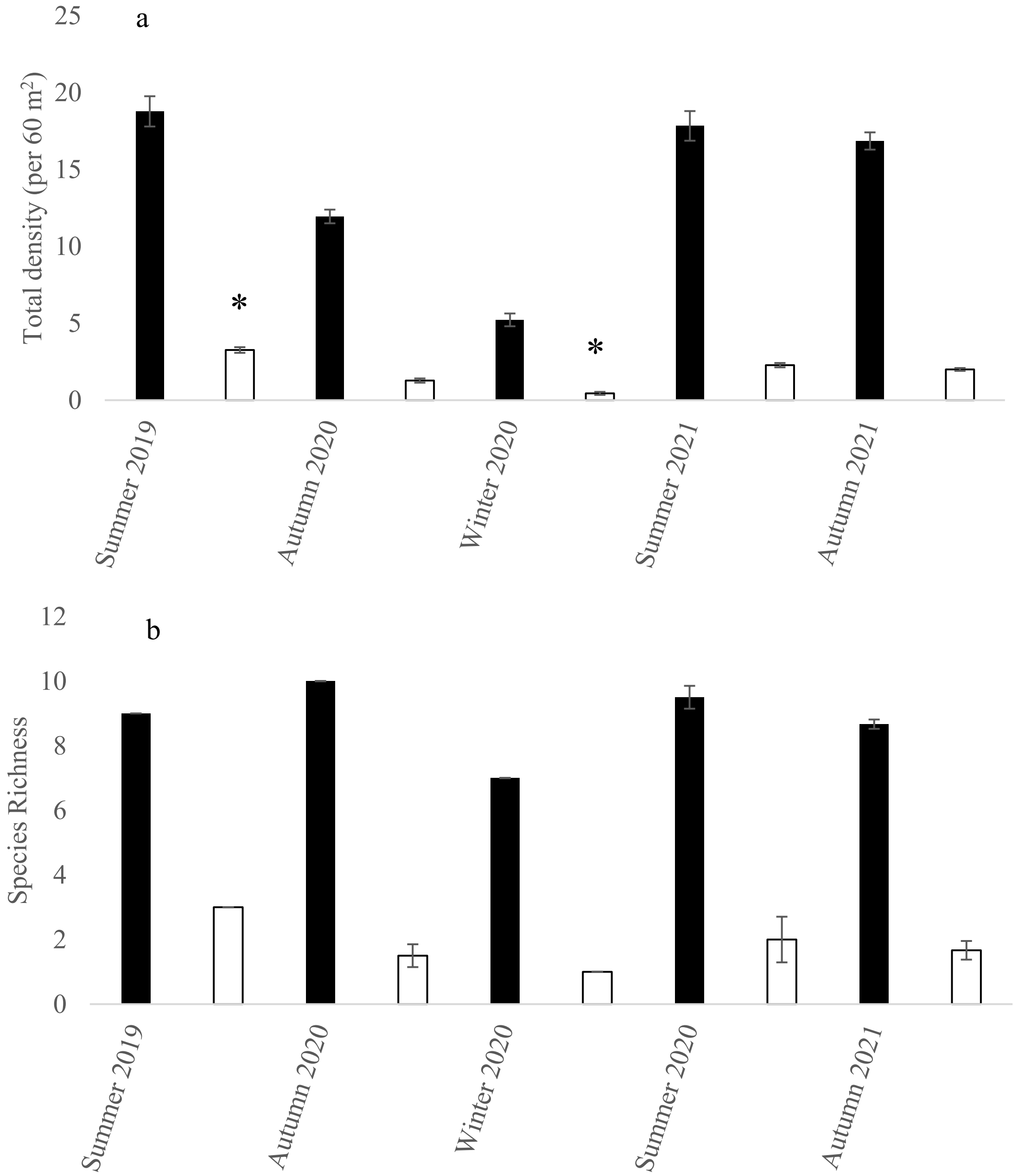


*Figure 6a) Fish density (per 60 m^2 ± SE) of tropical (white) and temperate (black) fish species and b) species richness (± SE) within SYCOGA through sampling seasons Summer 2019, Autumn 2020, Winter 2020, Summer 2021, and Autumn 2021. Significance between seasons indicated with *. Errors bars indicate standard errors. n= 9.*

