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Restoration of kelp beds on degraded temperate rocky reefs

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ABSTRACT

The loss of kelp beds has been observed across the globe, often as a result of overgrazing by urchins, but also facilitated by other factors that reduce kelp bed resilience. While kelps are restricted to temperate waters, their local distribution and abundance are limited by the availability of suitable substrate, light conditions, and wave climate. Natural recovery of kelp beds can be limited by short dispersal distances for spores, and the stabilizing feedbacks of alternate reef states. The loss of ecosystem services provided by kelp beds and the lack of natural recovery is driving interest in restoration among land managers and researchers. Restoration attempts for these temperate rocky reef ecosystems to date have had mixed success, and lessons learned may be location specific, requiring further work to inform restoration efforts in different systems.

The study area for this thesis is Port Phillip Bay, part of the Great Southern Reef (GSR) which stretches across southern Australia. *Ecklonia radiata* is the dominant kelp across the GSR, and *Heliocidaris erythrogramma* is the urchin of concern in Port Phillip Bay. *Ecklonia radiata* is a relatively small kelp with large morphological diversity across environmental gradients. Port Phillip Bay has a history of anthropogenic environmental disturbances including catchment-based pollution, introduction of invasive species, and removal of several large fishes through overfishing. In recent years, overgrazing by *H. erythrogramma* has been blamed for vast losses of *E. radiata* cover in the Bay.

I begin this thesis by conducting a baseline survey of reef condition, urchin density, and urchin roe marketability across Port Phillip Bay. This allowed identification of specific management actions at a small (1 ha) spatial scale. I then explore three specific components of kelp restoration: 1) the use of kelp mimics to reduce sediment accumulation in the absence of an adult kelp bed; 2) the spatial scales over which natural recruitment can occur, and preferences for different substrate orientations and levels of shading; and 3) factors affecting success of transplanting juvenile kelp for restoration. The final chapter draws together the lessons from these four chapters in a management plan for kelp forests and urchins. Specific management actions were categorized at a 1 ha scale, allowing areas at highest risk to be identified, and actions to be prioritized based on management priorities and available resources. I observed divergent effects on sediment accumulation across sites, suggesting the artificial kelp behaves differently in slightly different environmental conditions. I observed most new kelp recruited within tens of meters from the nearest kelp bed, but densities and distances could not be explained by modelled local currents. I confirm the reduced sediment accumulation and low light conditions under a kelp canopy are associated with higher recruitment, and found vertical surfaces saw a tenfold increase in recruit density. However, I did not separate the effects, so the higher recruitment may have been due to one factor and in spite of the other. My transplant study demonstrated a potentially scalable restoration technique and highlighted the sensitivity of restoration spatial and temporal context. I also identified shallow exposed bommies as a potential source of juvenile sporophytes where high recruitment is coupled with very low likelihood of survival to maturity. Insights from this thesis can inform small scale interventions within the broader context of the Bay. My thesis identifies specific small scale kelp management actions appropriate within the broader context of Port Phillip Bay, but the lessons can be translated for application more broadly. My findings, some of which contrasts with previous studies, highlight the nuances in management of complex temperate reef ecosystems.

DECLARATIONS

This is to certify that:

1. The thesis comprises only my original work towards the PhD, with contributions as indicated in the Statement of Co-Authorship.
2. Due acknowledgement has been made in the text to all other material used.
3. The thesis is fewer than 100,000 words in length, exclusive of tables, maps, bibliographies, and appendices.

Tristan Graham

April 2023

STATEMENT OF CO-AUTHORSHIP

I am the primary author of all chapters in this thesis. My three supervisors are included as co-authors on all chapters, while other authors contributed to individual chapters as outlined below, in alphabetical order. The thesis is presented as a "thesis with publications", with chapters 2 to 5 prepared as manuscripts for publishing in peer reviewed journals. It was necessary, therefore, for some overlap in content, particularly in the introductions of each chapter where I review relevant literature. Chapter 5 has been published in *Restoration Ecology* and is available here: https://doi.org/10.1111/rec.13536. A signed co-author authorisation form and declaration for Chapter 5 is included in the submission of this thesis.

Chapter 1: Not for individual publication. Co-authored by Elisabeth M. A. Strain, Rebecca L. Morris, Stephen E. Swearer. TG wrote the draft, ES, RM, and SS provided editorial comments.

Chapter 2: Unpublished material not yet submitted for publication. Co-authored by Elisabeth M. A. Strain, Fletcher Warren-Myers, Paul Carnell, Rebecca L. Morris, Stephen E. Swearer. Survey design based on Worthington and Blount (2003) with modifications by PC, SS, and TG. Fieldwork organised by TG, with diving support from NCCC (University of Melbourne) and Blue Carbon Lab (Deakin University). Lab assessment of urchin roe led by FW-M. TG processed the data. TG analysed the data, with support from ES, RM, PC, and SS. TG wrote the manuscript, ES, FW-M, PC, RM, and SS provided editorial comments.

Chapter 3: Unpublished material not yet submitted for publication. Co-authored by Elisabeth M. A. Strain, Maryam Abdolahpour, Rebecca L. Morris, Stephen E. Swearer. RM conceived original idea, RM and TG undertook the initial fieldwork, MA and RM did the wave flume tests and drafted the corresponding methods section, TG designed the field experiment, TG wrote the manuscript, ES, RM, and SS provided editorial comments.

Chapter 4: Unpublished material not yet submitted for publication. Co-authored by Elisabeth M. A. Strain, Rebecca L. Morris, Stephen E. Swearer. TG designed the experiment with input from ES, RM, and SS. TG led fieldwork, with diving and processing support from NCCC (University of Melbourne). TG did the analysis of results, with support from ES, RM, and SS. TG wrote the manuscript, ES, RM, and SS provided editorial comments.

Chapter 5: Published in Restoration Ecology in August 2021. Co-authored by Elisabeth M. A. Strain, Rebecca L. Morris, Stephen E. Swearer. TG, SS, ES, RM conceived and developed experiment design; TG led experiment preparation, setup, monitoring, and completion; SS provided resources for field work; TG did analysis and wrote initial draft manuscript; SS, ES, RM provided feedback and edited the initial manuscript and revisions.

Chapter 6: Not for individual publication. Co-authored by Rebecca L. Morris and Stephen E. Swearer. TG wrote the manuscript, SS, and RM provided editorial comments.

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TABLE OF CONTENTS

CHAPTER 1 - GENERAL INTRODUCTION

Background

Species that have a capacity to create, modify, or maintain habitats are labelled *ecosystem engineers*, and these can have profound impacts on biodiversity and ecosystem function (Miller et al., 2018). Through modifications to the biotic (e.g., access by predators) and abiotic (e.g., shading, water flow) environment they control access to resources, and therefore habitat suitability, for other species (Jones et al., 1994). Ecosystem engineers can even drive biodiversity outside the immediate area, for example by providing or distributing food (Surugiu et al., 2021). With widespread ecosystem degradation worldwide, the protection of key ecosystem engineers provides flow on effects of supporting a plethora of other species and maintaining important ecosystem services.

Kelps are impressive ecosystem engineers, they may modify the current speeds (Gaylord, 2007; Hondolero, 2017), reduce understory light (Clark, 2004), and provide habitat among holdfasts and fronds. They are also foundation species, playing an important role in the structuring of ecosystems. They are found on coastlines across the worlds temperate and polar regions (Wernberg, Krumhansl, et al., 2019), and they are powerhouses of primary production with some of the fastest growth rates of any species in the world (Mann, 1973). They can support huge diversity and biomass of other species, both in the immediate vicinity and at a distance through production of drift (Vanderklift, 2008; Filbee-Dexter, 2016; Miller et al., 2018). Darwin (1839) famously compared kelp forests to intertropical terrestrial forests and declared *"if in any country a forest was destroyed, I do not believe nearly so many species of animals would perish as would here from the destruction of kelp"*.

Unfortunately, the degradation of kelp forests has been observed across the globe. Some of the major drivers of kelp forest degradation include: ocean warming and heat waves; excessive nutrient or sediment loads; and removal of predators leading to overgrazing by herbivores (Filbee-Dexter & Wernberg, 2018). These drivers of kelp forest degradation interact, with impacts of one driver often reducing resilience of kelp to other drivers. For example, overfishing may reduce the resilience of kelp beds to poleward range expansion of herbivores (Ling et al., 2009). It is difficult for kelp beds to recover following anthropogenic disturbances without the removal or reduction of stressors (e.g., disease or predation of urchins) and favourable conditions for recovery (e.g., spore supply and a clear substrate for settlement) (Filbee-Dexter & Scheibling, 2014). In some cases recovery after a short disturbance may be possible where immature or alternate life stages lay dormant under the canopy (Carney & Edwards, 2006). When passive recovery is unlikely, because the drivers of kelp forest degradation remain, or an alternate stable state has established, kelp recovery may require external intervention.

Kelp restoration can build on this understanding of the drivers of kelp forest degradation and barriers to recovery to inform ecologically meaningful interventions (Campbell et al., 2014). The definition of ecosystem restoration adopted in this thesis is *"the process of assisting the recovery of an ecosystem that has been degraded, damaged, or destroyed"* (Society for Ecological Restoration International Science and Policy Working Group, 2004). Drivers of kelp forest degradation should be addressed first, with consideration given to possible interactions between drivers at various spatial and temporal scales (e.g., global warming of sea surface temperatures and increased local nutrient load from urban runoff) (Morris et al., 2020). Restoration can be applied pre-emptively to existing degraded kelp bed (to enhance health and resilience), or following kelp loss (to recover lost services), and other management actions like afforestation can be applied to new locations (e.g., artificial reefs to offset degraded kelp forests) (Marshall, 2003; Eger, Layton, et al., 2022). A wide range of techniques have been applied to achieve this restoration or afforestation, including relatively passive measures like establishment of marine protected areas (to enhance predator pressure on herbivores) or the subsidisation of urchin fishers to reduce urchin numbers, to more active measures like quickliming or culling of urchins, seeding areas using the deployment of spore bags, transplantation of sporophytes, or introduction of artificial substrate, as well as culturing and genetic manipulation of transplants (Bernstein, 1982; Morris et al., 2020). The appropriate action for a particular site depends on the local context including drivers of kelp forest degradation, species of kelp, and social and political factors. Scalability of many of these interventions remains an issue, with current methods often too expensive to scale up (Eger, Marzinelli, et al., 2022) and scaling effects may be present, like patch size effects by (Layton et al., 2019). It is important to understand the ecosystem services being recovered, and have clearly defined and measurable goals (Morris et al., 2020). In many cases details of specific techniques (e.g., transplanting), or attributes (e.g., spore dispersal) may not yet be understood for the local context or species. We need to make use of the available knowledge, while appreciating the limitations of transferring conclusions between systems.

The Great Southern Reef (GSR) is a temperate reef system extending along more than 8,000 km of southern Australia (Bennett et al., 2016). It is very important to both the local and national economy, producing an estimated \$10B.yr^{-1} from fishing and tourism alone, along with many other ecosystem services (e.g., Bennett et al., 2016). The GSR extends over a wide range of environmental conditions, from the tropical limits in the north to much cooler waters on the west coast of Tasmania. Drivers of kelp forest degradation across the GSR have varied, highlighting considerations across temporal and spatial scales for management of these important ecosystems. In the west, ocean warming, heat waves, and tropicalization have resulted in a kelp range contraction over 100 km, with kelp beds being replaced with algal turf matrix (Wernberg et al., 2016). In the east, warming waters have led to tropicalization of herbivorous fish (Verges, 2016) and allowed the urchin *Centrostephanus rodgersii* to expand southward to Tasmania, where they have produced extensive urchin barrens. Eutrophication and loss of urchin predators have also contributed to observed degradation of kelp forests. A recent study of *E. radiata* along the Victorian coastline linked observed declines to multiple environmental variables and projected future declines under IPCC climate change scenarios (Young et al., 2022).

Ecklonia radiata (C. Agardh) J. Agardh is the dominant kelp species across the GSR and is also found around Aotearoa New Zealand and South Africa. Its morphologic plasticity allows it to thrive in a range of environmental conditions (Miller et al., 2011; Wernberg, Coleman, et al., 2019). The movement of *E. radiata* under hydrodynamic flow creates a sweeping of the reef, preventing sediment or algal turf build-up, and promoting the growth of coralline algae (Melville, 2001). Preventing sediment and turf build-up is essential for successful recruitment of kelp itself, and this is a major stabilizing factor of both *E. radiata* beds and the alternate urchin barrens or algal turf matrices. The spore dispersal kernel of *E. radiata* and recruitment patterns are not well understood, and microscopic gametophytes (the intermittent life stage between spores and macroscopic sporophytes) have never been observed in the field (Wernberg, Coleman, et al., 2019). *E. radiata* is susceptible to warming waters and heatwaves, tropicalization of herbivores, and poor water quality (Wernberg, Coleman, et al., 2019). Some restoration techniques have been trialled for *E. radiata*, including urchin removal, spore dispersal through adding bags of reproductive adults to reefs, and transplanting of juvenile and adult sporophytes. Patch dynamics for transplantation have also been studied, recommending a minimum patch size of 2 m^2 with a density of $15.m^{-2}$ (Layton et al., 2019). Recent observations have also confirmed the ability for holdfast reattachment (e.g., Graham et al., 2021) of transplanted kelp and successful holdfast fragmentation (pers. obs.).

The study area for this thesis is Port Phillip Bay, a large shallow bay in south-east Australia. The city of Melbourne sits on the northern shore of the Bay, with suburbs extending down the eastern and western shorelines. The Bay is used extensively by the local population for recreation and supports several commercial fisheries. The shoreline of the Bay is dotted with rocky reefs, including basalt flows in the north-west, and a range of sedimentary formations (Bird, 1993). The reefs range from flat and continuous platforms to complex boulder reefs. The Bay's reefs were once covered in dense E. radiata beds, but in recent decades many of these have collapsed to form urchin barrens or become covered in algal turf (Carnell & Keough, 2019). Previous work has shown that overgrazing by the local urchin, *Heliocidaris* *erythrogramma*, is a clear driver of this degradation, likely supported by other stressors such as turbidity, eutrophication, and high water temperatures (Johnson et al., 2015). Projections of *E. radiata* cover under IPCC climate change scenarios suggest the Bay will be impacted relatively little compared to the open coast (Young et al., 2022).

Thesis Outline

In **Chapter 2** I begin the thesis with a seaweed and sea urchin survey aimed at understanding the current condition of the rocky reefs in Port Phillip Bay and addressing the primary stressor to kelp beds in the Bay. The urchin survey component looked at both the quantity (distribution and abundance) and quality (marketability) of the native urchin *H. erythrogramma*, to identify both the risk to kelp beds and options available for their removal. I considered four reef states in the vegetation survey, informed by implications for kelp management. Vegetated (>50% foliose macroalgae cover) subsites were classified as *E. radiata* dominant if more than half the vegetative cover was *E. radiata*, otherwise classified as mixed macroalgae. Unvegetated subsites were classified as turf dominant if more than half the unvegetated cover was turf, otherwise classified as bare. I developed a flow chart to guide the classification of subsites to assist in prioritization of management actions including methods of urchin removal. These are two vital steps in a restoration project as they guide the selection of sites and methods and ensures the cause of degradation is appropriately managed.

I found very little kelp dominated reef and a high proportion of denuded reef, either bare or covered by turf. Individual subsites were identified as priority areas for specific interventions (e.g., wild catch harvesting of urchins, collection of urchins for ranching, ongoing monitoring). I also investigated methods to interpolate survey results across all reefs in the Bay, finding that hard substrate availability and low urchin density/biomass are important factors for predicting the presence of vegetation. I found the definition of urchin density at a spatial scale greater than the subsite risks overlooking critical spots requiring management intervention, despite 70% of the variance in urchin density occurring at the region scale.

Next, in **Chapter 3**, I explore the development and experimentation of an artificial kelp mimic intended to temporarily provide the positive feedback processes associated with kelps to assist a reverse phase shift back to the kelp bed state. I describe the development of a simple to assemble kelp mimic, informed by measurements of natural kelp, to produce the sweeping motion under wave conditions to help reduce sediment accumulation and thus providing suitable substrate for recruitment, as well as protecting juvenile transplants and deterring urchins. I observed a significant reduction in organic mass accumulation under the artificial kelp at one site, while differences between the control and artificial kelp were non-significant for all other measures including survival of juvenile transplants and urchin densities. I present results from the experimental field deployment highlighting additional design considerations such as the fouling and disintegration of materials under field conditions, the need for greater spore supply, the importance of tracking individual sporophyte transplants, and the necessity for deployments to be retrieved after use with minimal impact to the reef.

In **Chapter 4** I explore the spatial scales of natural recruitment from existing kelp beds to better understand the circumstances in which provision of suitable substrate alone may enable recovery of kelp beds. I also investigate the effects of substrate orientation and canopy conditions on kelp sporophyte recruitment rates to increase recruitment success during restoration projects. I present results showing the presence of juvenile sporophytes was mostly within tens of meters of the extant bed, in a direction not dictated by predominant local currents. This suggests the prediction of recruitment from existing beds will require further investigation, rather than simply applying a travel time in a hydrodynamic model. I present results from the manipulative experiment showing significantly more sporophytes recruited to vertical surfaces than horizontal, and significantly more under an *E. radiata* canopy than no canopy. I did not observe the artificial kelp providing the sweeping and shading benefits of the real kelp canopy, and the 5x increase in recruitment I observed under artificial kelp compared to the control was not statistically significant at α = 0.05. While vertical tiles and tiles under kelp both saw less sediment accumulation and lower light, an interaction between the two was not observed, indicating vertical substrate is beneficial but is not a complete substitute for the habitat conditions provided by a natural kelp canopy.

In the final data chapter, **Chapter 5**, I explore the factors affecting the success of transplanted juvenile kelps. Transplanting sporophytes is a useful method to quickly restore the services of kelp beds, including the provision of spores for recruitment of the next generation. This is particularly useful given the large proportion of reefs across the Bay that are unvegetated and often well outside the expected natural recruitment distances of extant kelp beds, as well as the lack of recruitment observed after deploying spore bags in Chapter 3. Here I present a method of transplanting stage I and II sporophytes (sensu Kirkman, 1984), attaching holdfasts to basalt tiles with silicon air tubing. I observed no significant loss of sporophytes associated with translocation, nor from deployment directly to barren areas without urchin exclusion fences, likely due to the time of year and availability of other food on the reef for the urchins. I identified a possible sink population of juvenile sporophytes on shallow reefs where the increased drag forces from large adult fronds likely led to mortality in the background population. I observed the presence of an adult canopy hindering the development of transplants, including growth, reattachment, and maturation. Overall, the transplant method was successful, with many transplants reattaching their holdfasts and maturing to stage III with sporophylls. The method can be scaled up easily at a cost in line with other macrophyte restoration work.

In **Chapter 6** I present a case for developing a wholistic spatial management plan for urchin management and kelp restoration and demonstrate how this could inform specific restoration actions. I discuss how the work to date on kelp restoration can come together to provide resources for future restoration activities. I also discuss some persistent research gaps.

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CHAPTER 2 - MANAGEMENT OF ROCKY REEFS FOLLOWING KELP HABITAT DEGRADATION DRIVEN BY OVERABUNDANT URCHINS

Abstract

Overgrazing by urchins is a key driver of kelp forest degradation on temperate rocky reefs and results in the formation of alternative stable states with poorer ecological service provision. Understanding the status and relationships between reef state (vegetated with foliose algae vs. bare) and abundances of urchins is essential for informing targeted management actions such as urchin harvesting or culling. Here I exclude turfing and coralline algae from the 'vegetated' category. I examined the current distribution of macroalgal cover (including kelp) and reef state, urchin density, and roe quality in Port Phillip Bay, Australia, and compared these metrics to a baseline study from 2002. I also explored the potential for environmental variables (i.e., bathymetric derivatives, lidar reflectance, and spectral wave model outputs) to predict reef state. Clear differences were observed in reef state among regions, with all subsites near the Bay opening identified as vegetated. Across the entire Bay only a single subsite was dominated by kelp, and more than half the subsites were bare. Urchin density varied greatly by region, consistent with the previous survey, however, densities had increased since that survey, most notably in the north of the Bay. The relationship between reef state and urchin density was consistent with hysteresis. These findings suggest reefs within Port Phillip Bay are mostly in a degraded state and are subject to increasing grazing pressure from urchins. A flow chart for reef management is presented, taking into consideration reef state, urchin

density, and roe quality to determine which interventions are most likely to provide the greatest benefit.

Introduction

Kelp beds are incredibly productive ecosystems across the world’s temperate rocky reefs, providing food, shelter, and nutrient uptake, along with flow-on ecological services including water treatment, commercial and recreational fishing, and tourism (Smale et al., 2013; Bennett et al., 2016). Kelp population dynamics are impacted by a range of local and regional stressors (Steneck et al., 2003; Krumhansl et al., 2016). Warming waters, increased wave energy, eutrophication, selective fishing, increased sediment loads, and introduced species can all reduce the fitness of kelp and other canopy-forming algae (Strain et al., 2014; Filbee-Dexter & Wernberg, 2018). The cumulative effect of these stressors makes kelp beds more susceptible to overgrazing by sea urchins (Rogers-Bennett & Catton, 2019).

The collapse of productive kelp beds to impoverished urchin barrens, devoid of foliose algae, with low productivity, species diversity, and structure, is a well-documented global phenomenon (Ling et al., 2015). Stabilizing mechanisms of the kelp state are replaced with stabilizing mechanisms of the alternate state, including a dietary shift of urchins from drift algae to live (attached) algae including recruits (Perreault et al., 2014; Kriegisch et al., 2019), which creates a hysteresis (Ling et al., 2019). Critical urchin densities for barren formation and maintenance have been identified in some cases. For example, the long spined sea urchin *Centrostephanus rodgersii* can produce a barren at 4-10 individuals m^{-2}, but only require 0.2-1.2 individuals m^{-2} to maintain it (Ling & Johnson, 2009). In contrast, the purple urchin *Heliocidaris erythrogramma* can produce a barren at 8 m^{-2}, with 4 m^{-2} maintaining it (Kriegisch et al., 2016). These thresholds, however, are likely to vary spatially with environmental conditions, with variation in algal growth rates and drift production, and given the ability of kelp to thrive in a range of environmental conditions due to their high morphological plasticity (Fowler-Walker et al., 2005). High light and nutrient conditions following canopy loss may favour the growth of matting algae, which combined with sediment can form an algal turf matrix that presents a barrier to kelp recruitment (Gorman & Connell, 2009; Layton et al., 2019). Thus, following collapse due to urchin overabundance, an impoverished state may persist even with no urchins present.

While natural recovery of kelp beds has been observed, the presence of these stressors makes natural recovery less likely. Consequently, interventions may be required to assist recovery, and various restoration methods have been developed. An important first step in any kelp restoration project is addressing the major driver of kelp forest degradation / resistance to recovery, which in many cases is urchin overabundance. A common method of urchin control is culling which generally involves divers smashing urchins with hand-held tools (Tracey et al., 2015; Guarnieri et al., 2020). Utilizing divers engaged in other activities to cull urchins as a secondary activity, such as alongside harvesting abalone, has led to inconsistent results with uneven culling effort in trials (Sanderson et al., 2016). Alternatively, urchins may also be harvested by commercial fishers, however, in some cases the roe quality in areas of concern may not be suitable for market, requiring a ranching period to improve the quality (Pert et al., 2018).