4.3.2 Comparison of assemblage parameters between coral habitat and directly adjacent rocky reef habitat within SYCOGA.

Overall fish density was significantly greater (ranging between 4 – 10 times greater) on the coral habitat compared to temperate rocky reef habitat (two-way ANOVA, $F_{1,64} = 75.94$, p = 0.003, Fig. 7). Fish density did not significantly differ among sampling months (two-way

ANOVA, $F_{3,64} = 0.711 = 0.559$, Fig. 7). There was no interaction between sampling months and habitat type (two-way ANOVA, Interaction term, $F_{3,64} = 0.695$, p = 0.559).

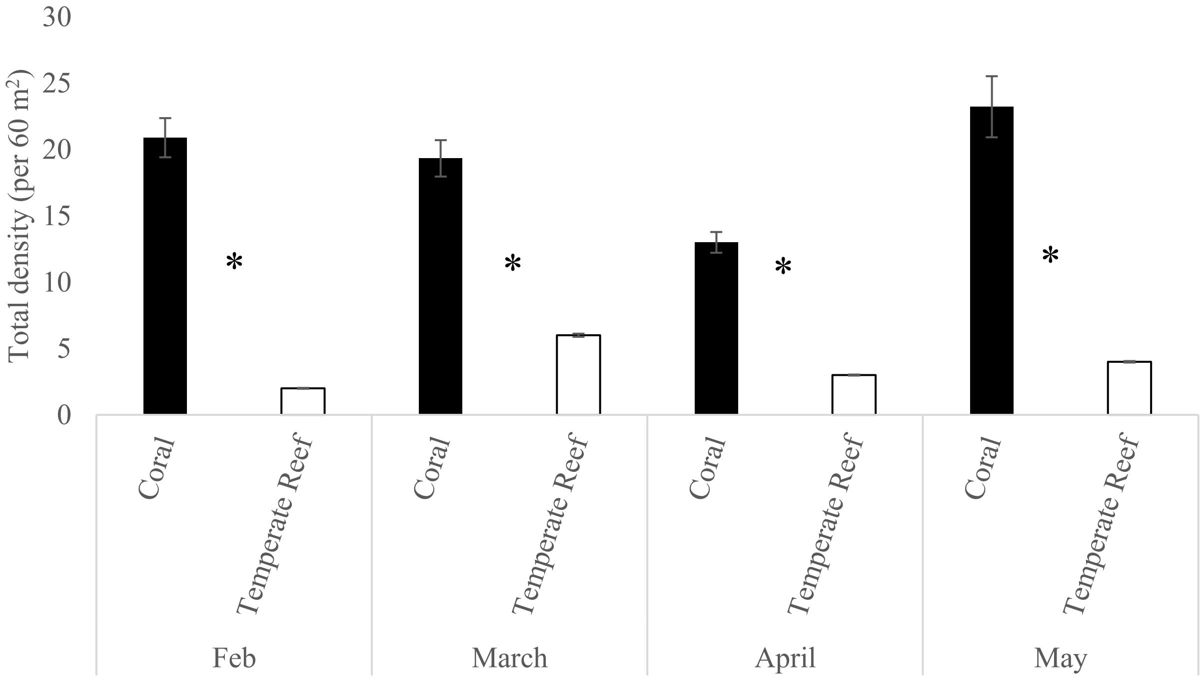


*Figure 7 Fish density (per 60 m^2 ± SE) of both tropical and temperate individuals combined on coral habitat vs temperate reef over four sampling months within SYCOGA. * Indicates significance at $p < 0.05$.*

4.3.3 Comparison of assemblage parameters between SYCOGA and Northern Sydney rocky reef habitat

In 2021, SYCOGA supported 2.8 times greater key tropical vagrant densities than 2020 (Tukey's, q = 4.595, p = 0.007) and 5.4 times greater than 2019 (q = 6.556, p = 0.0001) (Fig. 4). There was a significant interaction between sampling year and location (Northern Sydney rocky reefs vs SYCOGA coral bed) for key tropical fish density (ANOVA, Interaction term, $F_{2,36} = 7.67$, p = 0.002, Fig. 8). In 2021, SYCOGA contained: ~ 48 times higher key tropical vagrant densities than the Northern Beaches rocky reef sites (q = 9.187, p = 0.0001), and 7 times greater in 2020 (q = 5.014, p = 0.001); however, no significant differences were observed within 2019 (p = 0.064) (Fig. 8) when recruitment was lower.

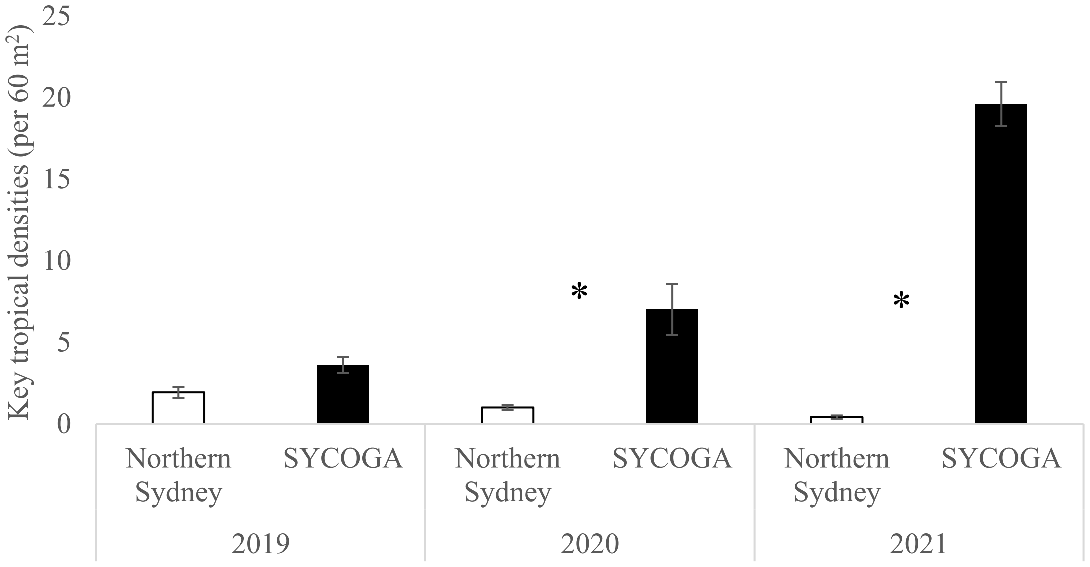


*Figure 8 Key tropical vagrant species densities across years (2019, 2020, and 2021) between Northern Beaches temperate rocky reef sites and SYCOGA. * Indicates significance between sites within years at p < 0.05.*

4.3.4 Comparison of assemblage parameters between SYCOGA and northern established *P. aliciae* habitat.

There was a significant interaction in total fish density between location (SYCOGA, Broughton Island, and Cabbage Tree Island) and densities of tropical or temperate species type (two -way ANOVA, Interaction term, $F_{2,\ 44} = 8.867$, p <0.001). Broughton Island contained ~ 3 times higher temperate density than SYCOGA (p = 0.005) and 13 times than Cabbage Tree Island (p < 0.001). SYCOGA was also found to have ~ 5 times higher a temperate density than that of Cabbage Tree Island (p < 0.001). There was no difference in overall density of tropical fish alone among the three sites.

4.4 Discussion

Range-expanding coral *P. aliciae* habitat that has been recently established in Sydney supported higher densities of both temperate and vagrant tropical reef fishes than nearby rocky reef habitat, indicating its potential importance as novel fish habitat in temperate south-eastern Australia. This study is the first to describe a comprehensive species list for both tropical and temperate species on this novel coral habitat. We also observed the seasonal variability and decline of fish assemblages on temperate reefs during the cooler months of the year, which included both tropical (e.g., *T. lunare*) and temperate species (e.g., *P. microlepis*). An increase in fish density each year relative to temperate habitat was also recorded throughout the study period.