Urchin culling is expensive and labour intensive, and while costs may be recovered through harvesting, this is dependent on catch effort and roe quality. Furthermore, if not targeted properly, these urchin removals may not flow on to positive impacts on vegetative cover. It is important, therefore, to carefully target resources to where they can have the greatest benefits relative to costs. For example, prevention of barren formation through selective harvesting of urchins may be more cost effective than restoration of a lost kelp bed (Miller et al., 2022).

This study considers the reefs of Port Phillip Bay (hereafter the Bay), in south-eastern Australia. The Bay is part of the Great Southern Reef, a 7M ha area of temperate reef stretching along the coasts of 5 states. *Ecklonia radiata* (C. Agardh) J. Agardh is the dominant kelp across the Great Southern Reef, whose ecological services of fishing and tourism are much valued, while other services are yet unquantified (Bennett et al., 2016; Gaylard et al., 2020). These ecological services are likely concentrated in the Bay due to its high human population and the provision of important spawning and nursery grounds for several important commercial and recreational fishery species. In 2002 a stock assessment was undertaken in the Bay to assist in the development of a commercial fishery for the urchin *Heliocidaris erythrogramma* (Worthington & Blount, 2003). This stock assessment quantified the acceptable catch quota based on extrapolated urchin biomass and the assumption that urchins in barrens would not be suitable for harvesting due to their poor condition. In 2015 a study of the effects of *H. erythrogramma* and anthropogenic stressors on the rocky reefs of the Bay was completed (Johnson et al., 2015), highlighting the loss of *E. radiata* and high densities of *H. erythrogramma* in the Bay, as well as their ability to create barrens at densities over 8 m^{-2} and to maintain them at densities over 4 m^{-2}. It also identified positive feedback mechanisms of the kelp bed, urchin barren, and turf-sediment states.

In this study I have undertaken the first combined survey of reef state, urchin density, and roe quality, to provide important baseline information to inform the development of a spatial management plan for the Bay's reefs. The survey allowed me to explore spatial variation in each variable as well as their interdependencies. Anecdotal evidence suggests urchin densities have increased across the Bay and kelp cover has reduced. I use the information from the survey to identify areas at high risk of collapse/potential for recovery, and what restoration intervention to apply to maximize the chance of success while minimizing the cost. My findings challenge several assumptions underlying current urchin management, with possible implications for commercial fishing. The survey approach presented here provides a useful framework for managing and restoring temperate reef ecosystems globally.

Methods

I designed a survey to observe current reef state, and the distribution, size, and roe quality of the native urchin *Heliocidaris erythrogramma* in Port Phillip Bay. The Bay was divided into regions following (Worthington & Blount, 2003), with the addition of a Port Phillip Heads region (PP) to cover the south of the Bay (Figure 1). The seven regions were further divided at smaller spatial scales by reef, site, and subsite, as summarized in Table 1, with an attempt to spread surveys spatially, and across depths at the subsite level.

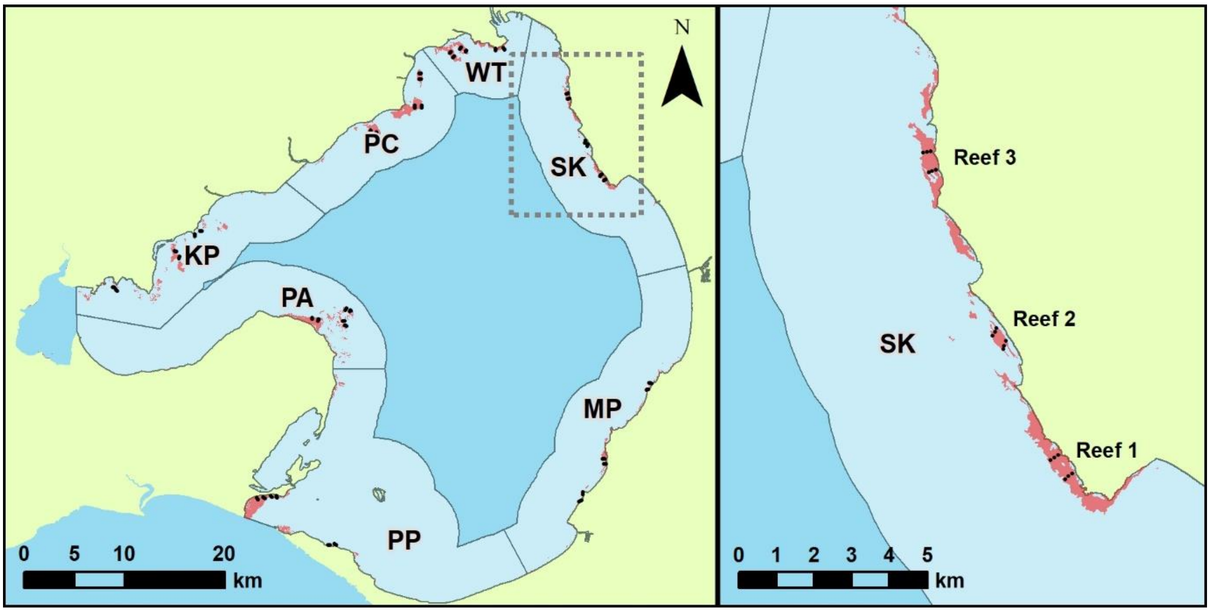


Figure 1 Distribution of surveys in Port Phillip Bay. Pink polygons = rocky reefs, black dots = subsites. PP = Port Phillip Heads, PA = Portarlington, KP = Kirk Point, PC = Point Cooke, WT = Williamstown, SK = St Kilda, MP = Martha Point. Inset (dashed rectangle) shows distribution of subsites across three reefs in the St Kilda region.

Table 1 Design of the 2002 (Worthington & Blount, 2003) and current surveys.

Number	2002	2019/2020	Spatial scale
Regions	6	7	20 km
Reefs per region	2	3	5 km
Sites per reef	2	2	500 m
Sub-sites per site	2	3	100 m
Transects per sub-site	6	6	10 m

Surveys

I undertook surveys between late October 2019 and late February 2020. At each subsite, two divers each ran three 5 x 1 m transects, which were haphazardly placed on the reef approximately 7.5 m apart. Along each transect, divers counted *H. erythrogramma* in two size classes: small (<35 mm) and large (>35 mm) and took a 1 m^2 photoquadrat. The shallow depth at some subsites required four photos to capture the 1 m^2 quadrat, which were later stitched together, and reduced to the original photo dimensions. The Coral Point Count (CPCe 4.1) tool was used to classify photos, with 10 points randomly assigned to each photo and categorized as either *Ecklonia radiata* (E), Mixed macroalgae (M), bare (B), or turf (T), with a fifth class (X) used to classify points that could not be identified (e.g., on the transect tape). This method resulted in approximately 60 points per 60 m covered by transects (avg. 1 m^{-1}), about half that described in the reef life survey methods manual (available online: https://reeflifesurvey.com/methods/) with 100 points per 50 m transect (avg. 2 m^{-2}).

Roe-assessment

I collected urchins between 21 October 2019 and 18 November 2019, corresponding to their harvesting season. From each subsite, the first 7 urchins of 35 mm or greater were collected and bagged. Bags were kept in eskis filled with sea water on the boat during diving operations, and oxygen was provided via bubble rocks during transport. On return to the laboratory, I transferred the urchin bags to sea water tanks and processed them within 2 days.

I measured urchin test diameters and mass and noted test and spine colour prior to opening. I then measured roe mass and calculated gonad index (GI) as the proportion of roe mass to total mass. Roe colour, texture, firmness, and grade, was classified following Pert et al. (2018), with a minimum GI threshold of 10% (Table S1).

Data manipulation and statistical analysis

Each data row included subsite identity, which was used to summarize the data to a dataframe with each row representing a subsite, including means, standard deviations, and counts for each data type. Urchin counts were converted to densities (m^{-2}) and categorized as high (>8 m ^{2}), moderate (4-8 m^{-2}), or low (<4 m^{-2}) based on threshold densities for overgrazing and recovery of *E. radiata* by *H. erythrogramma* (Kriegisch et al., 2016). Due to the rarity of *E. radiata* dominated points in the coral point count dataset, *E. radiata* and mixed macroalgae were combined and are referred to herein as vegetated reef. All other points were considered unvegetated, with bare and turf being subsets of the unvegetated reef category. The coral point count classes were converted to proportion of each reef class and the class representing the highest proportion was selected as the dominant class for that subsite.

Generalized linear models (GLM) were then developed in R (v. 4.0.0) using the glmmTMB (v. 1.0.1) package (Brooks et al., 2017; R Core Team, 2020). I tested the effect of location on vegetated classification using a binomial model with nested effects, first using all random effects to find variance contributions, then with as many fixed effects as could be included without compromising the model fit (2 fixed, 3 random, levels = [region [PP, PA, KP, PC, WT, SK, MP], reef [1, 3, 3], site [1, 2], subsite [A, B, C], photoquadrat [1:n]]). This was repeated for the unvegetated points to differentiate turf from bare reef, large urchin density and biomass density, as well as the urchin density and roe quality parameters. A square root transformation was also done on the urchin biomass density, informed by a BoxCox recommendation using the MASS (v. 7.3.51.5) package (Vernables & Ripley, 2002).

Interpolation of results across the Bay

Similar GLMs were then used to investigate the relationship between potential explanatory factors and reef state as summarized in Table 2, in the hope of enabling the interpolation of survey results to un-surveyed reefs. Factors considered included data from the survey (urchin density and biomass density), elevation and bathymetric derivatives, LiDAR reflectance, and spectral wave model results. The bathymetric and LiDAR reflectance datasets were provided by the Victorian Government's Department of Environment, Land, Water, and Planning (DELWP) for this project, with a resolution of 2.5 m. Both had been processed from a range of original data sources, and the reflectance dataset had been normalized (Allemand et al., 2017). Spectral wave values were from an uncalibrated spectral wave model run in MIKE 21 using design 1% AEP wind conditions. The explanatory variables were first tested for correlation (grouping shown in Table 2). Two sets of GLMs were then developed combining uncorrelated variables either with or without interaction terms. Bayesian Information Criterion (BIC) were used to rank models and select the most appropriate combination of explanatory factors. Since urchin density and biomass were correlated, the model sets could be divided into those using density, those using biomass, and those with no reference to urchins.

Since urchin density data was not available outside the immediate survey subsites, the values had to be averaged at a larger spatial scale. Most of the variance in urchin density and urchin biomass density was at the regional scale, so they were averaged at that level, with all other predictor variables averaged at the reef level. The resulting formulas were then rearranged to allow the expression of urchin density or biomass relating to a threshold likelihood of vegetation, set at 50%. Equations 1 and 2 show this rearrangement, with *a* representing the intercept, *c* representing the coefficients, and x_1 and x_2 representing the predictor variables.

$$\frac{e^{(a+c_1x_1+c_2x_2+\cdots)}}{1+e^{(a+c_1x_1+c_2x_2+\cdots)}}=0.5 \qquad \text{eq. 1}$$

$$x_1=\frac{(a+c_2x_2+\cdots)}{-c_1} \qquad \text{eq. 2}$$

Table 2 Summary of explanatory factors investigated.

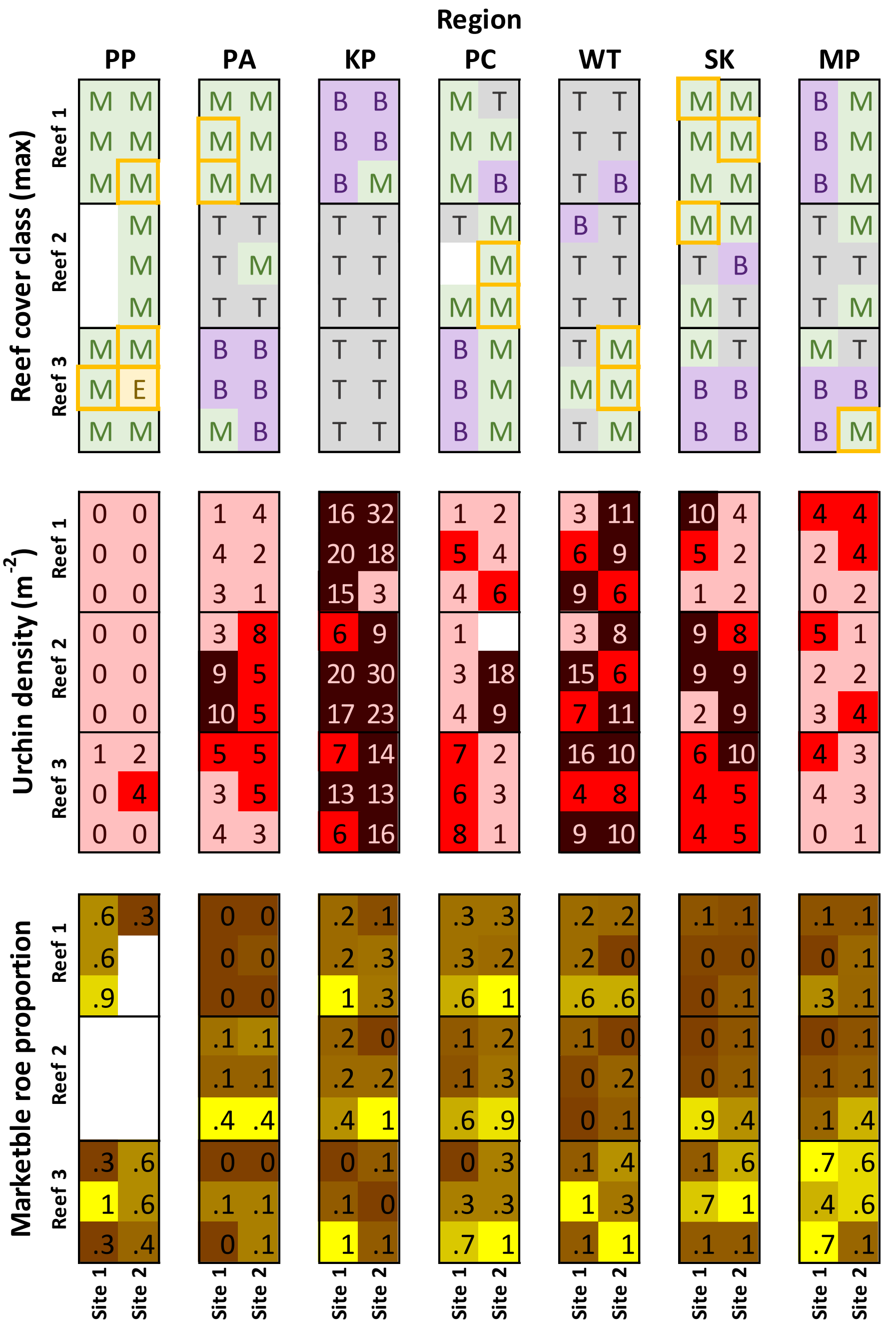
Source	**Factor**	**Transformation**	**Proxy for**	**Grouping**
Survey	Large urchin density	Divided by 5 to give (m^{-2})	Grazing pressure	a
	Large urchin biomass	square-root	Grazing pressure	a
DEM	Elevation (mean)		Various (inc. light)	b
	Elevation (sd)		Depth variation	c, d
	Rugosity	Area / Planar Area -1	Depth variation	c
	Slope			c
	Maximum curvature			d
	Bathymetric Position Index (BPI)		Relative elevation locally	e
LiDAR	LiDAR Reflectance (mean)		Substrate hardness	f
	LiDAR Reflectance (sd)		Variability in substrate hardness	g
Spectral wave model	Maximum wave orbital velocity		Wave exposure at bed	h
	Peak wave period		Wave exposure	i

Results

Reef states, urchin densities, and roe marketability

The dominant reef classification, average urchin density, and proportion of marketable roe for each subsite are presented in Figure 2. More than half the subsites surveyed (66/122, 54%) were classified as unvegetated, either bare (27, 22%) or covered with algal turf (39, 32%); four out of 122 subsites were not able to be classified due to a lack of photos. Four (4/21, 19%) reefs were unvegetated at all subsites (2 x KP, 2 x WT), while only five (24%) had no unvegetated subsites (3 x PP, 1 x PA, 1 x SK). *E. radiata* was observed at 13 subsites (11%), all of which were vegetated, but only dominant at a single subsite. Mixed macroalgae was the most common classification (56, 46%) and vegetation was completely missing from only five subsites (4%). At the regional scale, KP had only a single subsite vegetated, and this was accompanied by high urchin densities (>8 m^{-2}) across all but four subsites. The next most unvegetated region was WT, which had the second highest urchin density.

Urchin densities were higher across all regions compared to the 2002 survey (Figure 3). The increases were statistically significant in four regions for large urchins, and all six regions for small urchins. A clear gradient in urchin densities was observed, from high in the north-west to low in the south-east. Urchin densities at KP remained much higher than any other region, including eight of the ten highest density subsites. The only subsite in KP with low urchin densities was also the only vegetated subsite. Eight subsites (6%) had 100% marketable roe, and 19 (16%) had greater than 50% marketable roe.



Region

Reef cover class (max)

	PP		PA		KP		PC		WT		SK		MP	
	Site 1	Site 2	Site 1	Site 2	Site 1	Site 2	Site 1	Site 2	Site 1	Site 2	Site 1	Site 2	Site 1	Site 2
Reef 1	M	M	M	M	B	B	M	T	T	T	M	M	B	M
	M	M	M	M	B	B	M	M	T	T	M	M	B	M
	M	M	M	M	B	M	M	B	T	B	M	M	B	M
Reef 2		M	T	T	T	T	T	M	B	T	M	M	T	M
		M	T	M	T	T		M	T	T	T	B	T	T
		M	T	T	T	T	M	M	T	T	M	T	T	M
Reef 3	M	M	B	B	T	T	B	M	T	M	M	T	M	T
	M	E	B	B	T	T	B	M	M	M	B	B	B	B
	M	M	M	B	T	T	B	M	T	M	B	B	B	M

Urchin density (m^{-2})

	PP		PA		KP		PC		WT		SK		MP	
	Site 1	Site 2	Site 1	Site 2	Site 1	Site 2	Site 1	Site 2	Site 1	Site 2	Site 1	Site 2	Site 1	Site 2
Reef 1	0	0	1	4	16	32	1	2	3	11	10	4	4	4
	0	0	4	2	20	18	5	4	6	9	5	2	2	4
	0	0	3	1	15	3	4	6	9	6	1	2	0	2
Reef 2	0	0	3	8	6	9	1		3	8	9	8	5	1
	0	0	9	5	20	30	3	18	15	6	9	9	2	2
	0	0	10	5	17	23	4	9	7	11	2	9	3	4
Reef 3	1	2	5	5	7	14	7	2	16	10	6	10	4	3
	0	4	3	5	13	13	6	3	4	8	4	5	4	3
	0	0	4	3	6	16	8	1	9	10	4	5	0	1

Marketble roe proportion

	PP		PA		KP		PC		WT		SK		MP	
	Site 1	Site 2	Site 1	Site 2	Site 1	Site 2	Site 1	Site 2	Site 1	Site 2	Site 1	Site 2	Site 1	Site 2
Reef 1	.6	.3	0	0	.2	.1	.3	.3	.2	.2	.1	.1	.1	.1
	.6		0	0	.2	.3	.3	.2	.2	0	0	0	0	.1
	.9		0	0	1	.3	.6	1	.6	.6	0	.1	.3	.1
Reef 2			.1	.1	.2	0	.1	.2	.1	0	0	.1	0	.1
			.1	.1	.2	.2	.1	.3	0	.2	0	.1	.1	.1
			.4	.4	.4	1	.6	.9	0	.1	.9	.4	.1	.4
Reef 3	.3	.6	0	0	0	.1	0	.3	.1	.4	.1	.6	.7	.6
	1	.6	.1	.1	.1	0	.3	.3	1	.3	.7	1	.4	.6
	.3	.4	0	.1	1	.1	.7	1	.1	1	.1	.1	.7	.1

Figure 2 Subsite classification by highest percentage cover (top), urchin density (middle), and proportion of marketable roe (bottom)). Subsite initials: E = Ecklonia radiata, M = mixed macroalgae, B = bare, T = turf. Orange outlines indicate presence of E. radiata detected. Urchin densities coloured as high >8 (dark red), moderate (red), and low <4 (pink). Marketable roe proportion is coloured from brown (0) to yellow (1). Region initials: PP = Port Phillip Heads, PA = Portarlington, KP = Kirk Point, PC = Point Cooke, WT = Williamstown, SK = Saint Kilda, MP = Martha Point. White cells indicate missing data.

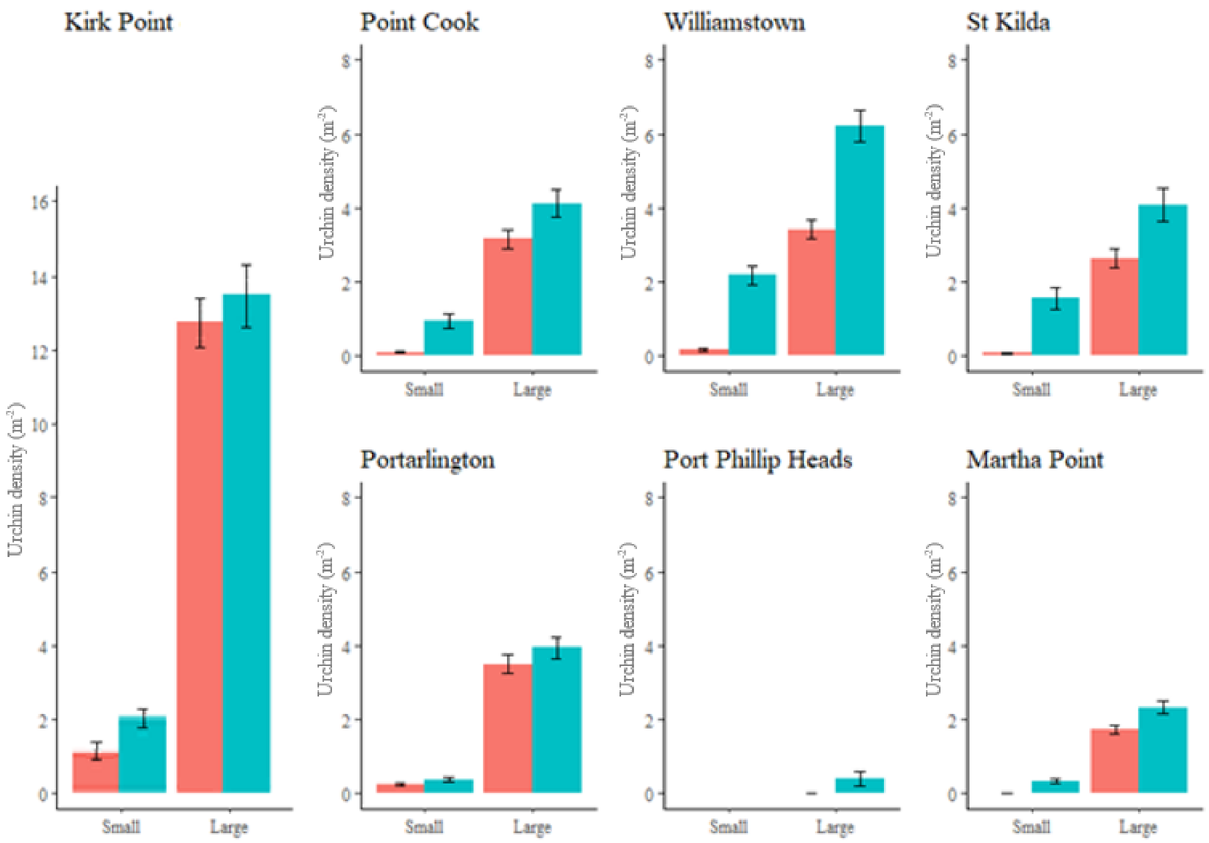


Figure 3 Urchin densities by region and size. Red bars show the previous survey (2002) observations, while blue bars show the current survey observations. Note that urchin surveys were not conducted at Port Phillip Heads in 2001.

Spatial patterns of variance

Variance in reef state (vegetated vs. non-vegetated) was greatest at the subsite and regional scales while variance in the distribution of turf among non-vegetated reefs was greatest at the reef and subsite scales (Table 3). For urchin density and biomass density the greatest variance was at the regional scale, followed by the subsite scale (Table 3). Marketable roe variance was greatest at the subsite level, closely following the variance distribution of gonad index (GI) despite roe firmness, good colour, and good texture showing greatest variance at the regional and reef scales. While the variance distributions for test diameter and total mass were similar, neither matched the distribution for roe mass.

Table 3 GLM results showing variance contributions from each spatial scale for reef state (top) and urchins (bottom).

Reef State	**Vegetated**				**Turf (Non-Vegetated)**			
Source	**df**	**χ^2**	**Pr(>χ^2)**	**% Var**	**df**	**χ^2**	**Pr(>χ^2)**	**% Var**
Region, Rg	6	165	$<2.2\text{E}^{-16}$	25	6	52	$<2.3\text{E}^{-09}$	15
Reef, Rf(Rg)	14	197	$<2.2\text{E}^{-16}$	17	14	158	$<2.2\text{E}^{-16}$	31
Site, St(Rf)	-	-	-	9	-	-	-	0
Subsite, Ss(St)	-	-	-	27	-	-	-	27
Photo, Ph(Ss)	-	-	-	22	-	-	-	27
Urchins	**Large Urchin Density**				**Urchin Biomass Density$^{0.5}$**			
Source	**df**	**χ^2**	**Pr(>χ^2)**	**% Var**	**df**	**χ^2**	**Pr(>χ^2)**	**% Var**
Region, Rg	6	315	$<2.2\text{E}^{-16}$	70	6	103	$<2.2\text{E}^{-16}$	47
Reef, Rf(Rg)	14	115	$<2.2\text{E}^{-16}$	10	-	-	-	5
Site, St(Rf)	-	-	-	0	-	-	-	0
Subsite, Ss(St)	-	-	-	15	-	-	-	45
Drop, Dp(Ss)	-	-	-	4				
Residual					-	-	-	3
Urchins	**Test Diameter**				**ln(Total Mass)**			
Source	**df**	**χ^2**	**Pr(>χ^2)**	**% Var**	**df**	**χ^2**	**Pr(>χ^2)**	**% Var**
Region, Rg	6	1306	$<2.2\text{E}^{-16}$	65	6	1254	$<2.2\text{E}^{-16}$	63
Reef, Rf(Rg)	-	-	-	3	-	-	-	3
Site, St(Rf)	-	-	-	2	-	-	-	1
Subsite, Ss(St)	-	-	-	2	-	-	-	0
Residual	-	-	-	28	-	-	-	33
Urchins	**Roe Mass$^{0.3}$**				**Gonad Index$^{0.5}$**			
Source	**df**	**χ^2**	**Pr(>χ^2)**	**% Var**	**df**	**χ^2**	**Pr(>χ^2)**	**% Var**
Region, Rg	6	280	$<2.2\text{E}^{-16}$	24	6	208	$<2.2\text{E}^{-16}$	12
Reef, Rf(Rg)	-	-	-	8	-	-	-	13
Site, St(Rf)	-	-	-	2	-	-	-	3
Subsite, Ss(St)	-	-	-	19	-	-	-	28
Residual	-	-	-	48	-	-	-	44
Urchins	**Good Colour**				**Good Texture**			
Source	**df**	**χ^2**	**Pr(>χ^2)**	**% Var**	**df**	**χ^2**	**Pr(>χ^2)**	**% Var**
Region, Rg	6	162	$<2.2\text{E}^{-16}$	63	6	16.2	0.013	0
Reef, Rf(Rg)	-	-	-	14	-	-	-	91
Site, St(Rf)	-	-	-	0	-	-	-	0
Subsite, Ss(St)	-	-	-	23	-	-	-	9
Urchins	**Firmness**				**Marketable Roe**			
Source	**df**	**χ^2**	**Pr(>χ^2)**	**% Var**	**df**	**χ^2**	**Pr(>χ^2)**	**% Var**
Region, Rg	6	4.03	0.673	100	6	101	$<2.2\text{E}^{-16}$	25
Reef, Rf(Rg)	-	-	-	0	-	-	-	23
Site, St(Rf)	-	-	-	0	-	-	-	0
Subsite, Ss(St)	-	-	-	0	-	-	-	52

Relationships in the data

Due to the lack of *E. radiata* in the Bay, I was unable to verify the previously observed relationship between urchin density and kelp cover. Instead, I plotted percentage cover of mixed macroalgae against urchin density (Figure 4), finding a negative relationship between urchin density and percentage cover and few vegetated reefs with high urchin densities.

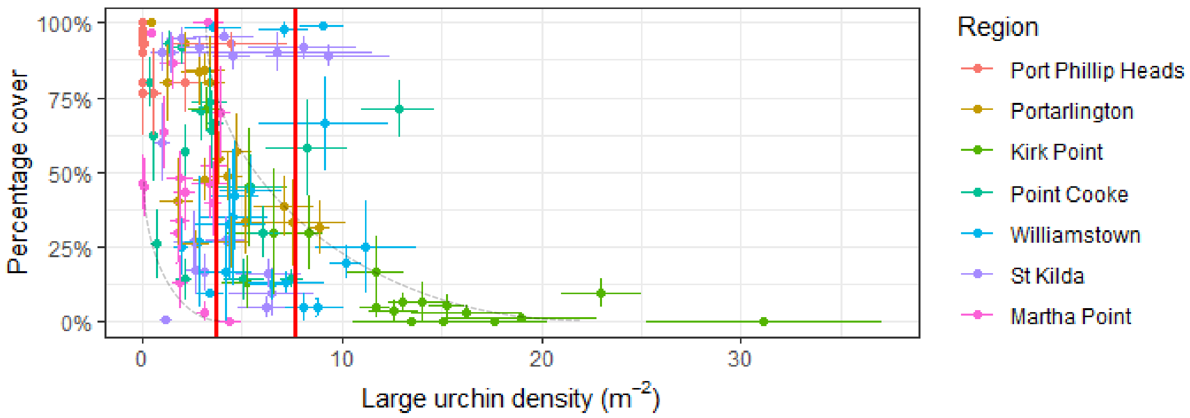


Figure 4 Percentage cover of macroalgae by large urchin density (m^{-2}). Regions are colour-coded, and confidence bands show +/- 1 SE. Dashed line shows general trend of reduced percentage macroalgal cover with increasing urchin density. Vertical red lines indicate the urchin density thresholds for phase shifts from E. radiata bed to H. erythrogramma barren (8 m^{-2}) and the reverse (8 m^{-2}).

Urchin test diameter declined with increasing urchin density across the whole dataset, as was observed by (Worthington & Blount, 2003). However, this relationship was driven largely by differences in urchin densities among regions; however, the relatively small within-region variation resulted in no evidence of a relationship when splitting the dataset by region (Figure 5).

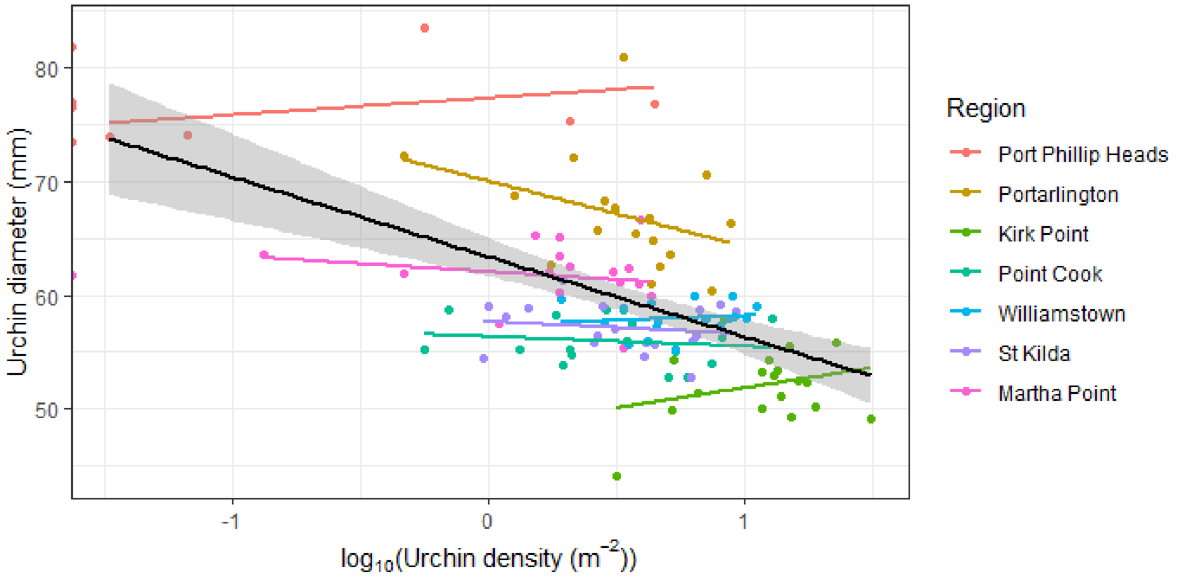
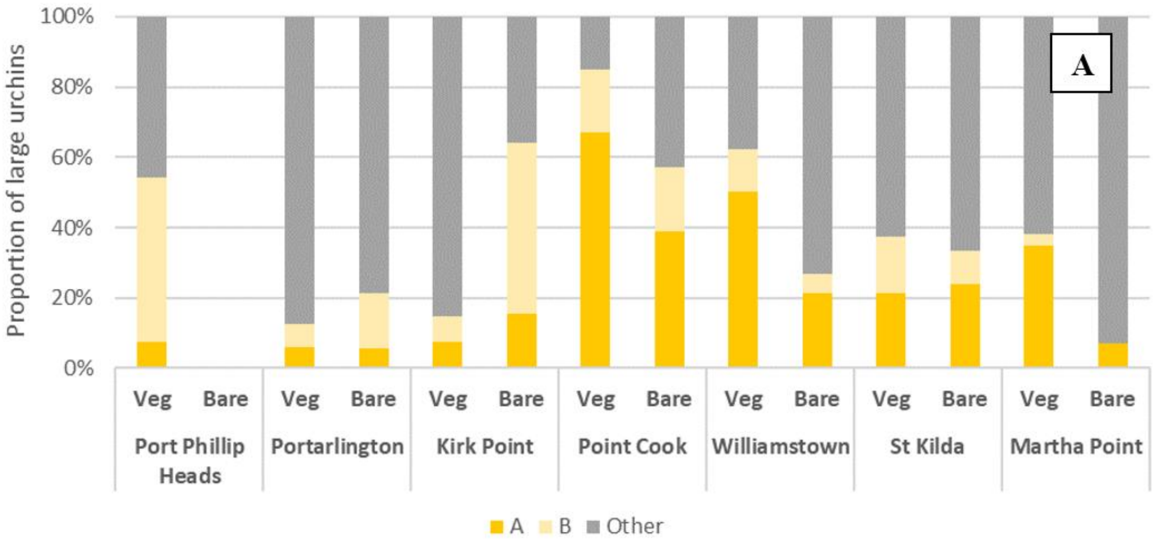


Figure 5 Urchin diameter (mm) and density (m^{-2}) coloured by region with trend lines. Black line shows linear trend across all regions.

There was no significant effect of reef state on the proportion of marketable roe at the regional scale and mean values did not consistently favour vegetated reefs (Figure 6). More than half the roe was marketable from the vegetated reefs at PP, PC, and WT, and the unvegetated reefs at KP and PC. There was also no significant effect of urchin density on the proportion of marketable roe (p = 0.652).



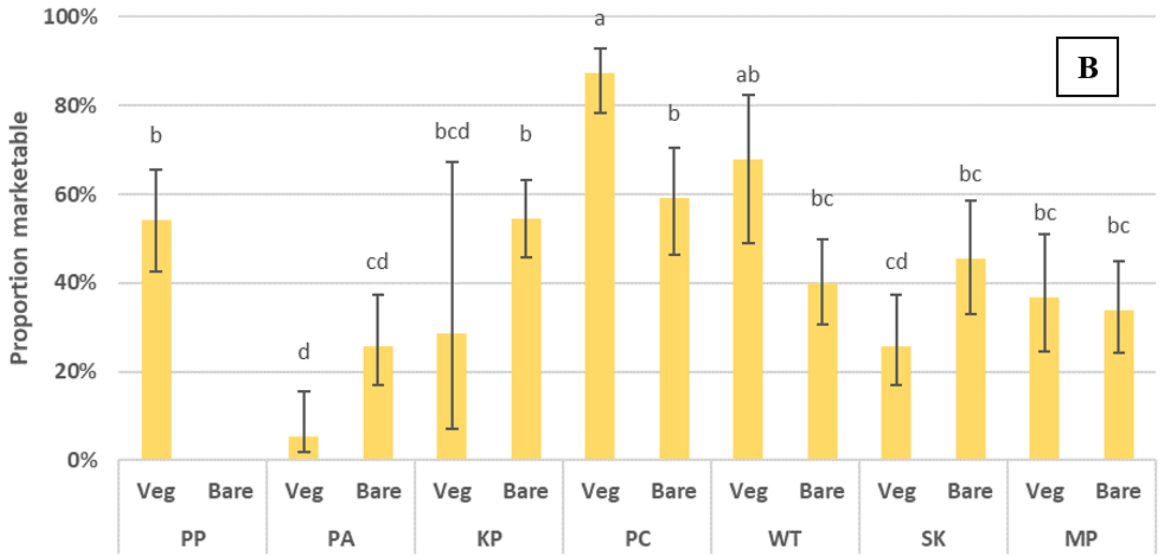


Figure 6 Roe grades (top) and percentage of marketable roe (bottom) for large urchins with GI > 10% on vegetated and bare reefs in each region. Note: no bare reefs were observed in Port Phillip Heads. Error bars show 95% confidence intervals, and shared letters indicate no statistically significant difference in values.

Interpolation

Neither urchin density nor urchin biomass density were selected in best performing models as predictors of turf presence (Table 4), suggesting herbivory has little impact on whether unvegetated reefs are covered with turf algae and allowing prediction across the Bay based on the raster data alone. Regionally averaged urchin density was selected, however, as a highly significant variable in the modelling of reef state (vegetated vs. non-vegetated). The best performing model (Table 4) for the prediction of vegetation also included LiDAR reflectance, indicating a preference for solid substrate. Rearrangement of eq.1 to eq. 2 and applying the LiDAR reflectance values indicates a significantly lower urchin biomass threshold at Martha Point (0.1 x), as illustrated in Figure 7. These formulas may be applied to predict vegetation across all reefs in the Bay.

Table 4 Final GLM's selected by BIC for predicting vegetation state (top) and turf presence (bottom).

Vegetated Reef

Scale	BIC	Formula
Subsite	111.85	Urchin_Density_Subsite (-ve) + Curvature (+ve) + LiDAR_Reflectance (-ve)
Site	114.78	Urchin_Density _Site (-ve) + Curvature (+ve) + LiDAR_Reflectance (-ve)
Reef	124.00	Urchin_Density _Reef (-ve) + LiDAR_Reflectance (-ve)
Region	117.96	Urchin_Biomass_Region (-ve) + LiDAR_Reflectance (-ve)
Bay	146.71	Curvature (+ve) + LiDAR_Reflectance (-ve)

Turf

Scale	BIC	Formula
All	66.96	Depth (-ve) + Area (-ve) + Rugosity (+ve) + Tp (-ve)

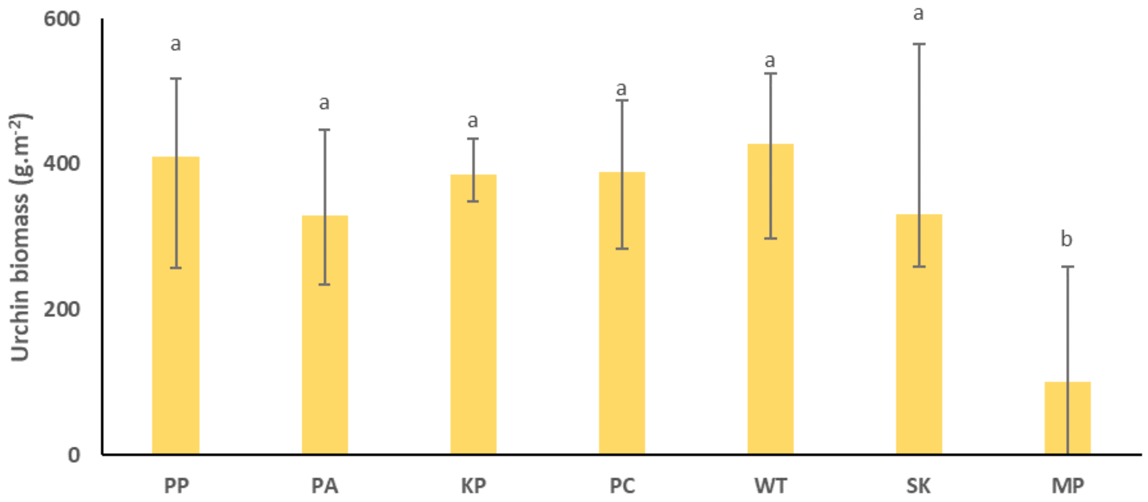


Figure 7 Threshold urchin biomass (g.m^{-2}) for 50% vegetative cover by region. Error bars show 95% confidence intervals, and shared letters indicate no statistically significant difference in values.

Discussion

Overall, these results suggest the Bay's rocky reefs are in poor condition with most predominantly unvegetated. This lack of kelp and other canopy algae represents a significant gap in ecological services, providing an economic case for their protection and restoration. Kelp was present at only 11% of subsites, all of which were classified as vegetated. Coupled with the presumed short dispersal distances of *E. radiata*, this may suggestlimited natural spore supply to unvegetated reefs. Urchin densities were above kelp carrying capacity (8.m^{-2}) at six vegetated subsites indicating a risk of overgrazing, and above kelp recovery capacity (4.m^{-2}) at fifty unvegetated sites, suggesting natural recovery was unlikely. The high proportions of marketable urchins across different reef states suggests wild catch harvesting can play an important role in managing urchin densities in areas of interest. The results also suggest that several assumptions underlying the current calculation of total allowable catch may not be valid, and an adjustment to the current quota may be justified. For example; the overabundance of urchins may pose a greater risk than that of serial depletion, urchins within barrens may provide meaningfully to the commercial catch, and the 2% of urchin biomass value may be overly conservative.

Changes in reef state and urchin density since 2002

By comparing the results of the current survey with the previous urchin survey by Worthington and Blount (2003) and the habitat maps used in their calculations (Ball & Blake, 2007), I can identify several important changes in urchin densities, and the relationships between urchin density, reef state, and roe quality. Urchin densities have increased across all regions, breaching the 4.m^{-2} threshold for natural kelp recovery at Point Cooke, Williamstown, St Kilda, and Portarlington. This suggests a likely reduction in the capacity of reefs in these regions to recover kelp beds, highlighting the urgency of protection. An overabundance of urchins and the subsequent loss of canopy algae were not concerns considered by Worthington and Blount (2003), as they were instead trying to ensure stocks were not serially depleted. They did, however, suggest ongoing surveys to monitor the urchin densities in the Bay to inform quota limits. Along with reporting data from the urchin fishery, surveys could give a better understanding of both the risks of serial depletion and any variation in threshold densities across the Bay.

The total allowable commercial catch (TACC) for the Bay was calculated as 2% of the estimated biomass of urchins on vegetated reefs excluding Portarlington (DEPI, 2014). Using the same methods to reassess the TACC considering this new data, the recommended TACC would increase from 60 T to 90 T (Figure 8). This was driven primarily by increases in urchin biomass on vegetated reefs in St Kilda (+771 T) and Williamstown (+512 T). A slight increase in Point Cooke (+273 T) offset a decrease in Kirks Point (-239 T). This recalculation is still based on the conservative approach currently used aimed at avoiding serial depletion of urchins.

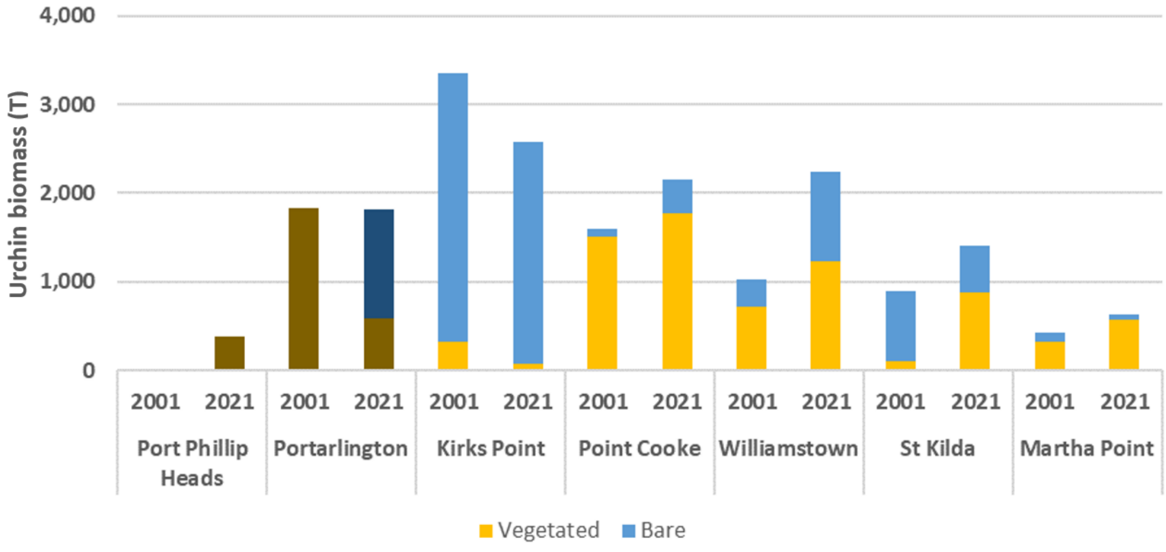


Figure 8 Comparison of estimated urchin biomass by region and vegetation state (vegetated or bare). Darkened colours for Port Phillip Heads and Portarlington indicate that they did not contribute to the TACC estimate.

Observations by Worthington and Blount (2003) of a negative relationship between urchin density and test diameter, and poorer roe condition on barren reefs, led to a recommendation to exclude barrens from the total allowable catch calculation. Consequently, the current commercial urchin quota is based on an estimated urchin population on vegetated reefs, with the assumption that urchins on barrens are unsuitable for harvesting. My study, however, contradicts this view, as I found no evidence of reduced test diameter or proportion of marketable roe attributed to either high urchin density or a lack of vegetation on the reef. In fact, 19 (15%) of subsites were classified as barren but had urchins suitable for harvest, suggesting the presence of barrens in the Bay should not restrict the urchin quota. Thus, barrens may contribute meaningfully to commercial catches, and commercial fishing may be a realistic option for urchin reductions where they are needed on unvegetated reefs.