The inter-seasonal variability in tropical and temperate species within this study have mirrored previous research observing fish temporal recruitment variabilities within Sydney. Both tropical and temperate species experienced declines in densities throughout the cooler winter/autumn months. Specifically all but one tropical species (*T. lunare*) were absent from the censuses throughout the winter months, likely due to mortality. This decline in abundance of reef species appears to be a common characteristic of high-latitude reefs, as seem by Vaughan, Shiels & Burt (2021) in which nine species observed accounted for 70% of the divergence in community structure and seven of those species were more abundant in summer than winter within the Arabian Gulf. Booth *et al.* (2007) suggested that Sydney's proximity to the EAC separation zone gives greater exposure to EAC eddies which may alter inter-annual variability in assemblage composition. *T. lunare* was consistently the most abundant tropical species observed throughout the study, is similarly abundant throughout the tropical Indo-Pacific region (Parenti and Randall, 2011), and is known to be a highly opportunistic predator. *T. lunare*, while individuals persisting through the winter were observed, had reduced density during the cooler months of April and June 2020. Within SYCOGA this species is potentially the first expatriated tropical species to form reproducing populations as mating practices have been observed (W. Gladstone *pers. obs.*). As previous studies have shown (Figueira *et al.*, 2009; Figueira and Booth, 2010) mortality is not solely based on the ability of a warm-adapted individual to withstand temperatures below its critical thermal threshold. Seasonal mortality in tropical vagrant fish may be a result of reductions in physiological and behavioural capacity. Eme and Bennett (2008) found that warm-adapted damselfishes demonstrated metabolically induced reductions in feeding rates even when temperatures were above critical thermal limits. Similarly, the pale-tail damselfish (*Pomacentrus trichrouris*) found within the Arabian Gulf shows reductions in distance from refugia and feeding rates during winter sea-surface temperatures (D'Agostino *et al*., 2020). *T. lunare's* potential predators (J. Sear *pers. comm.*) which may be a cause of the declining numbers during the June-August seasons in combination with reduced metabolic and physiological characteristics. Lower temperatures may also indirectly affect through reduced escape ability of tropical species (Figueira *et al.,* 2019).

A reduction in abundance of temperate fishes also occurred through June and into August. *Parma microlepis* and *Parma unifasciata* are two temperate damselfish that were the most abundant species throughout the study. Both species are endemic to the east coast of Australia: *P. microlepis* is one of the most abundant reef fishes in NSW, primarily throughout southern NSW and *P. unifasciata*, is most commonly found in the northern coastal region (Kingsford and Battershill, 1998). Juveniles and adults are observed throughout urchin barrens (Tzioumis and Kingsford, 1995; Galaiduk *et al.*, 2013). While temperate species such as *P. microlepis* are not expected to decline nearly as much throughout the cooler winter seasons (see Figueira *et al.,* 2009, 2018), it may be a result of the reduction of typically high algal mat coverage in temperate reefs (Millar, 1999), which is an important component of Parma diet (Tzioumis and Kingsford, 1995). Future studies could consider the effects of the inter-seasonal variability of food availability on temperate and tropical species abundance within a growing temperate coral reef environment.

Impacts of range-expanding herbivorous grazers and scrapers such as the parrotfish, *Calotomus japonicus*, in southern Japan (Mezaki and Kubota, 2012), or the poleward movement of the habitat engineering sea urchin (*C. rodgersii*) (Ling *et al.*, 2008), has resulted in a monotypic algal turf dominated benthic habitat in temperate systems, which has been described as 'habitat simplification' (Agostini *et al.*, 2021). Tropicalisation was identified in Japan's Tosa Bay under increasing sea-surface temperatures over the period 2008 to 2010, due to grazing of kelp forests, and the infilling of tropical corals has resulted in the dominance of tropical fish within temperate communities (Nakamura *et al.*, 2013). In contrast, SYCOGA does not demonstrate simplification, because there has been an infilling by habitat-forming corals on which both tropical and temperate species were concentrated compared to surrounding kelp, barren rock, and algal mat habitats in this study, exhibiting tropicalisation. Therefore, the novel coral gardens in Sydney concentrate (higher densities, more vagrant species) fish and may facilitate tropicalisation and also temperate fish assemblages.