Categorization tree

I have developed a categorization tree (Figure 9) to guide selection and prioritization of management actions, pulling together our understanding of the Bay's rocky reefs, interactions between urchin density and reef state, and considerations of marketability. The final categories are marked with letters, which are referred to herein to discuss management approaches. The first distinction made is vegetated status, with vegetated reefs considered more desirable. Vegetated subsites with low urchin densities (A) are considered healthy (Wernberg et al., 2019) and at low risk of overgrazing by urchins, so no action is immediately required at these sites. Likewise, vegetated subsites with medium urchin densities (B) require no immediate action, however, they are priority areas for monitoring, as a sudden increase in urchin densities could put them at risk of overgrazing. There may also be variation in the carrying capacity of vegetated reefs, for example, increased wave action may reduce the grazing ability of urchins allowing persistence of kelp with high urchin density (Kawamata, 2010). Removal of urchins from vegetated reefs with high urchin densities is a high priority, acknowledging that protection of existing vegetation is cheaper than its restoration after being lost (Eger et al., 2020; Eger et al., 2022). Where urchins are too small (<35 mm) to be commercially harvested (C), they should be culled. If urchins are large with marketable roe (D) they should be targeted for commercial harvest, while large urchins with poor roe quality (E) can be conditioned in aquaria or sea cages prior to sale (Pert et al., 2018; Warren-Myers et al., 2019).

Non vegetated reefs that are not turf dominated may provide better opportunities for recovery. Urchin densities first need to be reduced below 4.m^{-2}, with removal methods depending on test size and roe quality, as discussed above. Following urchin removal, or where urchin densities are already low, natural recovery may be expected where spore supply is present (F) and monitoring of these reefs could provide important insights into the natural recovery process. Where no kelp is present (G) more active restoration methods are likely required, such as the provision of spore bags, seeding with inoculated substrate, or transplantation (Chang, 2000; Coleman & Wernberg, 2017). Subsites dominated by a sediment-turf matrix (H, I) present an additional challenge in restoration. Restoration of these sites is likely to be more expensive given the additional step of turf removal, however, some active methods such as transplanting with a sweeping artificial substrate may overcome this obstacle (Fredriksen et al., 2020; Graham et al., 2021).

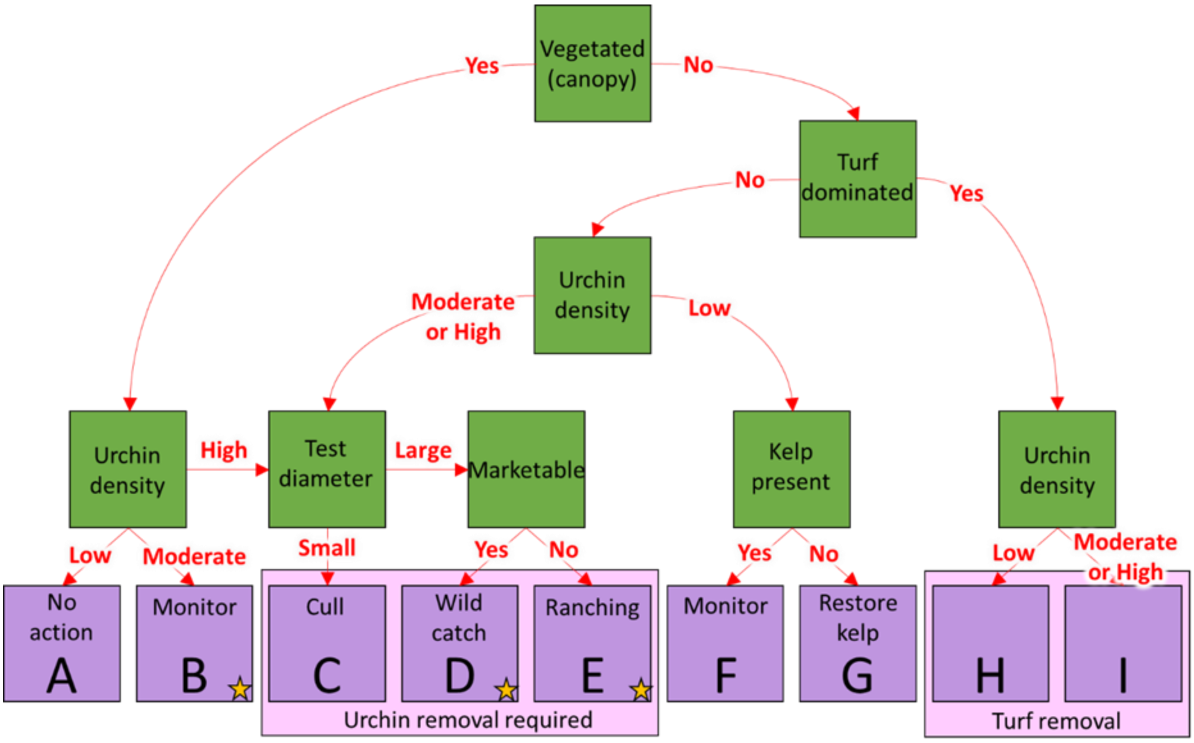


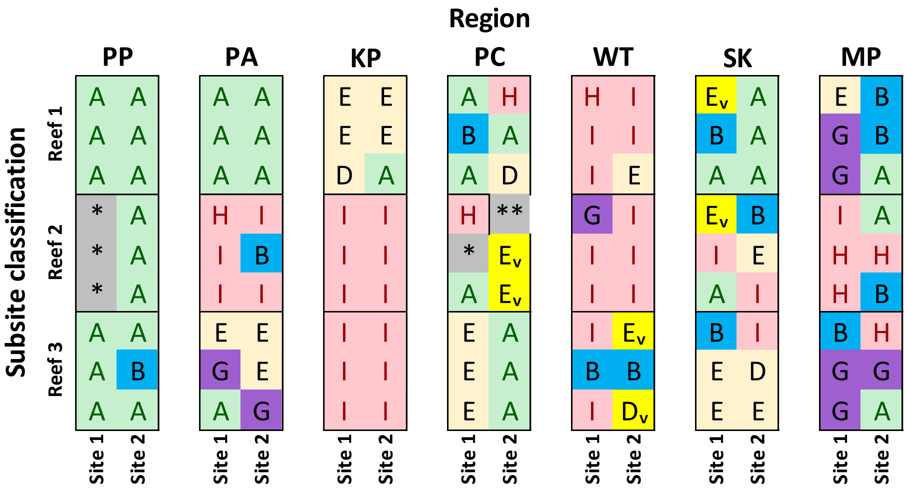
Figure 9 Categorization tree for reef management actions. Green boxes contain questions, red text the responses, and purple boxes the resulting actions. Stars indicate priority actions with greatest return for effort.

Actions for subsites

By applying the categorization tree presented in Figure 9 to the data collected in my survey, I can identify subsites suited to different management options (Figure 10). Six subsites (PC22B, PC22C, WT32A, WT32C, SK11A, SK21A) were identified as top priority for harvesting due to the risk of overgrazing from a critically high density of urchins. One of these (WT32C) had 100% marketable roe at 106 g.m-2, representing around 130 kg roe of which 86% was grade A, so should be targeted for commercial wild catch. Nearby at WT32A roe was underdeveloped, with an average GI just under 10%, resulting in only 43% of urchins marketable. This subsite would be better suited to harvesting of urchins for ranching, likely producing 100% grade A roe in a short time (Pert et al., 2018). PC22B had a higher density of roe (125 g.m-2), however, poorer colour and firmness meant only 27% was marketable, 30% of observed urchins were small, and the reef is within the Point Cooke Marine

Sanctuary, making it unavailable for the commercial fishery. This would be a location for culling, with potential for natural recovery due to the presence of *E. radiata*.

Twelve subsites were identified as high priority for monitoring, as they are currently vegetated with moderate urchin densities (PP32B, PA22B, PC11B, WT31B, WT32B, SK11B, SK22A, SK31A, MP12A, MP12B, MP22C, MP31A). PP32B is of particular interest, given it is the only subsite in the entire survey dominated by *E. radiata*. All of these should be monitored so that if increased urchin densities are observed, they can be removed. Eight subsites were identified as bare, with low urchin densities, suggesting possible natural recovery of vegetation, although five of these were at MP where the urchin carrying capacity appears to be much lower (Figure 7). Nineteen subsites were identified as bare, with moderate or high urchin densities. Three of these had 100% marketable roe, making them ideal for commercial wild catch harvest. No bare or turf dominated subsites contained any *E. radiata* making it unlikely urchin removal in those areas would result in natural kelp recovery (Burek et al., 2018).



	PP Site 1	PP Site 2	PA Site 1	PA Site 2	KP Site 1	KP Site 2	PC Site 1	PC Site 2	WT Site 1	WT Site 2	SK Site 1	SK Site 2	MP Site 1	MP Site 2
Reef 1	A	A	A	A	E	E	A	H	H	I	E_v	A	E	B
	A	A	A	A	E	E	B	A	I	I	B	A	G	B
	A	A	A	A	D	A	A	D	I	E	A	A	G	A
Reef 2	*	A	H	I	I	I	H	**	G	I	E_v	B	I	A
	*	A	I	B	I	I	*	E_v	I	I	I	E	H	H
	*	A	I	I	I	I	A	E_v	I	I	A	I	H	B
Reef 3	A	A	E	E	I	I	E	A	I	E_v	B	I	B	H
	A	B	G	E	I	I	E	A	B	B	E	D	G	G
	A	A	A	G	I	I	E	A	I	D_v	E	E	G	A

*Figure 10 Subsite management category based on categorization tree. A = no action required, B = monitor, C = cull, D = wild catch, E = ranching, F = monitor, G = restore kelp, H = turf removal, I = turf removal. The subscript $_V$ indicates vegetated reefs. * = A, F, G, or H; ** = A, B, or E.*

Interpolation across the Bay's rocky reefs

The high proportion of variance in urchin density at the regional scale suggests regional estimates may be sufficient for predicting non-surveyed reefs. Applying this method to the actual survey, however, leads to mis-categorization of high priority subsites. Specifically, the four vegetated subsites at risk of collapse due to high urchin densities at PC and SK would be missed due to regional average urchin densities being below 8.m^{-2}, while two additional subsites at WT would have been added, as well as the sole vegetated subsite at KP. This highlights the need for high resolution surveys of urchin densities to meaningfully understand current reef conditions. Such data may be available to managing authorities through abalone and urchin fishery data.

Conclusion

This study has demonstrated the importance of incorporating information about multiple components of an ecosystem into surveys to understand relationships and plan interventions. Here I have combined reef state, urchin density, and roe quality data to identify sites most at need of restoration effort, sites that could be targeted for commercial harvesting with co-benefits for reef health, and those with the greatest chance of recovery. While the survey and categorization tree presented in this study is specific to a particular bay in southern Australia, the approach is broadly applicable to understanding and managing urchin overabundance on temperate reefs worldwide.

Appendices

Table 5 Roe classification system for commercial quality H. erythrogramma. A and B grades are considered marketable. ‘F’ = firm, ‘NF’ = not firm. Table source (Pert et al., 2018).

Colour	Texture	Firmness	Grade
Bright orange or yellow	Fine	F	A
		NF	B
	Medium	F	A
		NF	B
	Coarse	F	A
		NF	B
Pale/dark orange or yellow	Fine	F	B
		NF	C
	Medium	F	B
		NF	C
	Coarse	F	C
		NF	C
Black, brown, or grey	Fine	F	D
		NF	D
	Medium	F	D
		NF	D
	Coarse	F	D
		NF	D

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CHAPTER 3 - USING ARTIFICIAL KELP TO FACILITATE RECOVERY OF NATURAL KELP BEDS

Abstract

Healthy kelp beds have positive feedback mechanisms that assist their persistence. These often include sweeping sediment from the reef, deterring herbivores, protecting juveniles from light stress, and providing spore supply. Following collapse of a kelp bed, the lack of these mechanisms reduces the capacity for recovery. As with other ecosystem engineers, the deployment of artificial mimics may assist recovery by re-establishing some of these mechanisms in the short-term while natural kelp establishes. Here we step through the development of an artificial kelp mimic from field measurements of adult sporophytes, through to optimization of sweeping motion in a wave flume, and finally testing with a field deployment at two sites. Our treatments included four types of artificial kelp, which were pooled to a single 'artificial unit of kelp (AUK)' treatment if non-significant. When testing for effects on mass accumulation, we found a significant interaction between treatment and site, suggesting the behaviour of the mimics is highly dependent on local factors such as fine-scale hydrodynamics. Heavy fouling and damage to the artificial kelp in the field highlighted the importance of caution when transferring lessons from a controlled lab environment to a real field setting.

Introduction

Species within an ecosystem interact with one another as well as the local abiotic environment. When the impacts of a specific species result in profound modification to the ecosystem, their capacity to act as an *ecosystem engineer* is of particular ecological interest (Jones et al., 1994). These modifications may be directly related to their form, such as when the structure of large trees provides habitat for aquatic insects (Frank, 2004), or when submerged macrophytes reduce light penetration, promote thermocline development, reduce flow rates, or enhance sedimentation (Carpenter & Lodge, 1986). Alternatively, they may be more indirect, such as when urchins graze down kelp beds removing a key primary producer and provider of structural habitat (Estes & Palmisano, 1974). Understanding these processes is important for predicting or managing change in ecosystems, such as a restoration project.

Natural selection on ecosystem engineering traits means it is typical for the engineer's fitness to improve with the changes it makes to the local environment. Such a positive feedback mechanism can lead to a more stable state (Kéfi et al., 2016). For example, the presence of seagrass can reduce suspended sediment loads allowing more light to penetrate the water column which helps seagrass growth (van der Heide et al., 2011; Adams et al., 2016). Such effects are often enhanced at scale with increasing patch size and/or density (van der Heide et al., 2021). With reduced cover, or complete loss of the ecosystem engineer, conditions become worse for the engineer and an alternative stable state may instead be reinforced. With loss of seagrass for example, the sediment load in the water column can increase, reducing light at the bed, and making recovery of the seagrass more difficult (Adams et al., 2016).

Kelps are valuable ecosystem engineers that are common on temperate rocky reefs across the globe. They support a wide range of species through provision of structural habitat, food, and modification of abiotic conditions (Jones et al., 1994; Connell, 2003). Kelps may also produce conditions which promote their own fitness and hence stabilize the kelp bed state. For kelps whose fronds touch the bed and are subject to high sediment loads, sweeping of the substrate may help maintain suitable substrate for recruitment (Velimirov, 1984; Thomsen et al., 2004; Burek et al., 2018). Likewise, when exposed to high urchin densities, a whipping motion may reduce herbivore pressure on the kelp bed (Konar, 2000; Konar & Estes, 2003; Ling & Johnson, 2009). Increased patch size and density can lead to increased spore supply both through spore production and a reduction in current speeds within the kelp bed that results in spore retention (Graham, 2003).

When kelp beds are degraded or lost, these positive feedbacks that facilitate kelp recovery through modifications to the local environment are not present. Instead, the positive feedbacks promoting kelp resilience can be replaced by positive feedbacks stabilizing alternative reef states. A well-known alternative state is that of an urchin barren devoid of foliose algae, which typically occurs when grazing urchins are overabundant because of the removal of urchin predators (Estes & Duggins, 1995; Ling et al., 2015). Once a barren, a return to the kelp state can be impeded by a lack of the positive feedback mechanisms of the kelp state (high spore supply, and sweeping of sediment from substrate), along with the capacity of urchins to maintain the barren state even at low densities (Filbee-Dexter & Scheibling, 2014; Ling et al., 2019). A natural reversal of such a phase shift requires a rare window of opportunity, when urchin densities are reduced, for example due to disease, sufficient reef is free of sediment, and timing aligns with spore release at sufficient scale for natural recruitment to occur (Feehan & Scheibling, 2014; Kriegisch et al., 2016; Capelle et al., 2019).

Given the importance of positive feedback processes in stabilizing alternative reef states, the artificial introduction of those processes associated with kelps may assist in the reverse phase shift back to the kelp bed state. The transplantation of adult kelp may work if undertaken at sufficient scale (Layton et al., 2019). However, such interventions require large quantities of adult kelp, which may not be available, or may cause damage to the donor reef (Carney et al., 2005). Alternatively, a kelp mimic may be developed which can provide the same benefits. This approach has been applied in the restoration of other ecosystem engineering species, for example the use of artificial seagrass mats or porous material to stabilize sediment, thus improving recruitment and survival of seagrass transplants (Campbell & Paling, 2003; Carus et al., 2021; Fivash et al., 2021).

This study considers the locally dominant kelp of Australia's Great Southern Reef, *Ecklonia radiata* (Agardh, C.) Agardh, J., which has been depleted in areas of Port Phillip Bay, Victoria from overgrazing by the native urchin *Heliocidaris erythrogramma* (Kriegisch et al., 2019). My aim is to develop a kelp mimic with similar frond movement to natural kelps and to test its efficacy in the field at clearing sediment from the substrate, enhancing survival of the gametophyte stage through shading, and protecting transplanted juvenile sporophytes from urchin grazing. This paper steps through the design of the artificial kelp including initial field measurements and wave flume tests, followed by field deployment trials at two sites. I expect the reintroduction of these positive feedback mechanisms will enhance both natural recruitment and survival of juvenile sporophyte transplants by reducing sediment accumulation and urchin density when compared to a control with no canopy.

Methods

Measuring wave conditions

Wave loggers (RBR® *solo* D wave) were deployed at four kelp beds in Port Phillip Bay between December 2017 and April 2018 to record the wave conditions the kelp were exposed to (Morris et al., 2020). The loggers recorded wave height, H_s, and associated period, T in hourly bursts at 1 Hz for 17 minutes. The four locations were chosen based on the presence of kelp beds with adjacent barrens, Governor Reef in the west (144°43' E, 38°09' S), two at Williamstown in the north (144°53' E, 37°52' S), and Point Linley in the east (145°02' E, 38°13' S). Wave periods and heights were calculated following (Kamphuis, 2010), after filtering out waves less than 50 mm, which included all swell during the deployments. From these calculations, a representative selection was used to determine the maximum orbital velocities at the bed, which are summarized in Table 1.

Table 1 Wave conditions recorded in the field.

Still water level (m)	**Wave period (s)**	**Wave height (mm)**	**Maximum horizontal orbital velocity at the bed (m.s^{-1})**
6.0	3	100	0.11
2.0	3	100	0.13
6.0	3	300	0.32
2.0	3	300	0.39

Design of artificial kelp

The design of the artificial kelp was informed by efforts to ensure scalability, through a simple cheap design, sustainability in material selection, and functionality in terms of mimicking the sweeping behaviour of natural fronds. Jute webbing was chosen as an alternative to plastic (e.g., Bologna & Steneck, 1993) as it is a natural fibre, which can biodegrade avoiding marine plastic pollution. It can also be purchased in rolls of various widths making it convenient to test various designs. The length and width of the strips were determined through field measurements of natural kelp. Attachment method and number of fronds were determined through wave flume testing.

Morphometric data from a natural *E. radiata* bed at Williamstown in Port Phillip Bay, Australia (144°54′ E, 37°52′) were taken in March 2017. Adult sporophytes were randomly selected, then stipe, frond, and total lengths, as well as lateral blade width, were recorded. Mean lengths and standard deviations were 47 ± 15 mm, 299 ± 58 mm, and 346 ± 76 mm, respectively (n = 18). The widths of lateral blades were 50 ± 12 mm (n = 11). Adult stipe density was also determined by haphazardly dropping a 1 m^2 quadrat into the kelp bed; 6.9 ± 2.6 m^{-2} (n = 8).

To aid in artificial kelp construction, the complex geometry of *E. radiata*, consisting of a stipe, primary lamina, and lateral blades, was simplified to single, double, or quadruple fronds, standardized to a constant surface area (i.e., reducing width in proportion to frond number). Based on these measurements, and available material widths, kelp fronds were mimicked using strips of jute webbing 50 mm wide and 300-350 mm long.

Flume study

Initial testing of the sweeping motion at The University of Melbourne in November 2017 identified seven designs that varied frond length, width, number, and attachment (Table 2) for more comprehensive testing in more realistic conditions. These designs were tested in December 2017 in a wave flume (50 m long, 1.2 m deep, 1.2 m wide, with a still water depth of 0.7 m) at The University of Western Australia, where a greater range of wave conditions that more closely mimicked those recorded in the field could be explored. A programmable piston-type wave generator was positioned in the middle of the flume, with 1:10 sloped wooden beaches at either end to minimize reflection (Abdolahpour et al., 2017). Two artificial kelp of each design on chicken wire mesh were attached to the plastic mesh at the base of the flume using cable ties. They were then exposed to a range of wave conditions (Table 3) by varying wave heights (47 – 170 mm) and periods (3 – 6 s). The ends of the artificial kelp were coloured with fluorescent spray paint and each experimental run was videoed with two cameras. Frames from these videos were then classified as either sweeping or not sweeping for each artificial kelp present based on whether the fronds were in contact with the bed.

Table 2 Artificial kelp designs tested in the wave flume.

ID	Number fronds	Length (mm)	Width (mm)	Attachment
1x300x50T	Single	300	50	Tape
1x350x50T	Single	350	50	Tape
2x300x25T	Double	300	25	Tape
2x300x50K	Double	300	50	Knot
2x300x25K	Double	300	25	Knot
2x350x25K	Double	350	25	Knot
4x300x12.5K	Quadruple	300	12.5	Knot

Table 3 Wave conditions tested in the wave flume.

ID	Still water level (m)	Wave period (s)	Stroke length (mm)	Wave height (mm)	Maximum horizontal orbital velocity at bed ($m.s^{-1}$)
3s 47mm	0.5	3	100	47	0.11
3s 71mm	0.5	3	150	71	0.17
4s 106mm	0.5	4	300	106	0.25
6s 142mm	0.5	6	600	142	0.32
5s 170mm	0.5	5	600	170	0.39

Field trials

A field experiment was set up (18 October 2018 to 07 March 2019) to test the efficacy of the artificial kelp in reducing the accumulation of sediment, promoting recruitment of *E. radiata* from spore bags, and protecting juvenile transplants from urchin grazing. The experiment was replicated on two reefs in the north-west and north of Port Phillip Bay, namely Point Cooke (144°48′ E, 37°56′), and Altona Marker Reef (144°51′ E, 37°53′) (Figure 1). Both reefs have been known to support kelp beds, but no kelp was observed at either in the year leading up to this experiment. Both reefs are on Newer Volcanics basalt flows characteristic of the western side of the Bay. Point Cooke is a patchy reef that extends eastward off a south to east facing shoreline. The site was outside the eastern boundary of the Point Cooke Marine

Sanctuary and consisted of intermittent sediments (sand and gravel) and basalt boulders. At the time of this study, the reef was an extensive urchin barren, with urchin densities > 10 m^{-2} (Carnell & Keough, 2019). The elevation at the site was between -2.8 and -3.5 m AHD. Altona Marker Reef is located approximately 1.5 km offshore from a south facing shore. It is a patchy reef interspersed with sandy patches and basalt boulders. This site included mussel beds and areas covered by other species of canopy-forming macroalgae. Neither site had any *E. radiata* present during experiment setup. The initial experiment was designed to compare the artificial kelp to no canopy (control), *E. radiata* canopy, and *Undaria pinnatifida* canopy, however, the loss of the *E. radiata* and *U. pinnatifida* canopies to urchin grazing meant these treatments were discarded. Hence, only the control and artificial kelp components are described here.

Wave conditions at the two sites were extracted for a one-year period from a calibrated hydrodynamic model of the Bay (Tran, 2020). Maximum wave orbital velocities at the bed were calculated from these and a plot of these against the orbital velocities tested in the flume are provided in the supplementary material (Figure S1).

The experiment utilized an unreplicated block design (n = 6 blocks), with each block (a 3 x 3 m plot with a central star picket) containing one replicate artificial kelp canopy treatment (1.5 x 1.5 m quadrat) and one replicate no canopy (control) treatment (1.5 x 1.5 m quadrat) (Figure 2). Canopy algae was cleared from within both treatments, and fencing wire was laid down for the artificial kelp treatment, held in place with marine epoxy and rocks. Initial deployments of the artificial kelp made of jute fell apart before the experiment setup was complete, so it was decided to test a range of different materials. Hence, the artificial kelp treatment was divided into 4 quadrats each containing 10 artificial kelps made of jute, rubber, PVC, or HDPE. The artificial kelp were assembled from two 60 cm lengths 25 mm wide folded in half and cable tied together after looping around the fencing wire. On 18 October 2018, 3 basalt settlement tiles (30 x 150 x 300 mm) to measure sediment and turf accumulation were placed within each control, and 1 under each artificial kelp material at Altona. The same experiment was repeated at Point Cooke on 12 November 2018.

Juvenile *Ecklonia* were collected from Point Linley (144°54’ E, 37°52’) in the south-east of the Bay on 29 October 2018 and transferred to a recirculating seawater system. Ten juveniles were attached to each of 12 squares of gutter guard (approximately 100 x 100 mm) with silicon tubing. These squares of gutter guard were then deployed to the Altona site on 07 November 2018, being epoxied to the middle of the control quadrant or cable tied onto the fencing wire under the artificial kelp. Following early observations of juvenile losses, each square was reset to a total of 9 individuals on 09 November 2018. The juvenile transplant experiment was not replicated at Point Cooke because of the high urchin grazing pressure. Mesh bags containing fronds with reproductive tissue from ten adult sporophytes were attached to the central star pickets on 26 September and 18 October 2018 at Altona and on 25 October 2018 at Point Cooke.

Monthly surveys were done following the experimental set-up between November 2018 and February 2019. During these surveys, the number of juvenile transplants surviving was counted, and their stage of development noted (I = simple single lamina, II = simple lateral lamina, III = adult; sensu Kirkman, 1984). To explain any potential variations in survival rates among the treatments, all urchins present within each block were counted and culled using a knife or hammer. At the conclusion of the experiment, the settlement tiles were collected, and the accumulated turf was scraped off and dried in an oven at 60°C for 48 hours. The dried samples were then weighed before being burnt in a muffle furnace at 400°C for 16 hours to remove the organic fraction and again weighed. The organic component was then assumed to be the difference between the dried and ash masses.

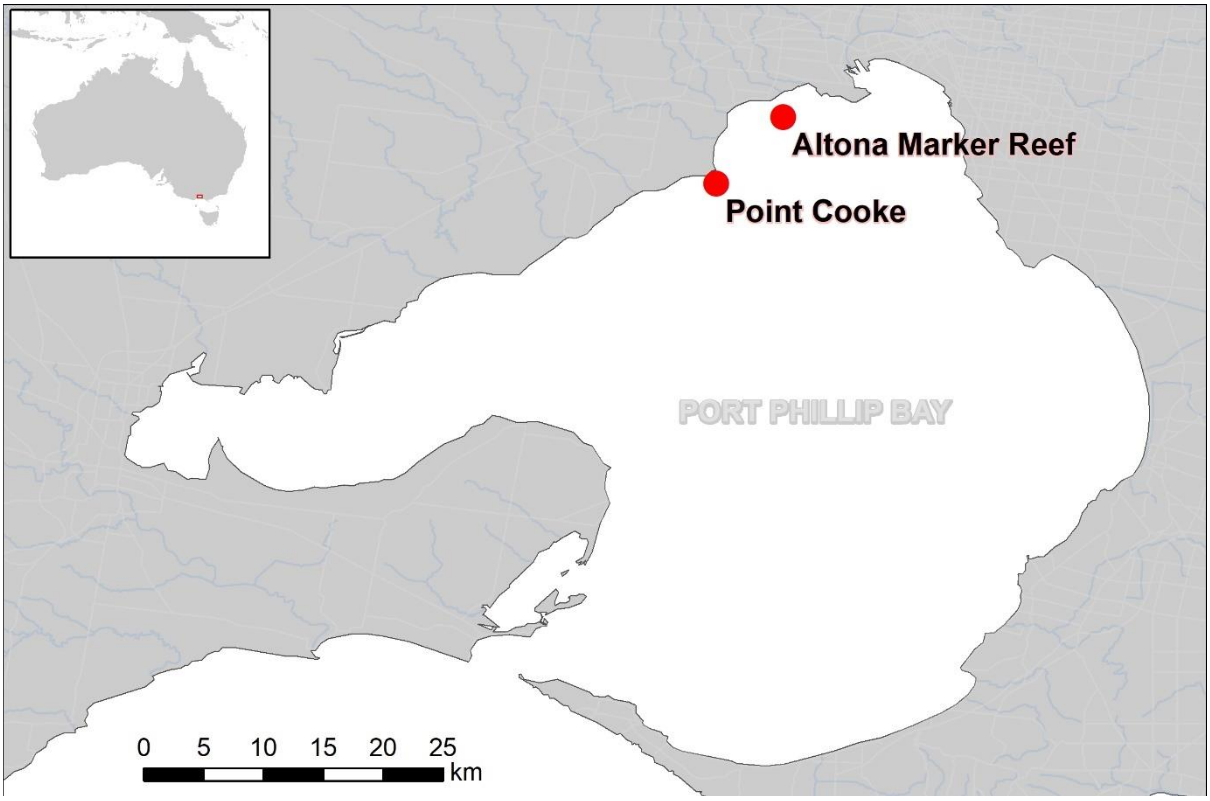

Figure 1 Location of experimental deployments.

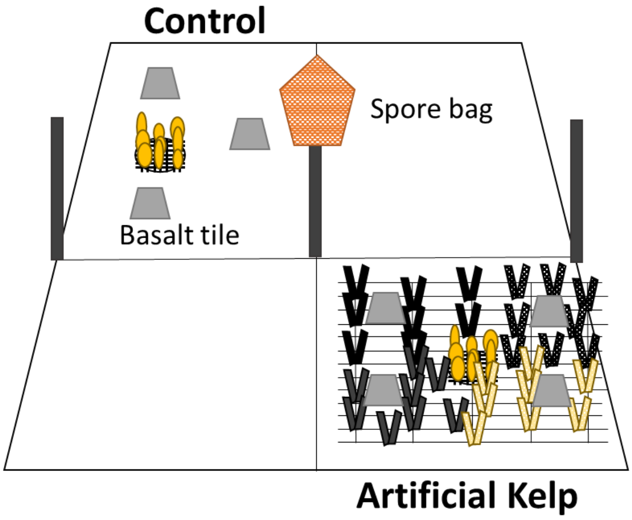

Figure 2 Schematic diagram showing one replicate block in the field experiment. Central star picket had a spore bag (orange pentagon) attached at the top and was adjacent to two 1.5 m quadrats containing either the control or artificial kelp treatments. Within the artificial kelp treatment were four types of artificial kelp (jute, PVC, HDPE, and rubber). Juvenile sporophytes attached to gutter guard were placed in the middle of each treatment, along with the basalt tiles (grey rectangles).

Statistical analysis

Data manipulation and analysis were done in R (v. 4.0.5). A series of GLMs were developed to test the effects of treatment (5 levels: Control, Jute, HDPE, Rubber, PVC) and site (2 levels: Point Cooke, Altona) on organic and inorganic mass accumulation, urchin abundance, juvenile kelp transplant survival and development, and retrieval of artificial kelp, as summarized in Table 1. Site was treated as a fixed factor to detect differences due to receiving environments. The block design was accounted for in the GLMs as a random factor nested within site, allowing treatments to be considered independent. Where no significant effect was observed for individual artificial kelp treatments, they were combined to a single artificial unit of kelp (AUK) treatment to provide additional power in the comparison between AUK and the control.

Organic mass accumulation was modelled (M1) with a single replicate of each treatment (material) per block, so the control was averaged at the block level to produce a balanced model. As individual treatments (material) had no significant effect on inorganic mass accumulation (M2a, $\alpha=0.05$), they were combined into a single artificial kelp treatment. For this model (M2b), the jute treatment was removed, as it was not maintained, leaving three replicates of the artificial kelp treatment, and three replicates of the control. Inorganic mass accumulation in this model (M2b) required a transformation ($^{\wedge}0.1$) to satisfy the Levene's test for homogeneity of variance, as recommended by the BoxCox function in the MASS (v. 7.3.51.5) package (Vernables & Ripley, 2002).

As urchin counts were carried out within the 1.5 m x 1.5 m treatment and control quadrats at each block, no data was collected at the individual material level (M3). An extra random factor was included in this model to account for repeated sampling over time (nMonths). Likewise, juvenile sporophyte transplants were placed at the centre of the artificial kelp treatment, so no material level data were available. As these were only deployed to the Altona site, the factor site was not included in these models (M4, M5). Again, a random factor for time was included. The final model tested the effect of treatment and site on retention of artificial kelp material (M6).

Table 4 Summary of generalized linear models (GLM) developed. M_org = organic mass, M_inorg = inorganic mass, T = Treatment (5 levels: Average control, Jute, HDPE, Rubber, PVC), S = site, B = block, S/(1|B) = random factor of block nested within site, Tx = Treatment (2 levels: Control, Artificial kelp), nUrch = number of urchins in the 2.75 m^2 area of the treatment, pcJuv = percentage of juvenile transplants remaining, SII_or_SIII = number of kelp that have matured to stage II or stage III, Ret = retrieval of artificial kelp, nMonths = number of months since deployment.

ID	**Response**	**Predictor variable(s)**	**Notes**
M1	M_org	T * S/(1|B)	
M2a	M_inorg	T * S/(1|B)	Individual treatments were non-significant, so were combined for greater power in M2b.
M2b	M_inorg$^{0.1}$	Tx * S/(1|B)	Transformation of response variable required to satisfy Levene test for homogeneity of variance.
M3	nUrch	(1|nMonths) * Tx * S/(1|B)	Urchins counted within the 1.5 m x 1.5 m area occupied by all artificial kelp, so no individual material level data available.
M4	pcJuv	nMonths * Tx + (1|B)	No individual material level data available. Juveniles not deployed to Point Cooke.
M5	SII_or_SIII	nMonths * Tx + (1|B)	No individual material level data available. Juveniles not deployed to Point Cooke.
M6	Ret	T * S/(1|B)	This includes both those artificial kelp fronds which were still attached and those that had dropped to the sea floor but were still present within the block.

Results

Flume study

Only one kelp mimic (5b) was observed sweeping 100% of the time for all five wave conditions, while a second (6a) swept 100% of the time for four of the five wave conditions (Table 5). The replicates of these two designs however did much poorer, with average sweeping times less than 30%. Averaging results from replicates, the best designs were #3 (54%), #5 (56%), and #6 (61%), all sweeping more than half the time (Table 5). These all utilized double fronds of 25 mm width, but with different attachment methods and slightly different lengths. In comparison those that used the wider 50 mm fronds (1, 2, 4) had average sweeping times of 0%, 26%, and 10% respectively (Table 5). A width of 25 mm was therefore chosen for the field deployments. Cable ties were used to attach the mimics in the field because the alternative materials used could not be tied or taped like the jute.

Table 5 Percentage of time mimics were sweeping. Kelp designs are listed on the left as (number of fronds x length of fronds in mm x width of fronds in mm and attachment method). T = taped, K = knotted. Design IDs include a or b indicating the two replicates of each design. Wave period and height are listed across the top.

Kelp design	**ID**	**Wave period (s), wave height (mm)**					**Mean**
		3, 47	**3, 71**	**4, 106**	**6, 142**	**5, 170**	
1x300x50T	1a	0	0	0	0	0	0
	1b	0	0	0	0	0	0
1x350x50T	2a	33	67	80	50	3	47
	2b	0	0	7	17	0	5
2x300x25T	3a	40	67	40	60	30	47
	3b	53	67	90	40	57	61
2x300x50K	4a	0	0	0	0	0	0
	4b	0	0	27	33	40	20
2x300x25K	5a	0	0	0	27	37	13
	5b	**100**	**100**	**100**	**100**	**100**	**100**
2x350x25K	6a	**100**	60	**100**	**100**	**100**	92
	6b	0	0	50	63	33	29
4x300x12.5K	7a	0	0	0	7	17	5
	7b	**100**	83	90	**100**	73	89
	Mean	30	32	42	43	35	36

Field deployment

Mass accumulation

Significant interactions were observed between treatment and site in both mass accumulation analyses. For inorganic mass accumulation, this interaction was only significant after combining artificial kelp treatments.

Organic mass. Organic mass accumulation (Figure 3 a) in the control at Altona was significantly higher (2.6x) than at Point Cooke, and was higher than all artificial kelp treatments, significantly against two (PVC and rubber). Despite this clear difference in background organic mass accumulation, artificial kelp treatments across both sites showed no significant differences (Table 6 a).

Inorganic mass. Background rates of sediment accumulation at the two sites were very similar. Mean values of inorganic mass accumulation under artificial kelp trended in opposite directions at the two sites resulting in a significant interaction effect (Figure 3 b). There was insufficient power in the experiment to differentiate treatment from controls, but the mean under the artificial canopies at Point Cooke were significantly higher (2.5x) than at Altona (Figure 3 b).

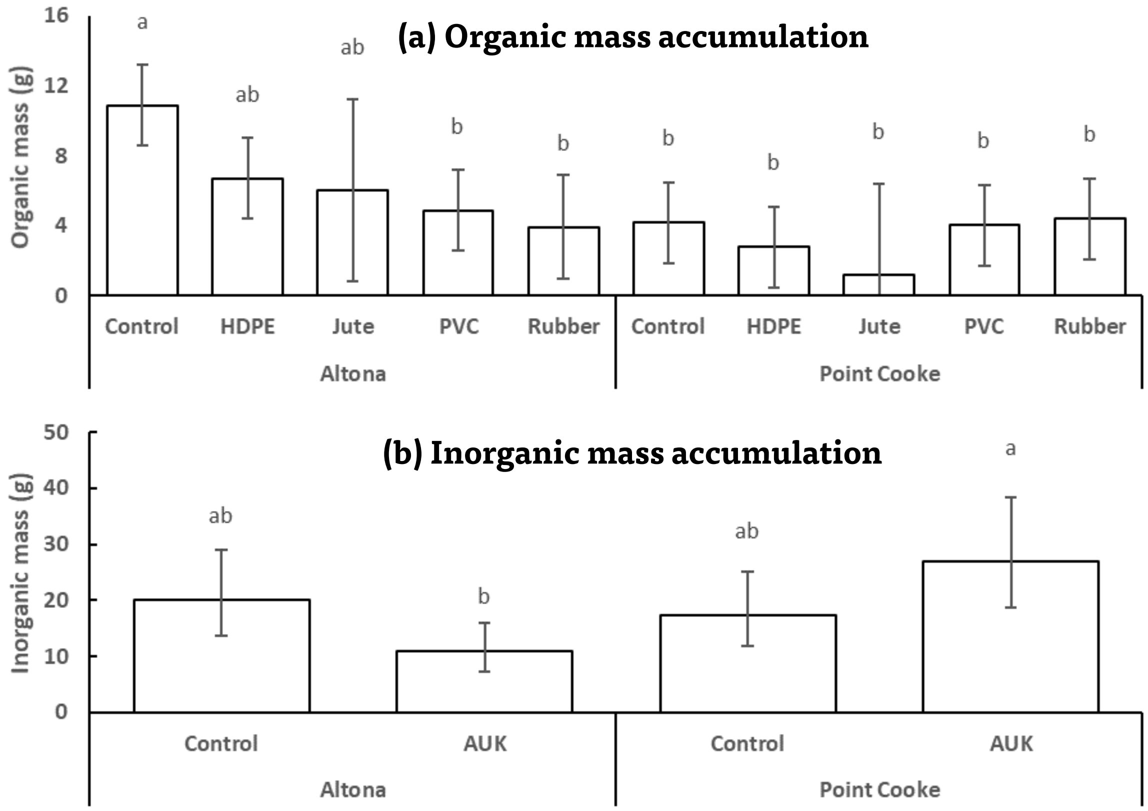

Figure 3 The effect of treatment and site on a) organic, and b) inorganic mass accumulation. All artificial kelp materials were averaged for inorganic mass. Error bars show 95% confidence intervals. Those that do not share a letter are significantly different (α = 0.05).

*Table 6 Analysis of Deviance Tables (Type II Wald χ^2 tests) for (a) organic, and (b) inorganic mass accumulation. Asterisks denote significance at alpha levels: * <0.05; ** < 0.01; *** <0.001.*

(a) Organic mass accumulation

Model term	**χ^2**	**Model df**	**p**	**Sig**
Treatment	10.82	4	2.87E-02	*
Site	14.45	1	1.44E-04	***
Treatment x Site	11.20	4	2.44E-01	*

(b) Inorganic mass accumulation

Model term	**χ^2**	**Model df**	**p**	**Sig**
Treatment	0.11	1	7.44E-01	NS
Site	4.39	1	3.61E-02	*
Treatment x Site	9.23	1	2.38E-03	**

Urchin abundance

There was no effect of treatment or site on urchin densities (Figure 4), with broad confidence bands for both factors. The average urchin density across the control and artificial kelp treatments was around 3.7 m^{-2}, while 95% confidence interval ranges were around 4.1 m^{-2}. The mean urchin density at Point Cooke was almost double (2.0x) that of Altona, but with high variability leading to a 95% confidence range of 10.3 m^{-2} (Figure 4 b).

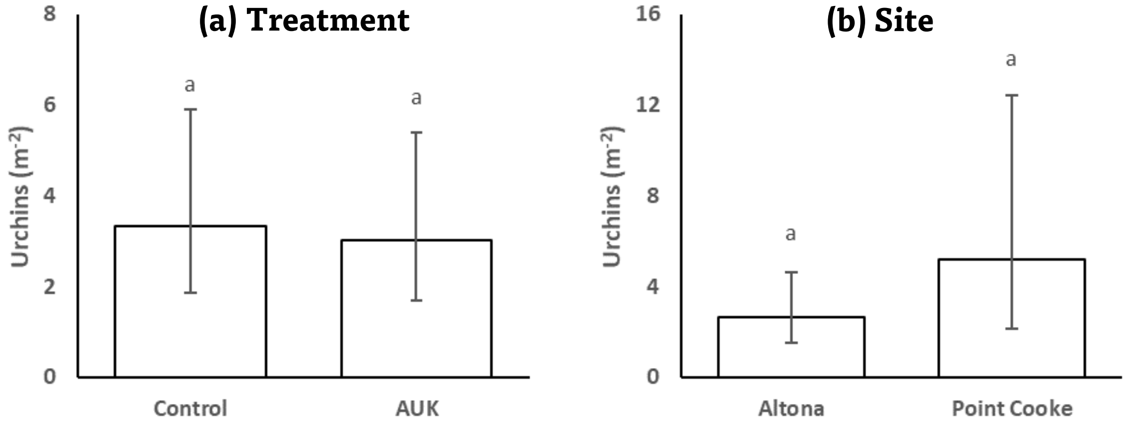

Figure 4 Urchin densities (m^{-2}) across treatments (a) and sites (b). Error bars show the 95% confidence interval. Bars that share a letter are not significantly different.

*Table 7 Analysis of Deviance Tables (Type II Wald χ^2 tests) for urchin density as a function of treatment and site. Asterisks denote significance at alpha levels: * <0.05; ** < 0.01; *** <0.001.*

Urchin density				
Model term	**χ^2**	**Model df**	**p**	**Sig**
Treatment	0.37	1	5.44E-01	NS
Site	1.72	1	1.90E-01	NS
Treatment x Site	0.01	1	9.03E-01	NS

Juvenile kelp survival and development

There was a significant (60%) loss of juvenile kelp transplants in the first month, then no significant loss over the two subsequent months (Figure 5). The presence of an artificial kelp canopy had no effect on survival of transplants (Table 8 a). While significant maturation was observed over the three-month deployment (Figure 6), no significant effect of treatment was observed (Table 8 b). By 3 months all remaining sporophytes had matured beyond stage I.

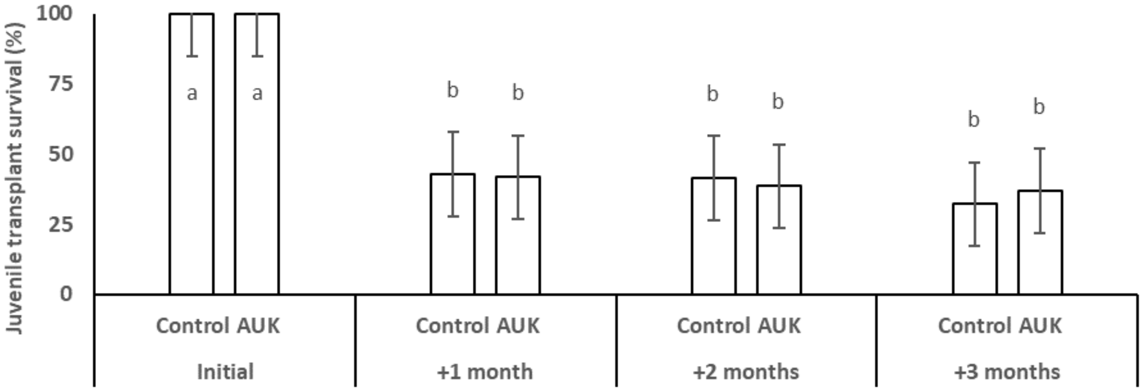

Figure 5 Survival of juvenile kelp transplants over experiment deployment. Error bars show +/- 95% confidence limits. Bars sharing letter show no significant difference.

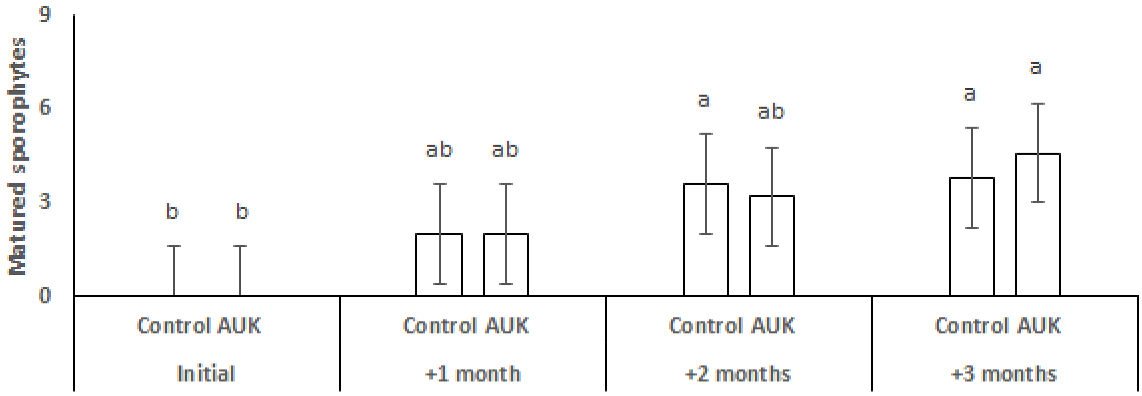

Figure 6 Number of sporophytes matured beyond stage I by month and treatment. Error bars show +/- 95% confidence limits. Bars sharing letter show no significant difference.