Broughton Island had higher tropical and temperate fish species densities than that of both SYCOGA and Cabbage Tree Island (12 km SW of Broughton), perhaps as a result of Broughton being further offshore and is therefore more likely to intercept the EAC. Possibly the increase in range-expanding corals and reduction of historically typical temperate habitat (such as algal mats and kelp forests), leading to a biotic homogenisation of this habitat may be a key driver of whether an environment has been tropicalised (Vergés *et al.*, 2016). An example of tropicalisation not occurring within Eastern Australia 'climate change hot spot' was documented by Mizerek *et al.,* (2021). Over the course of 23 years coral taxa and subtropical coral cover did not change throughout the Solitary Islands Marine Park (SIMP), despite significant increases in average sea-surface temperature. While long term habitat coverage of

SYCOGA would require a greater data set over a number of years to analyse, the coral habitat has been proliferating within the reserve.

Chapter 5: General Discussion

Increasing sea-surface temperatures and the strengthening of Western Boundary Currents (WBCs) have led to the range-expansion of tropical fishes and reef forming corals into temperate marine ecosystems (Booth *et al.*, 2007a; Barneche *et al.*, 2009; Fodrie *et al.*, 2010; Hobbs, 2010; Baird *et al.*, 2012; Nakamura *et al.*, 2013; Fowler *et al.*, 2018). The sub-tropical, range-expanding hard coral *Pocillopora aliciae* habitat has been present over the last decade, in Sydney temperate reef areas, but is now expanding and attracting a suite of tropical and temperate fishes (Booth and Sear, 2018).

The overall objective for this thesis was to understand the dynamics of tropical vagrant fishes as they settle and integrate into a novel temperate environment in south-eastern Australia and how the local fish assemblage might be affected by this expatriating coral habitat. Therefore, this thesis aimed to understand 1) the mechanisms by which tropical vagrant fish species locate rare and scarce habitat and conspecifics within an extra-natal environment, 2) how expatriating tropical vagrant and local temperate species utilise novel and often scarce coral habitat, and 3) whether or not this novel habitat facilitates tropical and temperate assemblages.

5.1 Key Findings

In Chapter 2 of this thesis, I investigated the ability of humbug damselfish *Dascyllus trimaculatus* individuals to locate rare coral habitat (*Pocillopora aliciae*) and conspecifics on temperate rocky reefs through olfactory and visual cues. This selection was uncovered by a series of aquarium preferences experiments using a four-way choice arena. Choice chambers have been commonly used to test visual, olfactory, or auditory abilities of tropical reef fishes however, most studies have observed responses to cues commonly found in a tropical environment and seldom outside of a species' natal habitat (Kingsford *et al.*, 2002; Wright *et al.*, 2005; McCormick and Manassa, 2008; Coppock *et al.*, 2013). Through the experiments conducted in Chapter 2, I found that *D. trimaculatus* individuals could employ olfactory abilities to locate novel coral habitat and used both olfactory and visual abilities to locate conspecifics. These findings emphasise tropical reef fish abilities to locate suitable habitat and conspecific individuals even in novel environments, and the further establishment and expansion of these tropical communities will provide a greater source of olfactory and visual cues to assist in recruitment than currently exists during the initial colonisation in SE Australia.

Following these discoveries, in Chapter 3 I observed small-scale habitat use and maximum movement distances (MMD) of tropical vagrant and temperate fish species throughout these coral beds to understand whether there was overlap or separation in how these species utilised the *P. aliciae* coral heads. Using direct behavioural observations of 14 fish species (four tropical, 10 temperate) I show that tropical individuals were eight times more likely to be found within the centre of coral heads than open boulder habitat which could greatly increase the availability of suitable habitat potentially accelerating tropicalisation in south-eastern Australia. This contrasted to temperate species, which were more likely to be found on the edge of coral habitat. Tropical individuals are also more common within the centre habitat (44% observed) than temperate species (7% observed). There were no significant differences in average MMD (movement distance over 15 min) between tropical and temperate individuals of a similar size, reinforcing the primacy of body size in fish movement (Nash *et al.*, 2015; Streit *et al.*, 2021). In this study, I have identified spatial separation and niche segregation which potentially facilitates coexistence of tropical and temperate species utilising novel and scarce poleward-expanding coral habitat within Australia's southeast.

Finally, in Chapter 4 I assessed whether or not these range-shifting *P. aliciae* coral beds are attracting both expatriating tropical and local temperate fish species and compared to rocky reef habitats nearby, and how these assemblages are changing over time. Fish densities and species richness were compared densities across seasons and between SYCOGA and other sites supporting typically temperate habitat around northern Sydney. Cooler winter temperatures throughout Australia's southeast is consistent with declines in abundance and densities of both tropical and temperate species and continues to be a significant bottle-neck for the establishment of tropical species in temperate environments (Figueira and Booth, 2010). Twenty fish species were identified associating with coral habitat in SYCOGA (8 tropical and 12 temperate). SYCOGA had significantly greater densities of reef fishes than surrounding temperate reefs within northern Sydney. Both temperate and tropical species were observed at much greater (66% greater on average) densities than directly adjacent non-coral rocky substrate. Furthermore, a key tropical vagrant species found on this coral habitat (Booth and Sear, 2018), *D. trimaculatus*, has been observed in densities of up to 100x greater than those of surrounding temperate environments (D. Booth *pers. obs.*). While other tropicalised regions around the world have experienced domination of tropical species (Nakamura *et al.*, 2013), I suggest that this expatriating coral habitat within Australia's southeast is currently facilitating and concentrating high densities of both tropical vagrant and temperate species, which may aid in the tropicalisation of the surrounding region.

5.2 Future Research Directions

In this thesis, I observed the processes by which the range expansion of *P. aliciae* into SE Australia facilitates the movement of tropical reef fish. This thesis provides suggestions and improvements for future research looking at range expansion by tropical vagrant fish into temperate marine communities and the consequences of this.

In Chapter 2, I tested ability of humbug damselfish *Dascyllus trimaculatus* individuals to locate rare coral habitat (*Pocillopora aliciae*) and conspecifics on temperate rocky reefs through isolated olfactory and visual cues. Future studies should test the responses to multiple simultaneous cue configurations in non-laminar flows, which is closer to what is observed *in-situ* during settlement. Also, as observed through mixed modelling in Chapter 2, I suggest that future preference experiments should consider the effects of fish release direction on its resulting propensity for selecting a tank section where the cue is introduced. Habitat use and quality has been a heavily studied research topic, as habitat degradation of coral reefs worsen throughout the tropics in response to ocean warming, acidification, agriculture, and storm damage (Aronson *et al.*, 2003; Nash *et al.*, 2012; Pratchett *et al.*, 2014).

In Chapter 4, I observed range shifting *P. aliciae* coral beds are attracting high densities of both expatriating tropical and local temperate fish species compared to rocky reef habitats nearby, and how these assemblages are changing over time. I explained that cooling winter temperatures and winter mortality of tropical and temperate species were potentially responsible for the reduction in densities withing SYCOGA. However, further research may look at the seasonal variability in food availability within this temperate coral reef environment for not only tropical species but also temperate fish. *T. lunare* provides an interesting model for future studies, as it currently persists through the SE Australian winters, which may eventually be the case for numerous tropical species. With intensifying WBCs, warming ocean temperatures, and range shifts of habitat leading to tropicalisation in south-eastern Australia, we may also observe the full suite of fish trophic levels shift poleward.