*Table 8 Analysis of Deviance Tables (Type II Wald χ^2 tests) for juvenile kelp transplant (a) survivaland (b) maturation as a function of treatment and number of months. Asterisks denote significance at alpha levels: * <0.05; ** < 0.01; *** <0.001.*

(a) Survival of juvenile kelp transplants

Model term	**χ^2**	**Model df**	**p**	**Sig**
Treatment	0.00	1	9.73E-01	NS
nMonths	206.96	3	<2.00E-16	***
Treatment x nMonths	0.59	3	8.99E-01	NS

(b) Maturation of juvenile kelp transplants beyond stage I

Model term	**χ^2**	**Model df**	**p**	**Sig**
Treatment	0.03	1	8.54E-01	NS
nMonths	34.31	3	1.71E-07	***
Treatment x nMonths	0.64	3	8.87E-01	NS

Recruitment from spore bags

No recruitment was observed in control or artificial treatments at either site.

Retrieval of artificial kelp

None of the jute material was retrieved at the end of the experiment. There was no significant difference in retrieval of the other three materials, all averaging between 60 and 80% retrieval, significantly higher than zero (Figure 7). Retrieval rates were not impacted by site (Table 9).

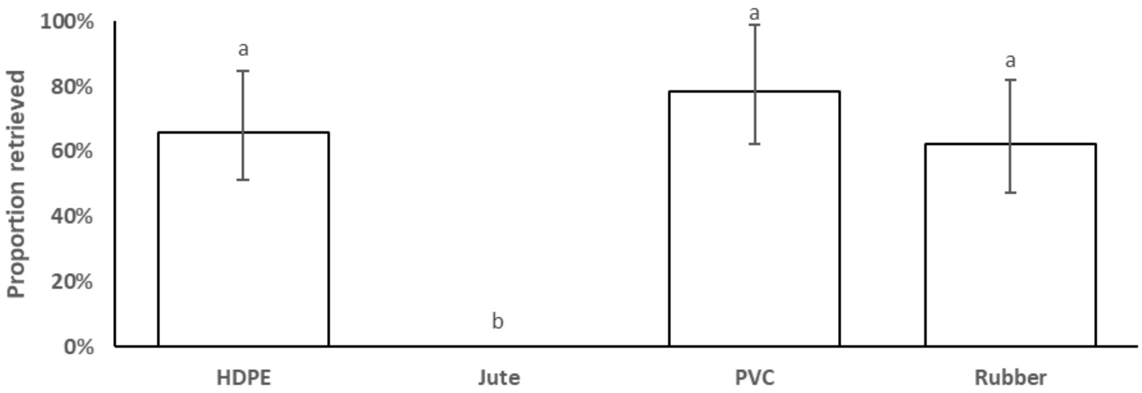

Figure 7 Retrieval rate of different artificial kelp materials. Error bars show 95% confidence limits. Bars that share a letter are not significantly different from one another.

*Table 9 Analysis of Deviance Tables (Type II Wald χ^2 tests) for retrieval of artificial kelp by material and site. Asterisks denote significance at alpha levels: * <0.05; ** < 0.01; *** <0.001.*

Retrieval of artificial kelp				
Model term	**χ^2**	**Model df**	**p**	**Sig**
Material	34.44	3	1.60E-07	***
Site	0.00	1	1.00E-00	
Material x Site	3.06	3	3.82E-01	

Discussion

Enhanced recruitment under artificial canopy

Adult kelp canopies provide at least four important mechanisms to support recruitment: provision of bare substrate by sweeping fronds under hydrodynamic flow (Burek et al., 2018; Layton et al., 2019); shading to light levels preferred by gametophytes for settlement (Tatsumi & Wright, 2016); spore supply; and reduced flow rate allowing spore settlement (Graham, 2003). This can lead to vastly higher (10x) recruit densities under a kelp canopy than a control with no canopy (see Chapter 4). My artificial kelp had the potential to provide three of these mechanisms, with the spores instead supplied via a spore bag containing fronds with sporophylls from ten adult sporophytes in the centre of each block (Dayton et al., 1984). No natural recruitment however was observed at either site in either the control or treatment tiles, nor the reef within each treatment. There are two possible factors that could have led to this result, either insufficient spore settlement densities or a lack of suitable substrate. Both hypotheses were tested in Chapter 4, by repeating the experiment in an extant bed where spore settlement densities were likely to be much higher, and by providing a vertical substrate which does not accumulate sediment, thus potentially maintaining suitable conditions for recruitment. These modifications resulted in average recruit densities under artificial kelp being five times greater than in controls (see Chapter 4).

Protection of juvenile transplants

Adult kelp canopies provide protection for juvenile sporophytes in the understorey by shading, producing drift (for urchins to eat instead of live fronds), and importantly deterring herbivores through lashing by fronds (Konar & Estes, 2003; Toohey & Kendrick, 2007; Kriegisch et al., 2019). Other macrophyte mimics have improved transplant survival through herbivory reduction and sediment stabilization (Campbell & Paling, 2003; Tuya et al., 2017). With my jute kelp mimic based on real frond dimensions and optimised for a sweeping motion under wave conditions, I expected to achieve some of this protective effect. Unfortunately, no effect was observed on either juvenile transplant survival or development in this study. The late change of material may have made the flume testing redundant, as various materials used to replace jute (rubber, PVC, and HDPE) may behave differently under the same flume wave forcing. About half the juveniles perished in the first month, followed by little loss by the end of the experiment. This is consistent with procedural losses such as from handling and attachment, but also suggests direct herbivore pressure may not have been intense enough to detect a protective effect. A similar lack of a protective effect was observed in a transplant experiment where alternative algae were abundant on the reef (Graham et al., 2021). The rapid loss of all adult kelp transplants to Point Cooke to herbivory drove my decision not to deploy juveniles to that site. In hindsight this may have provided an opportunity to test for any protective effect of the artificial kelp under intense herbivore pressure.

Effectiveness of frond sweeping

My results suggest the background rate of inorganic mass accumulation is very consistent at the two sites. The inorganic mass accumulation under artificial kelp at Point Cooke, however, was significantly higher (2.5x) than at Altona. This may have been the result of fine scale hydrodynamic differences between the two sites due to reef topography. The boulder reef at Altona may have concentrated wave energy resulting in flow rates capable of inducing the sweeping motion of the artificial kelp, while at Point Cooke the artificial kelp may have simply reduced flow rates without sweeping, acting similarly to the sediment trapping artificial seagrass mats used in seagrass restoration (Carus et al., 2021). This highlights the sensitivity of using a structure like my artificial kelp in slightly different hydrodynamic conditions, and raises more questions about how such effects may change with patch size (Layton et al., 2019). As with the adoption of porous media for sediment accumulation over a seagrass mimic (Fivash et al., 2021), future work should focus on provision of the service of sweeping, without necessarily mimicking the structure of the kelp sporophyte (van der Heide et al., 2021). For example, by using anchored and buoyed chains that can rub across the reef.

Given the lack of effective sweeping, it is not surprising that the artificial kelp also failed to deter urchins. This lack of effect may have been further enhanced by the large variance in urchin densities at the spatial scale of my experiment. As the sweeping and lashing motions were the mechanism for provision of clear substrate free of urchins, it follows that without achieving these, the expected improvements to recruitment and juvenile protection would also be lost.

Material selection for fronds

Early in the setup of the field experiment it became obvious that the jute design was unsuitable. It became heavily fouled, mostly with filamentous algae, and broke apart quickly. The limited time it was deployed in the wave flumes, and the clean water used, meant that it worked well under laboratory conditions, but conditions in the Bay were quite different. By the end of the third month, no jute remained. In comparison, roughly 60-80% of the other materials were retrieved at the completion of the experiment. The natural decay of the jute could be considered beneficial if done over an appropriate time frame, such as after new recruits or juvenile transplants have grown to provide the same sweeping (van der Heide et al., 2021). Modifications may also need to be considered to reduce fouling which can cause the artificial kelp to droop and potentially not provide the required sweeping (Harris & Chester, 1996).

The performance of the jute kelp is therefore difficult to establish. It produced the widest 95% confidence intervals for mass accumulation, potentially due to conditions varying more across the deployment, initially with all artificial fronds present, reducing to none at the end. Although rubber could be used as a natural alternative to jute, as it performed similarly to the two plastic artificial kelp, further research could be undertaken into preventing the jute strips from unravelling, such as applying epoxy to the cut ends.

Considerations for field deployments

The use of chicken wire in the wave flume was successful, but in the field, I had difficulties securing it to the bed. While it did conform well to the contours, it was flexible enough to bend off pegs and thin enough to pull through epoxy. Bungee ties worked well to secure the chicken wire on individual boulders but stretching over multiple boulders resulted in the wire sitting well above the bed in some areas. I instead progressed to a stronger fencing wire 2 mm thick which held its shape when bent. The 320 x 110 mm openings also meant fronds of the artificial kelp had more sweeping access to the reef, and I disturbed the reef less when removing the fencing at the end of the experiment. The condition of the fencing wire at the end of the experiment was not suitable for redeployment, so additional materials would need to be purchased when extending the restoration area.

The ecological benefits of effective sweeping are clear, but further work is required to develop a design that provides effective sweeping under the necessary conditions. It is possible a more practical design may be achieved which is not based on the size and shape of real kelp. For example, weighted and buoyed ropes may provide the necessary scouring effect, much like the scour rings around moorings, however care would need to be taken to ensure excessive scour is avoided (Broad et al., 2020). The simplicity of such a design would allow it to be used at greater scale and be adapted to different reef geometries.

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Supplementary

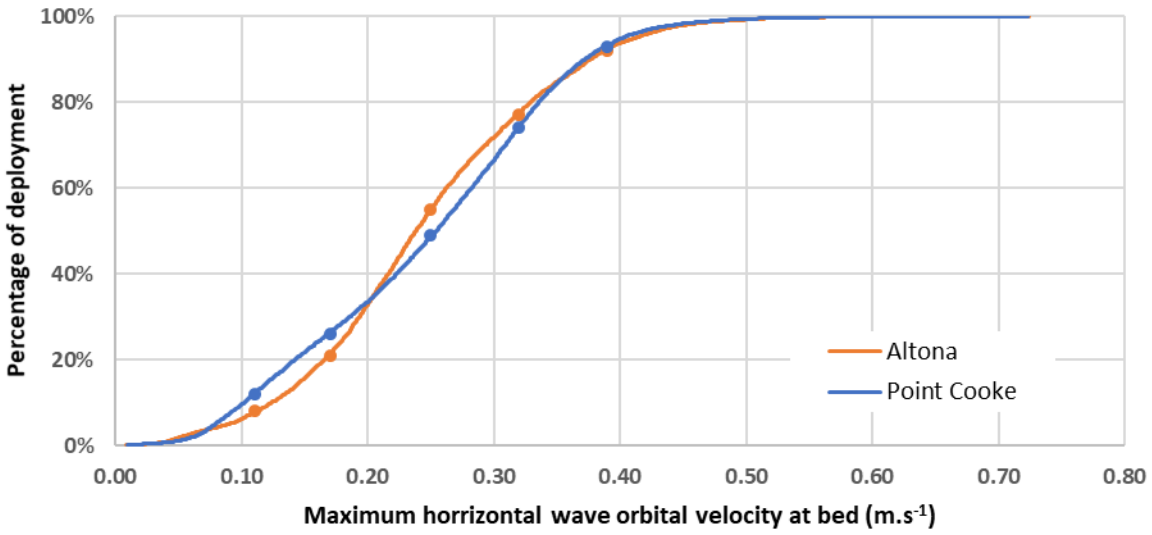


Figure S1 Cumulative distribution of wave orbital velocities at the bed for deployment sites, derived from hydrodynamic model. Points indicate the orbital velocities tested in the flume study.

CHAPTER 4 - RECRUITMENT PATTERNS AND EFFECTS OF OVERSTORY CANOPY AND SUBSTRATE ORIENTATION ON RECRUITMENT SUCCESS OF THE KELP *ECKLONIA RADIATA*: IMPLICATIONS FOR RESTORATION

Abstract

Kelps are a primary habitat forming species, providing a range of ecological services. Their declines across the globe, along with the services they provide, highlight the need for their restoration. Recruitment of new kelp is essential for the long-term survival of kelp beds. It is important, therefore, to understand the environmental conditions and spatial scales over which recruitment is likely. I undertook surveys to investigate the distance from existing kelp beds that recruitment was occurring and how that was related to current speeds. I also looked at how local factors of substrate orientation and canopy cover affect recruitment, along with some possible explanatory mechanisms (sediment accumulation and light reduction). I observed rapidly reduced recruitment with distance from the kelp bed, down to 0.05 m^{-2} at between 26 and 85 m from the bed. The distance from the bed was not explained by current speeds. *Ecklonia radiata* recruited most successfully to vertical substrates and

under a natural canopy; treatments with reduced sediment accumulation and reduced light. This study demonstrates both supply and non-supply side effects on recruitment, while highlighting an incomplete understanding of the processes driving successful recruitment.

Introduction

A decade of restoration has been declared to address observed degradation of ecosystems worldwide (UN General Assembly, 2019). As habitat forming species are the basis of many ecosystems, they are a particularly important component to consider in ecosystem restoration. On temperate marine reefs, kelps (order Laminariales), along with other canopy forming Fucoids, are the primary habitat forming species (Teagle et al., 2017). Kelps have among the fastest growth rates of any species on Earth and are often likened to terrestrial tropical rainforests for their support of high biodiversity (Darwin et al., 1839; Rassweiler et al., 2018). They also provide a range of ecological services including water treatment, commercial fishing, tourism and recreation, as well as spiritual and cultural values (Whiteoak et al., 2020; Andrews, 2023). Observed degradation of kelp forests in many regions of the world, along with the ecosystem services they provide, highlights the need for their restoration (Wernberg, Krumhansl, et al., 2019).

Several approaches have been trialled for restoration of kelps and Fucoids, that vary depending on the species, key stressors leading to their decline, and the current state of the reefs. In some cases, the removal of stressors, such as overgrazing of herbivores (sometimes associated with overfishing of their predators), or high nutrient levels, may be sufficient to see natural recovery of kelp beds (Breen et al., 1982; Gorman & Connell, 2009; Ling et al., 2010; Lefcheck et al., 2018). In other cases, such as when kelps have been lost from a region, and natural recolonization is unlikely due to the typically short dispersal distances of spores, more active approaches may be required (Wernberg, Krumhansl, et al., 2019). Provision of spore sources in the form of mesh bags full of reproductive tissue, known as spore bags, is one method of providing spores where natural supply is limited (Dayton et al., 1984). Local spore supply can also be artificially enhanced by transplanting adult kelp, which may provide additional services such as sweeping of the substrate and altering small scale hydrodynamics that can increase spore settlement and survival (Kennelly, 1989; Graham, 2003). Mimics of adult kelp may provide these additional services without the added financial and environmental costs associated with removal of adult kelp from an existing reef or the cultivation of kelp. Such an approach has been successfully applied to modify sediment grading and reduce herbivory in the restoration of seagrass (Campbell & Paling, 2003; Tuya et al., 2017). To identify which method(s) may be suitable, restoration projects should first consider if the environmental conditions of the site will enable natural recovery, as well as the status of local populations of the target species to determine the likelihood of recovery and the spatial scales over which it is likely to occur.

Assessing the status of local populations is challenging, as kelp beds are inherently dynamic, with shifts in spatial distributions often clearly visible year to year (North, 1976; Bell et al., 2020). Persistence of the bed is therefore contingent on successful recovery after disturbance, including expansion by recruitment beyond the boundary of the remnant bed (Ambrose & Nelson, 1982; Dayton et al., 1992; Deiman et al., 2012). Successful recruitment, normally determined at a point when juvenile sporophytes are visible to the naked eye, is a measure that includes spore settlement, the production, growth and fertilization of gametophytes, and the production, growth, and survival of sporophytes until the point of observation (sensu Keough & Downes, 1982). The specific environmental requirements of each of these life stages must therefore be met for successful recruitment, and hence persistence of the kelp bed.

While suitable environmental conditions are important, recruitment can still be limited by kelp spore supply. Not only do spores need to be present, but their concentration must be sufficiently high, so the developing male and female gametophytes are close enough for fertilisation to occur. While this can lead to some decoupling of the relationship between spore dispersal and recruitment, a clear relationship is still expected between recruitment and distance from the source kelp bed (Gaylord et al., 2006). When environmental conditions in unvegetated areas are suitable for recruitment, kelp recovery is likely to be a function of source spore density and currents that transport those spores across the area of interest. When recruitment declines with increasing distance from remnant beds, this would be consistent with recovery being dependent on local spore supply. Such relationships can be used to inform where additional interventions, such as the provision of spore bags, may be required.

For a restoration project to be successful, it must ultimately restore this natural recovery process, with minimal ongoing intervention (Morris et al., 2020). Restoration efforts would therefore be aided by an understanding of the environmental requirements for each life stage, and how these can be identified or facilitated in the field. Kelps generally require hard substrate to recruit onto, with excess sediment accumulation blocking access to this hard substrate and possibly smothering early life stages (Devinny & Volse, 1978; Dayton et al., 1984; Dayton, 1985; Airoldi, 2003; Strain et al., 2014). Previous observations of the impact of kelps on their local environment point to positive feedbacks, such as sweeping of the substrate by fronds by species like *Ecklonia radiata* in cases of high sediment load, and reduction of local water velocity, which can promote successful recruitment (Mohring et al., 2013; Mohring et al., 2014). The lack of these positive feedbacks away from existing beds may slow the expansion of kelp beds particularly in sediment or nutrient rich systems with high grazing pressure (Velimirov, 1984). Attempts at improving habitat suitability for successful recruitment through transplanting adult kelp, however, may have adverse impacts on donor reefs, be limited by supply, or show little success due to rapid herbivory (Layton et al., 2020; Graham et al., 2021). A kelp mimic may address these issues if they can provide similar services of sweeping, current reduction, and shading. Alternatively, the presence or addition of vertical substrate may be an alternative intervention to ensure the provision of suitable habitat for recruitment.

Ecklonia radiata (Agardh, C.) Agardh J., is the primary habitat forming kelp across Australia's Great Southern Reef, occupying open coasts, islands, and bays, and providing primary production and habitat in a range of environmental conditions (Dayton, 1985; Wing et al., 2007; Miller et al., 2011; Coleman, 2013; Krumhansl et al., 2016). Observed declines have been linked to heat waves and the migration of tropical herbivores from the north (Wernberg et al., 2016; Zarco-Perello et al., 2017), as well as eutrophication and over-abundances of the purple urchin *Heliocidaris erythrogramma* and long-spine urchin *Centrostephanus rodgersii* (Ling, 2008; Filbee-Dexter & Wernberg, 2018; Carnell & Keough, 2019). Reefs without *E. radiata* tend to exist in one of three alternate stable states depending on environmental conditions; urchin barren, sediment-turf matrix, or other mixed macroalgae (Wernberg, Krumhansl, et al., 2019). The first two of these states show reduced structural complexity and value for economically important fisheries (Filbee-Dexter & Scheibling, 2014; Filbee-Dexter & Wernberg, 2018; Chapter 2). Although no full-scale restoration effort has been undertaken for this native kelp, recent research investigating nutrient impacts, controlling urchin densities, and kelp patch dynamics provide useful knowledge to inform management of the drivers of kelp forest degradation (Layton et al., 2019; Ling et al., 2019).

Here I report on my observations of the abundance of kelp recruits relative to existing kelp beds to understand the spatial scale of recruitment, testing whether abundance declines with distance from the bed (due to reduced spore supply), and if so, whether the scale of recruitment can be explained by spore production and advection by local currents (simulated by a coupled hydrodynamic-spectral wave model). To explore drivers of variation in recruitment success at a more local level, I undertook a manipulative experiment within the kelp beds, investigating the independent and interactive effects of two environmental conditions on recruitment success: 1) the presence of a canopy; 2) and the provision of vertical surfaces. I predicted that both the canopy and the vertical substrate would result in higher recruitment, due to reduced sediment accumulation (through sweeping / falling off). I expected the effect of surface orientation would be greater in the absence of a canopy. I also tested whether a kelp canopy mimic can provide similar services to a natural E. radiata canopy (and thus similar recruitment success), as a practical alternative restoration approach where a kelp bed is not present.

Methods

Field surveys

Surveys were carried out at Point Linley (145°02′ E, 38°13′) and Williamstown (144°54′ E, 37°52′) to determine distances that E. radiata sporophytes could be found (i.e., successfully recruited) from natural kelp beds on rocky reefs. At each site, a 100 m transect tape was laid cross-shore through an existing kelp bed extending in both directions. A second 50 m transect tape was placed normal to this, running longshore and crossing the first transect near the densest part of the kelp bed. The rationale for these normal transects was to ensure the distances of observed recruitment from the bed were not biased by currents. Depth averaged current speeds were extracted at each site for a one-year period from a calibrated coupled hydrodynamic-spectral wave model of Port Phillip Bay Wave (Tran, 2020). These were tested as an explanatory factor in recruitment, with the expectation that stronger currents could support recruitment at a greater distance from the kelp bed. Along each transect, all kelp sporophytes within 2 m of either side of the transect tape were counted, with their stage and distance along the transect (chainage) recorded. Stage I sporophytes were defined by a single oblong blade, stage II sporophytes by simple and entire secondary blades, and stage III by compound lateral blades (sensu. Kirkman, 1984). Where kelp density was too high to carry out this method, the transect width was reduced to 1 m either side and the data were then binned into 5 m lengths and converted to sporophyte densities (m^{-2}) for each stage. Each bin, therefore, represented an area of 20 m^2, so the minimum detectable density was 1/20 m^{-2}. An initial survey at Point Linley was undertaken in late September 2019, but no data were collected at Williamstown as juvenile sporophytes were not observed during dives at that time. On 16-July-2020, a pre-recruitment survey was undertaken at both sites, finding only 2 stage I sporophytes, confirming that those identified in the post-recruitment survey would be new sporophytes rather than ones that had sat idle over winter with stunted growth. The final surveys were carried out on 07-October-2020 (Point Linley) and 14-December-2020 (Williamstown).

As the edge of the kelp bed was not always distinct, I tested the effects of different edge locations based on different adult density thresholds (from 1 m^{-2} to 5 m^{-2}) on the abundances of *E. radiata* recruits. The model with 4 adult sporophytes per square metre returned the lowest information criteria (AIC and BIC) scores and was therefore adopted as the most appropriate threshold. Generalized linear models (GLM) were then developed in R (v. 4.0.0) using the glmmTMB (v. 1.0.1) package (Brooks et al., 2017; R Core Team, 2020). I tested the effect of direction (fixed, 2 levels = longshore vs. cross-shore), distance from the edge of the bed (covariate, m) and site (fixed, 2 levels = Williamstown vs. Point Linley) and the interaction between these factors on the density of kelp recruits. Site was included as a fixed factor as the current and wave climates varied between them, and these were expected to be the key drivers of recruitment distances. Point Linley is more exposed to strong tidal currents and swell, while Williamstown is mostly exposed to wind waves. The density of stage I juveniles was transformed ($nSI^{0.1}$) to conform to the assumption of normality based on a BoxCox test using the MASS (v. 7.3.51.5) package (Vernables & Ripley, 2002). A lower-bound density threshold of 0.05 m^{-2} was adopted for determining the recruitment distance from the bed, since this is the minimum density detectable with the chosen survey method (i.e., 1 sporophyte in the 20 m^2 transect section).

Manipulative experiment

A manipulative field experiment was undertaken to determine the effects of canopy type and substrate orientation on the recruitment of kelp within a remnant bed. The experiment was undertaken at Williamstown (144°54′ E, 37°52′) in the north of Port Phillip Bay, Victoria, Australia. The reef is a basalt flow with crevices and boulders, with a maximum depth of around 3.5 m. At the end of March 2019, 24 blocks, marked with star pickets, were evenly spaced at 4 m intervals across the kelp bed, and each block (0.5 m radius around star picket) was randomly assigned to one of three canopy treatments: control (i.e., no canopy), *E. radiata*, or kelp mimics. At the start of April 2019 (Austral autumn) all existing canopy algae were removed from blocks assigned to kelp mimic and control treatments, while those in blocks at the *E. radiata* treatments were counted but not removed. For the kelp mimic treatment, chicken wire squares (900 mm x 900 mm) were placed on the reef and used to anchor 8 artificial kelp plants, giving a density over the tiles of 18 m^{-2}, matching the mean observed *E. radiata* density in the *E. radiata* treatment. The kelp mimics were made of two 600 mm x 25 mm HDPE strips of 500 µm HDPE folded in half and cable tied at the base (see Chapter 3). Within each block, 4 basalt tiles (300 mm x 150 mm x 30 mm) were placed as a standardised recruitment substratum for the kelp, with 2 tiles placed vertically lengthwise and cable-tied to the star picket, and 2 tiles placed horizontally on the reef next to the star picket. These were used to identify variations in recruitment based on substrate orientation (e.g., due to differences in light and sedimentation), ensuring observed juvenile abundance represented the full recruitment process from newly settled spores. All adult *E. radiata* within a 2 m radius of each star picket were counted as a proxy measure for spore supply. There was no significant difference in the abundance of adult kelp surrounding each treatment ($\chi^2 = 3.38$, df = 2, $Pr > \chi^2 = 0.184$), hence spore supply was considered equal across treatments.

Canopy treatments were maintained, and all tiles were monitored for visible *E. radiata* sporophytes on 8 occasions from mid-April 2019 until recruits were visible at most of the blocks at the end of November 2019. Light (illuminance) and sediment accumulation (dry mass) were measured as potential explanatory factors. Light under each of the canopy treatments was measured using HOBO light-temperature pendant loggers deployed in pairs (one on a vertical tile, and the other on a horizontal tile) attached with cable ties in a block of each canopy treatment. This allowed the relative light conditions to be approximated for each canopy treatment – tile orientation pair. The loggers were moved 4 times, recording at 15 out of the 24 blocks. Tiles were removed in mid-December 2019 and non-kelp algae were picked off by hand and stored. *E. radiata* sporophytes were identified by eye and classified according to which tile surface (face or edge) they had recruited to. The classified counts were then pooled across vertical and horizontal surfaces, and separately for the primary face (largest exposed face) only for further analysis. The accumulated sediment and microalgae were scraped off and stored for later analysis in the lab, where they were dried for at least 24 hrs at 60°C and weighed.

A series of generalized linear models (GLM) were used to test recruitment variation as a function of canopy treatment and surface orientation; and to investigate the potential explanatory factors of sediment accumulation and light (Table 1). All analyses were undertaken in R (v. 4.0.0) using the glmmTMB (v. 1.0.1) package, analyses of deviance/variance were assessed with the car (v. 3.0.8) package, and pairwise comparisons were tested using the lsmeans (v. 2.30.0) package with Tukey HSD adjustments (Lenth, 2016; Brooks et al., 2017; Fox & Weisberg, 2019; R

Core Team, 2020). Significance was determined with a Type I error threshold of $\alpha = 0.05$.

To test the effects of canopy and substrate surface orientation on juvenile recruitment, all *E. radiata* sporophytes identified on the vertical and horizontal surfaces, at the block level, were summed across all four settlement tiles. This juvenile count was fitted using a negative binomial model as a function of surface orientation and canopy treatment as well as interactions between the two. Block was added as a random factor to account for the nesting of surface orientation within a given location and canopy treatment. A natural log area offset was applied to account for differences in available horizontal and vertical surface resulting from ends of tiles always being vertical surfaces.

The effects of canopy treatments and tile orientation on sediment mass accumulation were tested using a GLM with a Gaussian fit. Mass accumulation per tile was transformed ($m^{-0.4}$) to conform to the normal distribution assumption based on a BoxCox test using the MASS (v. 7.3.51.5) package with the value rounded to one decimal place (Vernables & Ripley, 2002). Tile orientation and canopy treatment and their interaction were tested, and block was again included as a random factor.

The effect of canopy treatment and tile orientation on illuminance was tested using a GLM with a Gaussian fit. The selected measure for light was average illuminance between 08:00 and 16:00. Random factors of Block and Logger were included, and light was transformed ($E^{0.1}$) based on a BoxCox test.

Table 1 Summary of generalized linear models (GLM) developed. n_1 *= number of juveniles observed at the block level for a given surface orientation,* n_{SI} *= number of juveniles observed on the primary surface of tiles,* $m^{-0.4}$ *= transformed dry mass of accumulated sediment,* $E^{0.1}$ *= transformed average illuminance (lux), C = canopy treatment,* $O_{Surface}$ *= surface orientation,* O_{Tile} *= tile orientation,* O_{Light} *= light orientation, A = available area, B = blocking term linking data points at a given treatment. * = both individual and interaction terms, a/b = b nested within a, (1|a) = a is a random (intercept) factor with no gradient.*

ID	Response	Predictor variable(s)	Purpose
M1	n_1	$C * O_{Surface} + (1\|B) + \text{offset}(\ln(A))$	Test the effects of canopy treatment and surface orientation on recruitment.
M2a	$m^{-0.4}$	$C * O_{Tile} + (1\|B)$	Test the effects of canopy treatment and tile orientation on sediment accumulation.
M2b	$E^{0.1}$	$C * O_{Tile} + (1\|B) + (1\|\text{logger})$	Test the effect of canopy treatment and tile orientation on light conditions.
M03a	$n_{SI}^{0.1}$	Site * Direction * DistEdge + (1|Year)	Test to determine which factors and interactions are important.
M03b	$n_{SI}^{0.1}$	DistEdge + Direction + (1|Year)	Test the effect of distance from bed and direction on recruitment densities at each site.

Results

Survey results

The model indicated that the effect of distance from the edge of the kelp bed (distEdge4) was significant, with a reduction in juvenile abundance away from the beds. This effect, however, along with the effect of direction (shore parallel / shore normal), varied significantly with site (i.e., interactions were present). No significant interaction was observed between the distance from the bed and the direction. Splitting of the model by site then allowed the removal of all interaction terms, simplifying the model to only just two parameters: direction, and distance from the bed (Table 2). Juvenile densities at Point Linley declined rapidly with distance from the kelp bed, from 1.02 to 0.05 m^{-2} at 26 m from the bed in the cross-shore direction and from 2.27 to 0.05 m^{-2} at 35 m from the bed in the longshore direction (Figure 1). The decline in juvenile density at Williamstown was more gradual, from 1.04 to 0.05 m^{-2} at 85 m from the bed in the cross-shore direction and 0.28 to 0.05 m^{-2} at 45 m from the bed in the long-shore direction.

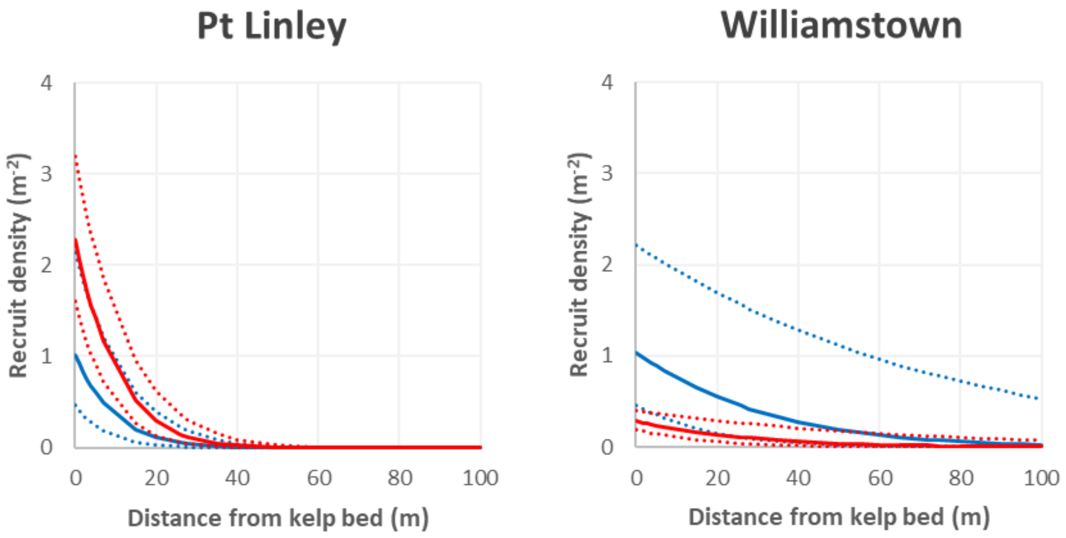


Figure 1   Fitted model results for juvenile density with distance from kelp bed at Point Linley (left) and Williamstown (right). Colours denote transect direction; cross-shore (blue) or along-shore (red). Dotted lines indicate +/- 1 S.E.

*Table 2 Analysis of Deviance Tables (Type II Wald χ^2 tests). Asterisks denote significance at alpha levels: * <0.05; ** <0.01; *** <0.0001.*

Initial model to find required terms:

Model term	**χ^2**	**Model df**	**p**	**Sig**
Site	0.59	1	4.44E-01	
distEdge4	46.31	1	1.01E-11	***
Direction	0.74	1	3.90E-01	
Site x distEdge4	7.16	1	7.46E-03	**
Site x Direction	8.17	1	4.26E-03	**
distEdge4 x Direction	0.00	1	9.76E-01	
Site x distEdge4	0.57	1	4.49E-01	

Point Linley model:

Model term	**χ^2**	**Model df**	**p**	**Sig**
distEdge4	43.14	1	5.10E-11	***
Direction	4.45	1	3.49E-02	*

Williamstown model:

Model term	**χ^2**	**Model df**	**p**	**Sig**
distEdge4	3.51	1	6.10E-02	
Direction	6.85	1	8.88E-03	***

Manipulative experiment

There were significant effects of canopy treatment and surface orientation on recruitment, sediment accumulation, and the light conditions, but no significant interaction between canopy treatment and surface orientation for any of the variables (Figures 2-4, Tables 4-6).

Recruitment

My results showed that kelp recruitment under *E. radiata* was significantly higher (8x) than the control, while the slightly higher (5x) recruitment under the artificial kelp was not statistically significant (see Figure 2a). Recruitment to vertical surfaces was significantly higher (10x) than that of horizontal surfaces (see Figure 2b). Despite the lack of a significant interaction, vertical surfaces under an *E. radiata* canopy had 100x higher recruitment than horizontal surfaces without a canopy.

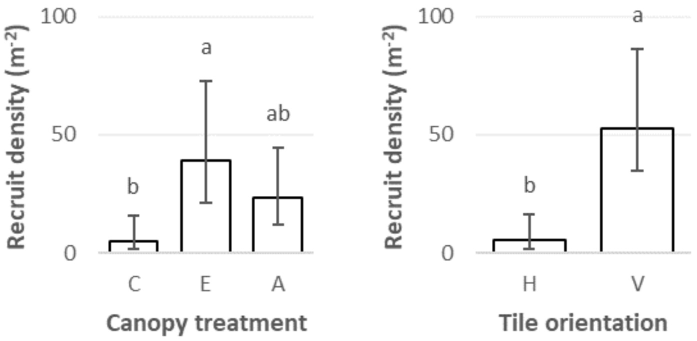


Figure 2 Mean density of recruits (m^{-2}) as a function of canopy treatment (left), and orientation (right). Tests were performed on the log scale. Bars indicate the 95% CI for the EM means. Means sharing a letter are not significantly different. C = Control (no canopy), E = E. radiata, A = Artificial kelp, H = Horizontal surface, V = Vertical surface.

Dry mass accumulation

Significantly lower sediment accumulation was observed on vertically oriented tiles (0.3x), and those under the *E. radiata* canopy (0.5x) compared to the control (Fig 3). However, sediment accumulation under the artificial kelp canopy was almost identical (0.9x) to that of the control. No significant interaction was observed between orientation and canopy.

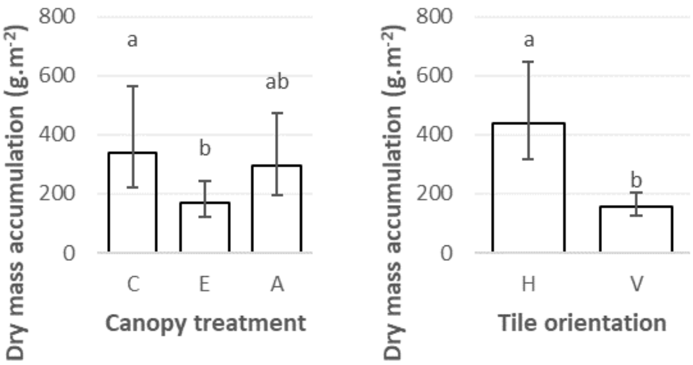


Figure 3 Dry mass accumulation (g) as a function of canopy treatment (left), and tile orientation (right). Bars indicate the 95% CI for the EM means. Means sharing a letter are not significantly different. C = Control, E = E. radiata, A = Artificial kelp, H = Horizontal surface, V = Vertical surface.

Light conditions

The *E. radiata* canopy reduced (0.3x) light levels significantly compared to the control, however, the artificial kelp canopy had no significant effect on light levels (1.3x) compared to the control (Fig 4). Light conditions on the vertical tiles were also significantly reduced (0.4x) compared to the horizontal tiles. No significant interaction was observed between orientation and canopy.

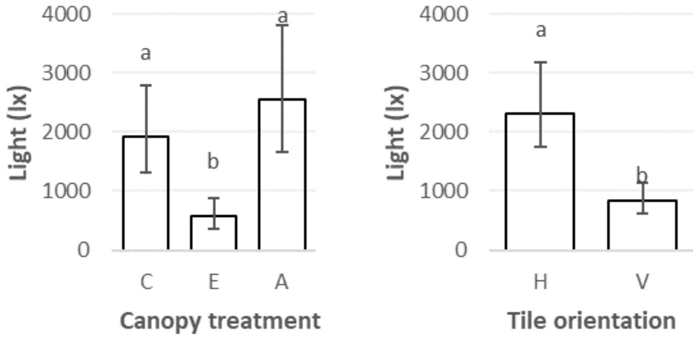


Figure 4 Average illuminance under each canopy treatment (left). Average illuminance by tile orientation (right). Bars indicate the 95% CI. C = Control, E = E. radiata, A = Artificial kelp, H = Horizontal tile, V = Vertical tile.

Discussion

Abundance of *Ecklonia radiata* juvenile kelp declined with distance from extant beds, indicating spore-supply limitation in this system, however, the distance juvenile kelps extended from the beds was not well explained by the prevailing local currents. Within the kelp beds, *E. radiata* recruited most successfully to vertical substrates and under a natural canopy; treatments with reduced sediment accumulation and reduced light. A non-additive positive effect on recruitment was expected of the *E. radiata* canopy with vertical substrate, with both relying on the mechanism of reduced sediment accumulation, however, this interaction was not observed, with the treatments instead showing an additive effect. The artificial kelp saw higher recruitment than the control despite having little impact on sediment accumulation or light. Combined, these results demonstrate both supply and non-supply side effects on recruitment, while also highlighting an incomplete understanding of the processes driving success.

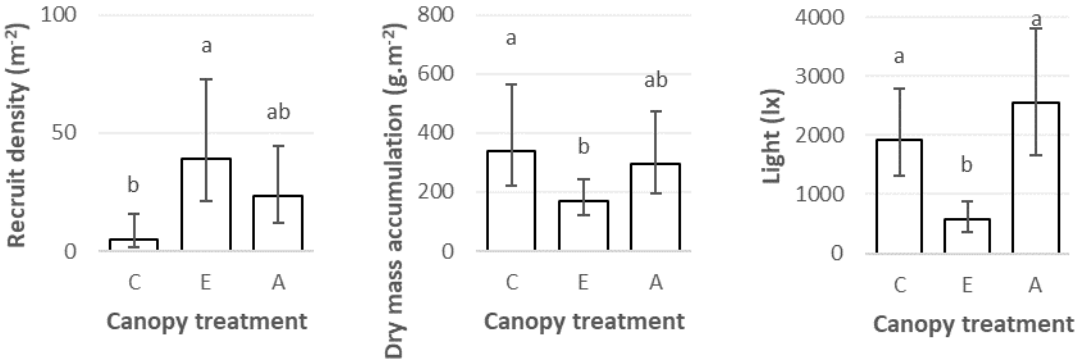
Distribution of juvenile kelp relative to the bed

To better understand the distribution of kelp recruits relative to extant beds, I present here a qualitative assessment by combining the results of the survey with recent hydrodynamic modelling of the Bay (Tran, 2020). The kelp beds at Pt Linley and Williamstown were of similar size (700 – 800 m^2) and average adult kelp density (10 – 12 m^2), with Pt Linley likely having roughly 30% more adult kelp in total. Hydrodynamic modelling of the Bay (Tran, 2020) showed distinct tidal current conditions at the two sites of this study. At Point Linley, a strong tidal signal was present with longshore flows in alternating directions (~0.05 $m.s^{-1}$), while at Williamstown a constant longshore current (~0.01 $m.s^{-1}$) was present running NW to SE. No cross-shore current was observed, likely due to the resolution and depth averaged nature of the model results. Given a typical spore suspension time of 2 hours, advection in these currents could lead to dispersion of spores, and potential recruitment, extending 360 m in the longshore direction at Point Linley, and 72 m to the SE at Williamstown, with no advection cross-shore. This contrasts with the results of my survey, with juvenile abundance in both longshore and cross-shore directions of a similar magnitude, and greater distances observed at Williamstown. Individual kelp plants distributed relatively evenly across the reef at Williamstown may have provided an important contribution to the observed juvenile abundance, while not overcoming the clear trend of reduced abundance with distance from the kelp bed. Alternatively, the higher current speeds at Pt Linley, while allowing spores to disperse greater distances, may also lead to over-dilution and hence reduced recruitment rates (Gaylord et al., 2006). Male and female gametophytes must settle sufficiently close to allow signalled release and attraction of sperm to eggs (Lüning & Müller, 1978; Tatsumi, 2018) so this could have resulted in sperm limitation and greater declines in recruitment with distances than prediction by spore dispersal alone. More detailed empirical studies (sensu Gaylord et al., 2006) are needed to properly identify the underlying mechanisms contributing to the rate of decline in natural recruitment away from remnant kelp beds in this system.

Ecklonia radiata canopy facilitation of recruitment

The presence of an *E. radiata* canopy facilitated higher densities of recruits. It is possible that the *E. radiata* canopy deposited spores directly below onto the tiles, however the experiment controlled for spore supply at the scale of 2 m by ensuring all treatments had similar adult densities at that scale, suggesting this is an unlikely explanation. Alternatively, it is possible the observed facilitation of recruitment below the *E. radiata* canopy was due to the fronds providing a suitable bare substrate through sweeping and reducing photo-stress to early life stages through shading. Sediment accumulation is a key driver of species composition on rocky reefs, with sediments able to smother, scour, or simply replace solid substrate with a mobile substrate, any of which could adversely affect recruitment (Devinny & Volse, 1978; Airoldi, 2003). Gametophyte settlement peaks at low light levels, similar to those found under an adult canopy, but subsequent growth is hindered (Tatsumi & Wright, 2016; Wernberg, Coleman, et al., 2019). As the sporophytes grow post recruitment, they have reduced need for clean substrate and shading, likely reaching light compensation around 0.35 to 5.0 g from which point more light is required to grow (Kirkman, 1981). While providing protection for these early life stages, and hence improving recruitment, the shading offered by the canopy may then stunt the growth and maturation of juvenile (Graham et al., 2021). Combined, these two studies suggest the relationship between adult *E. radiata* and the next generation can change from facilitatory to competitive over time. Similar observations have been made previously, with peak *Macrocystis pyrifera* germination within 2 m of adult plants, but competition for light resulting in a peak survival or stipe growth 8 m from adult plants (Dayton et al., 1984). While apparently adversely impacting on the growth of individual young sporophytes, this shift to a competitive relationship may enhance bed resilience by facilitating the accumulation of a dormant bank of *E. radiata* sporophytes/gametophytes beneath the canopy, enabling rapid regeneration following sudden canopy loss (Carney & Edwards, 2006).

Artificial kelp assist recruitment



Although the mean recruitment density under the artificial kelp treatment was 5 times that of the control, the effect was inconclusive with insufficient power at a significance level of α = 0.05 (i.e. there is more than 5% chance that the effect was random). Furthermore, this increase was not accompanied by the predicted decrease in both sediment accumulation and light conditions. This suggests my artificial kelp was not a good mimic for *E. radiata* and that some other factor may enhance recruitment success that was not measured here. Reduced water flow under natural canopies increases sediment deposition, which is then countered by sweeping leading to reduced sediment accumulation (Layton et al., 2019). The observed sediment accumulation under the artificial kelp canopy suggests that it didn't perform the sweeping function expected, suggesting the artificial fronds were insufficiently flexible under the relative weak currents at this site to make frequent contact with the substrate. While natural fronds of *E. radiata* can bend in any direction, the design process for the artificial kelp used here only considered the frond's movement as viewed from one side (i.e., in one plane). This may have reduced the area swept by the fronds compared to the natural kelp, which was already highly localized to a portion of the tiles (Figure 4). Consequently, this greater rigidity may have reduced current speeds, allowing for increased settlement of spores. Whether artificial kelp can enhance recruitment in restoration projects requires further investigation. In future, alternative designs should focus on mimicking specific functions such as flow reduction, or sweeping of the substrate, and may not necessarily look like natural kelp (e.g., buoyed, and anchored chains for substrate scouring).

Preference for vertical substrate

This study demonstrated higher recruitment success of *E. radiata* to vertical than horizontal substrates, despite kelp spore settlement potentially being higher to horizontal surfaces (Reed et al., 1992). This was coincident with both explanatory factors measured: lower sediment accumulation and lower light conditions. Reduced sediment accumulation ensures a greater available area of clear substrate on which spores can settle and/or survive (Valentine & Johnson, 2005), while the lowered light may reduce photo-stress on the very small stages (Wernberg, Coleman, et al., 2019). It is important to note that our study did not separate the effects of sedimentation from reduced light, so the higher recruitment may have resulted from reduced sedimentation in spite of lower light. Identifying this increased recruitment on vertical substrates under the conditions found in the Bay, is useful for informing the choice of intervention in a restoration context. For example, a natural reef with more vertical surfaces may have greater restoration success with provision of propagules alone, either drifting from an extant kelp bed or from mesh bags filled with reproductive kelp fronds (i.e., spore bags) placed on the reef. Conversely, a flat reef may require additional interventions such as removal of sediment or provision of alternative substrate, preferably with increased vertical surfaces (Deysher, 2002). This differentiation of reefs could be carried out easily at scale through the use of bathymetric derivatives such as rugosity, a measure of non-horizontalness of the reef (Kuffner et al., 2006).