5.3 Implications of Tropicalisation

The ramifications of the processes outlined throughout this thesis are not yet fully understood, however future projections may be found through what has been observed in other tropicalising regions around the world. The increased herbivory in temperate ecosystems led by poleward moving tropical fishes have exhausted many macroalgae populations (Nagai *et al.*, 2011; Vergés *et al.*, 2016), which, if not replaced by habitat-forming corals, leads to a significant drop in benthic biomass and species richness, as seen within the eastern Mediterranean (Vergés *et al.*, 2014c). However, when grazed and barren temperate reefs are infilled by range-expanding corals, diversity may be retained and in some cases increased (Rossier and Kulbicki, 2000; Yamano *et al.*, 2012), but the original assemblage structure and potentially function will be lost. There are still many unknown potential behavioural mechanisms between both tropical and temperate species that may be exhibited in this novel ecosystem, as this environmental shift is still in its early stages. However, it has been shown in south-eastern Australia that range-expanding tropical species show reduced foraging competency as water temperatures and lower aggression than temperate species as a result of lower sea temperatures, unfamiliarity with conditions, and/or decreased in abundance of fish of tropical origin (Coni *et al.,* 2021c). Tosa Bay, Japan, however, may foreshadow what is to come. Range expanding tropical fish species along with a range-expanding coral habitat has allowed tropical fish species to completely dominate and outcompete the local temperate population once winter sea temperatures as warm enough for these tropical fish to establish populations (Nakamura *et. al.,* 2013).

World fisheries have already observed the effects of tropicalisation through changes in composition of catch and the collapse of subtropical and temperate fisheries. The destruction of macroalga habitat throughout southern Japan caused by increasing poleward movement of tropical herbivorous fish, led to the collapse of the local abalone fishery in 2000, as the abalone relied heavily on the local *Ecklonia cava* habitat as food (Serisawa *et al.*, 2004). On a global scale, Cheung *et al.* (2013) observed increasing dominance of catches of warmer water species at higher latitudes and sharp declines in the proportion of subtropical species within lower latitudes across a 36 year period throughout 52 large marine ecosystems (regions which account for a majority of the world's fisheries). The targeting of these tropical herbivorous fish by local fisheries in tropical/temperate transition zones has been one management action that not only reduced the stress on temperate communities but supported temperate fisheries as historical stocks are depleted (Jansen *et al.*, 2016). While these tropical fishes have become an increasingly important component in fisheries catches in the Mediterranean (Bariche, 2005) and Australia (Gilby *et al.*, 2016), this does not solve the growing concerns of tropical communities which heavily rely on local fisheries (Sulu *et al.*, 2015). Through a combination of tropical habitat degradation, ocean warming, and acidification, Pratchett *et al.* (2011) concludes there will be a 20-50% decline in sustainable fisheries production in Pacific Island coastal environments by 2100.

5.4 Concluding Remarks

Future ocean warming of temperate marine ecosystems is likely to accelerate and magnify the successful establishment of tropical vagrant fish and coral species. Studying how the processes of settlement, habitat use, and recruitment is vital in understanding how tropicalisation occurs in temperate habitat. Anthropogenic driven climate change is altering marine habitats much quicker than terrestrial habitats, and while research must drive towards mitigation and protection, learning how ecosystems adapt and are impacted by these climate change processes are just as important. This thesis has shown that tropical vagrant fish species utilise olfactory and visual cues of habitat and conspecifics to locate and settle on scare novel reef habitat in temperate environments. I also explored niche separation of habitat use by invading reef fish and temperate species on range expanding *P. aliciae* habitat. Finally, how this habitat is facilitating and concentrating fish assemblages of both tropical and temperate origin and aiding in the tropicalisation of SE Australia. As stated throughout this thesis, the changes in temperate marine ecosystems as a result of climate change intensified processes (e.g., warming seasonal ocean temperatures and intensifying western boundary currents) are taking place around the world. It is my hope that this thesis contributes to further understanding the processes leading to tropicalisation of temperate environments as we experience continuous poleward shifts of tropical fish and habitat.

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