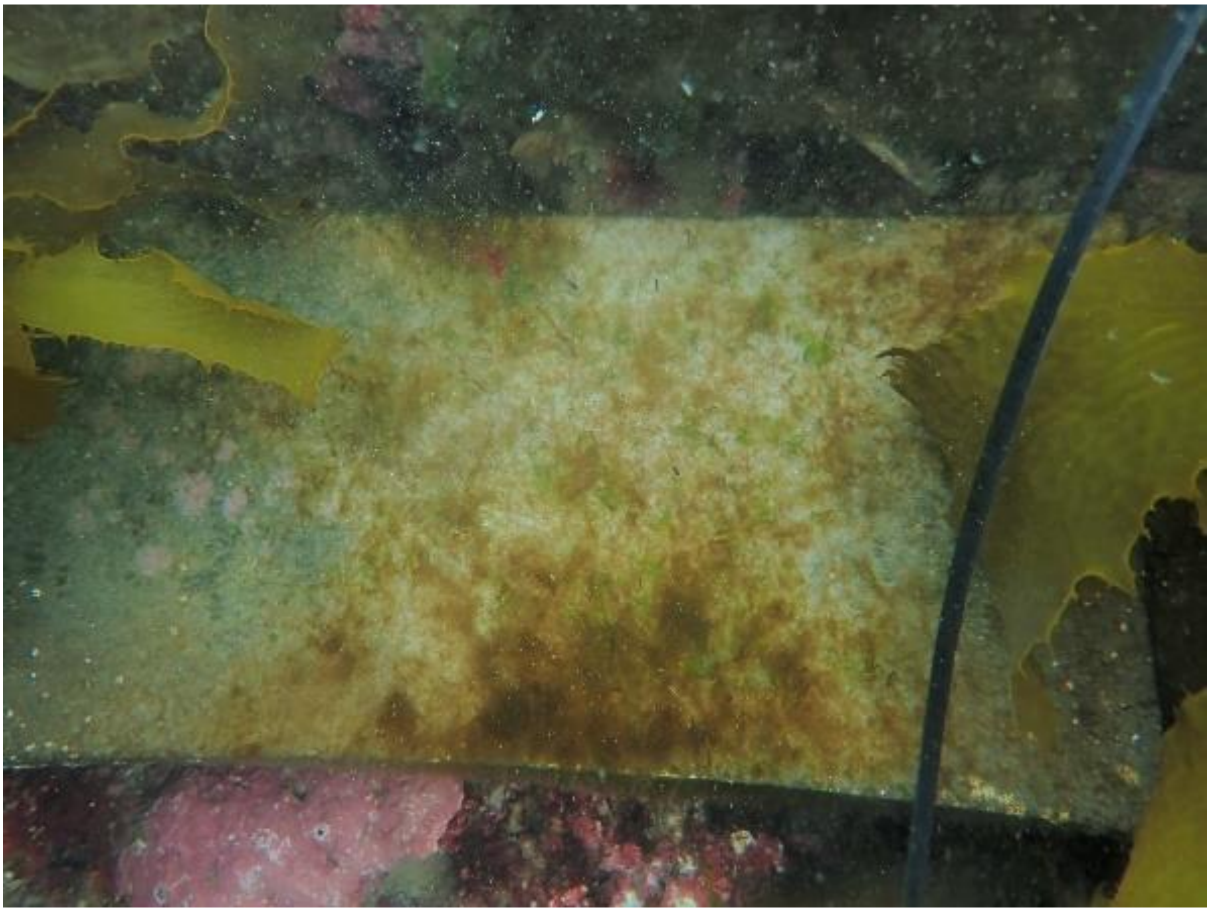


Figure 5 Highly localized sweeping of the tile by natural E. radiata fronds.

Summary

Here I have reviewed several factors of importance in kelp recruitment, an essential component of any kelp bed protection or restoration project. While further work is required to understand kelp dispersal and the mechanisms of recruitment failure, this study provides a starting point for spatial planning of restoration at scale by identifying the order of magnitude of distance recruitment is occurring from existing beds and identifying two environmental key factors that can limit recruitment success. Restoration of these habitat forming species is essential for healthy temperate reef ecosystems, having flow on benefits in nutrient uptake, and fishery productivity. Temperate reefs around the world are under increasing stress from climate change, urbanization, and over-fishing, and must not be overlooked in this decade of restoration.

Acknowledgements

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CHAPTER 5 - IDENTIFYING KEY FACTORS FOR TRANSPLANTATION SUCCESS IN THE RESTORATION OF KELP (*ECKLONIA RADIATA*) BEDS

Abstract

Kelp beds are a defining feature of temperate reefs worldwide, playing a fundamental role as ecosystem engineers and primary producers. Overgrazing by the native sea urchin *Heliocidaris erythrogramma* has driven a phase shift from kelp beds of *Ecklonia radiata* to barrens across much of Port Phillip Bay, Victoria. Here I present the results of a transplant experiment, which took juvenile *E. radiata* sporophytes from a source reef and attached them with silicon tubing to basalt tiles. Following an initial localized cull, I monitored the development and survival of individual *E. radiata* to investigate the drivers of loss during transplantation, including disturbance (control vs. procedural control), receiving environment (kelp canopy vs. no canopy), and translocation site (within vs. between reefs). I also investigated the role of holdfast reattachment and developmental stage on kelp survival. 69% of the kelp transplants survived over the 17 weeks, with no increased loss resulting from transplantation to a reef 41 km away. I observed high survival of transplants in the absence of ongoing urchin exclusion. Furthermore, the provision of a canopy is not

necessary and may result in adverse impacts on survival and development of juvenile sporophyte transplants presumably through competition for light. Individuals at the collection location (controls) were unlikely to survive to maturity suggesting their removal for transplanting is likely to have minimal impact on the kelp population of the donor reef. The methods used could be feasibly upscaled for rehabilitating or restoring kelp beds both in Port Phillip Bay and elsewhere.

Introduction

The need for ecosystem restoration worldwide to reverse adverse human impacts and address some of humanity's biggest challenges has recently been acknowledged, with 2020 being declared the United Nations Decade on Ecosystem Restoration (UN General Assembly, 2019). This declaration aims to achieve substantial upscaling of proven restoration methods to millions of hectares. Temperate reef ecosystems are one suitable target, as they are known to provide many important services but are currently widely degraded (Halpern et al. 2012; Krumhansl et al. 2016; Wernberg et al. 2019).

Kelps are large canopy-forming brown algae of the order Laminariales (Bolton 2010), an ecosystem engineer and defining feature of temperate reefs worldwide. They provide habitat and food for a range of species (Jones 1992; Hinojosa et al. 2015). Australia's Great Southern Reef, a 7M ha of kelp dominated temperate reef, is estimated to provide $130B/yr in waste treatment, fishing, and tourism, while most of its ecological values have not been quantified (Bennett et al. 2016; Gaylard et al. 2020). Despite their importance, kelp beds have suffered significant declines globally, with key drivers including warming, eutrophication, overfishing, storms, and overgrazing (Wernberg et al. 2019).

Degradation of kelp beds by the overgrazing of urchins is commonly associated with phase shifts to structurally simple algal turfs or bare rock, herein referred to as barren, which lack the services provided by kelp (Filbee-Dexter & Scheibling 2014). The shift from kelp bed to barren, a reef generally void of noncoralline algae, is understood to occur when a critical urchin density has been reached (Filbee-Dexter & Scheibling 2014). The critical density of urchins is species specific, with values of 4-10 m^{-2} for *Centrostephanus rodgersii* (Ling et al. 2009) and approximately 8 m^{-2} for *Heliocidaris erythrogramma*, triggering phase shifts in eastern Australia (Kriegisch et al. 2016). This alternate reef state is considered stable, as a much lower density of urchins is required for recovery of the kelp state, 0.2-1.2 m^{-2} for *C. rodgersii* (Ling et al. 2009) and 4 m^{-2} for *H. erythrogramma* (Kriegisch et al. 2016). The kelp free reef may be further stabilized through the development of turf, which is often associated with eutrophication and warming, which can inhibit natural recovery of kelp (Filbee-Dexter & Wernberg 2018). Alternatively, a macroalgal reef assemblage may form, suppressing the deteriorated reef state feedback loops and allowing kelp to re-establish (Wernberg et al. 2019).

Understanding the stability of these alternative stable states is important when considering kelp restoration options, whether for enhancing resilience of an existing kelp bed or re-establishing a lost kelp bed. For example, if a phase shift away from a kelp bed appears imminent due to high urchin density, removal of urchins may be the only action required (Leinaas & Christie 1996). However, if a stable algal turf has developed and no propagule supply is present, more active intervention may be required involving removal of turf or provision of substrate, provision of kelp spores, or transplanting of sporophytes (Morris et al. 2020).

Transplanting is an active restoration method involving the movement of kelp sporophytes from one location, either a donor reef or stock from lab culture to a receiver reef. Transplanting may be justified where background drivers for kelp forest degradation have been addressed but where spore supply or suitable settlement substrate remain low (Morris et al. 2020). While transplantation has rarely been implemented with kelps at scale, and only with mixed success (e.g., Sanderson 2003), the method has been used extensively in research (Fowler-Walker et al. 2005; Bennett et al. 2017; Layton et al. 2021) and for restoring other canopy-forming seaweeds such as crayweed (Fucales) (Campbell et al. 2014). These studies have used various life stages from microscopic gametophyte stages to adult sporophytes (Reeves 2017; Layton et al. 2019), however which stage is most appropriate to transplant is unclear as smaller kelp tend to acclimate more quickly, while larger kelp may survive better post-disturbance (Fowler-Walker et al. 2005; personal observation 2019). Furthermore, survival and growth of small transplants may require the presence of a canopy (Layton et al. 2019), while larger individuals can help facilitate a phase shift back to kelp bed by sweeping clean the surrounding reef, shading the understorey, and supplying spores (Reed & Foster 1984; Toohey et al. 2004; Wernberg et al. 2005). Lastly, the choice of donor reef should consider the availability of sporophytes of suitable size, the acclimation of those sporophytes, and the possible impacts to the donor reef of removing them.

Here I investigate transplantation as a restoration tool for kelp in Port Phillip Bay, Australia. *Ecklonia radiata* (Agardh, C.) Agardh J., is the locally dominant habitat forming kelp on Australia's Great Southern Reef stretching from Kalbari, Western Australia to Brisbane, Queensland (Bennett et al. 2016). High sea urchin (*H. erythrogramma*) densities have led to a rapid decline in kelp cover across many reefs in the Bay, particularly in the north (Carnell & Keough 2019). The non-native species, *Undaria pinnatifida* (Harvey) Suringar is often found emerging on these degraded *E. radiata* beds, providing similar canopy structure through winter and at least some equivocal services (Barrett et al. 2019), however its ability to provide adequate protection for juvenile *E. radiata* sporophytes has not been tested. In this region active restoration methods (sensu Morris et al. 2020) for kelp beds are necessary due to the high sea urchin densities, formation of an algal turf matrix inhibiting growth and survival of early life stages, and a lack of spore supply given the limited coverage of remnant kelp beds (Johnson et al. 2015). Three stages have been described in the development of *E. radiata* sporophytes based on their physical structure: stage I are defined by a single oblong blade, stage II by simple and entire secondary blades, and stage III by compound lateral blades (sensu Kirkman 1984). To develop an active restoration method, I measured the survival and development (holdfast reattachment and maturation to stage III) of juvenile (stage I and II) sporophyte transplants in different receiving environments over two sites, including fenced and unfenced barrens, *E. radiata* canopy, and *U. pinnatifida* canopy. A procedural control was included at the first site adjacent to where juvenile sporophytes were collected. The experiment was designed to test the following hypotheses:

1. The survival of juvenile sporophytes in the procedural control will be similar to that of non-disturbed individuals (with no urchin grazing pressure and similar environmental conditions);
2. The survival of juvenile sporophytes will be greater in the control compared to transplant treatments (high grazing pressure at restoration sites), however;
3. The survival of juvenile sporophyte transplants will be greater in fenced than unfenced treatments (lower grazing pressure);
4. There will be no difference in the survival of juvenile sporophytes translocated to barrens between locations (similar handling methods and receiving environments);
5. The survival of juvenile sporophyte transplants will be greater under a canopy (due to protection from excess light and urchin herbivory), however;

6. There will be no difference in survival of juvenile sporophyte transplants between *E. radiata* and *U. pinnatifida* canopies (as both have similar size and geometry);
7. Stage II transplants will have greater survival than stage I transplants (as greater loss was observed among small transplants in a pilot study), but;
8. Stage I transplants will show a higher rate of holdfast reattachment (due to their improved capacity for acclimation).

Methods

A transplant experiment was undertaken across two rocky reefs in Port Phillip Bay (hereafter the Bay), Victoria, Australia (Fig. 1a). Kelp sporophytes were sourced from Point Linley (145°02′ E, 38°13′ S) and deployed to barrens at Point Linley and Williamstown (144°54′ E, 37°52′ S). The Point Linley treatments were set up on 29 Aug 2019 and the Williamstown transplants set up on 04 Sep 2019. Point Linley Reef is located in the south-east of the Bay, between Mornington and Mount Martha. It is a sedimentary reef, presumably Sandringham Sandstone, with high relief interspersed by areas of sediment and mussel shells. The western side of the reef drops off to approximately 10 m depth, while the eastern side gradually shallows and transitions into a sandy beach (Fisherman's Beach). During the period of this study, the northern end of the reef was a barren whereas the southern section of the reef contained a kelp bed located primarily at approximately 4 m depth. The Williamstown East Reef is located in the north of the Bay. The reef is an outcropping of the Newer Volcanics plain which covers much of the western side of the Bay. The reef also contains boulders and extends from the modified shoreline to the north where basalt boulders have been assembled into breakwaters and a groin. The reef is relatively flat and generally about 3 m deep.

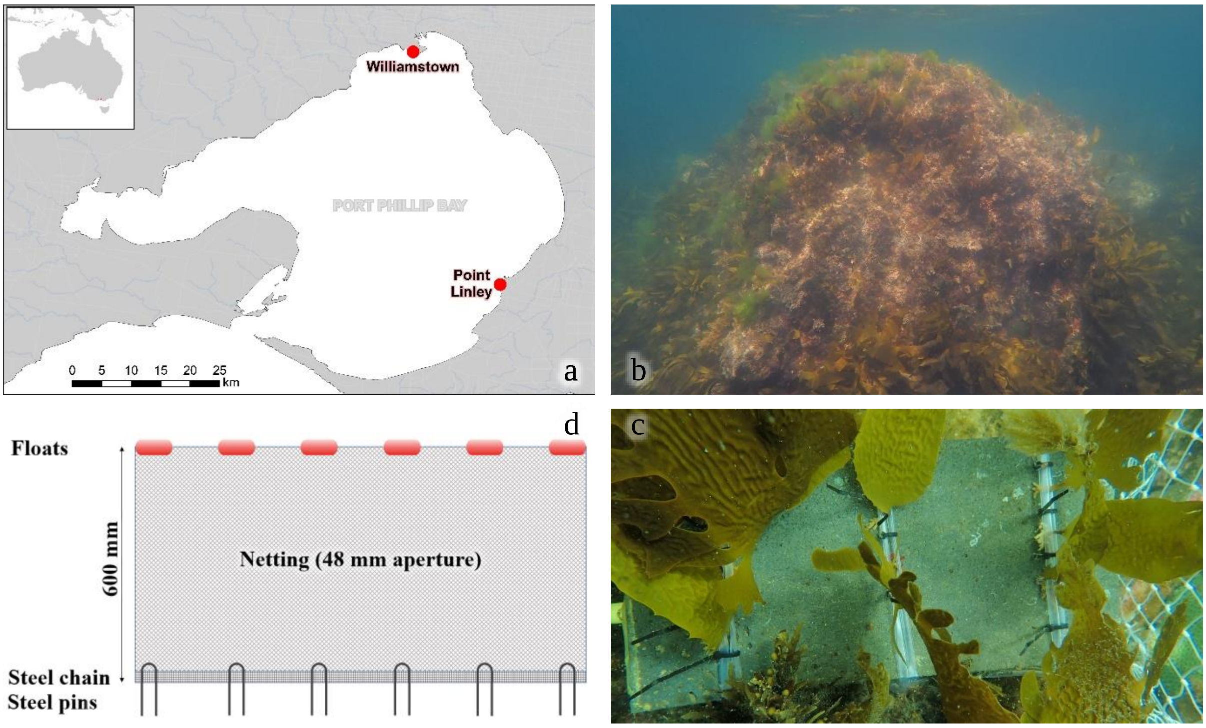

Figure 1. Clockwise from top left: a) Map of field sites; b) Boulder with juvenile sporophytes at the top and adults at the bottom; c) Basalt tile with juvenile sporophytes attached by silicon tubing around stipes; and d) Urchin exclusion fence design with floats along the top, chain along the bottom, and steel pins to secure the chain to the reef.

Large numbers of *E. radiata* juvenile sporophytes were observed on shallow vertical surfaces in remnant mussel beds, at the western end of the main kelp bed at

Point Linley Reef. These juvenile sporophytes were targeted for use in this experiment due to their availability and the scarcity of juvenile sporophytes elsewhere on the reef at the start of the experiment. The treatments are summarized in Table 1 and illustrated in Figure 2.

Table 1 Experimental treatments and their purpose.

ID	*Treatment*	*Location*	*Purpose*
1	Control	Point Linley	Determine background rate of survival
2	Procedural Control	Point Linley	Determine the loss associated with handling and reattachment (planned comparison to #1)
3	Barren	Point Linley	Determine success of transplantation to a local barren (planned comparison to #2)
4	Barren + Fence	Point Linley	Determine success of transplantation to a local barren with urchin exclusion (planned comparison to #3)
5	Translocation + Barren	Williamstown	Determine success of translocation to a distant barren (planned comparison to #3)
6	Translocation + Barren + Fence	Williamstown	Determine success of translocation to a distant barren with urchin exclusion (planned comparison to #4)
7	*Ecklonia* Canopy	Williamstown	Determine effect of canopy on transplant survival (planned comparison to #5)
8	*Undaria* Canopy	Williamstown	Determine effect of canopy type on transplant survival (planned comparison to #7)

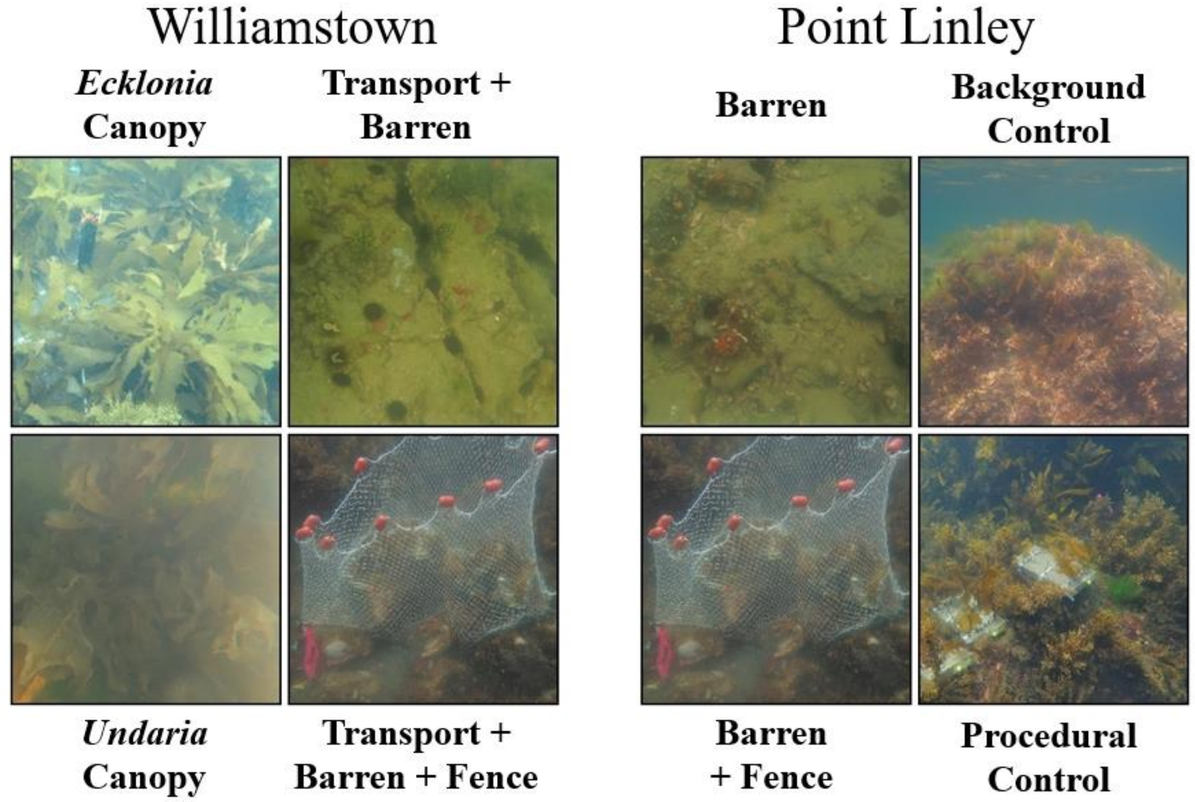

Figure 2. Schematic of experimental treatments across the two sites.

In late August, stage I and II sporophytes (48 of each) were randomly selected and removed from the donor reef, from depths of 1.2 to 2.0-m (Fig. 1b) and lifted to the dive boat. On the boat, individuals were randomly assigned to 12 basalt tiles (30 x 150 x 300-mm; 4-kg). The stipe of the individual was held between two pieces of silicon tubing that were wrapped around the tile and held together with cable ties; this secured the holdfasts of the transplants to the tiles (Fig. 1c). A total of four *E. radiata* juvenile sporophytes of each stage were attached to each tile, with positions randomly assigned. The transplants were kept on the boat for a total of 90-minutes, initially loose in eskis of fresh seawater, then once attached to the tiles, stacked in the same eskis with fresh seawater.

As a procedural control, four of the tiles were placed as close as possible on the donor reef within a 1-m^2 area (hereafter *Procedural Control*), these tiles were placed on a horizontal surface as it was not possible to reattach the tiles vertically onto the surface where the transplants were removed. Within a 1-m^2 area in an adjacent barren with no canopy algae, four tiles were placed (hereafter Barren). Another 1-m^2 area of the adjacent barren received tiles surrounded by an urchin exclusion fence (hereafter Barren + Fence). The exclusion fence was 600-mm high with a 48-mm aperture and was fixed to the reef along the perimeter of the 1-m^2 plot using a chain and metal pins, with sub-surface floats holding the fence stretched along the top (Fig. 1d). Stage I (x26) and stage II (x15) sporophytes on the donor reef were tagged as controls (i.e., were not removed or placed on tiles; hereafter Control). At the time of deployment, all urchins found within the 1-m^2 area of each treatment was removed, with the assumption that this would be a necessary step in any restoration project to protect transplants from urchin herbivory. No urchins were encountered in either the Control or Procedural Control at the time of deployment.

In early September 2019, 64 individuals of each stage were collected from the donor reef and attached to basalt tiles, as before. These tiles were then deployed at Williamstown in groups of four, placed in 1-m^2 areas. The first group was to a barren (hereafter Translocation + Barren), the second also to a barren with an urchin exclusion fence (hereafter Translocation + Barren + Fence), the third under an *E.*

radiata canopy (hereafter *Ecklonia* Canopy), and the fourth under an *U. pinnatifida* canopy (hereafter *Undaria* Canopy). The *Ecklonia* and *Undaria* Canopies were standardized by ensuring they had a similar number of stipes during deployment (17 *Undaria*, 14 *Ecklonia* at deployment, thinned to 14 each). Ideally tiles would have been spaced further apart but I were limited by the availability of *Ecklonia* and *Undaria* beds at Williamstown and barren area at Point Linley. As such, treatments were placed closer to one another to minimize spatial effects.

Monitoring of the transplants was undertaken at Point Linley in weeks 2, 3, 4, 5, 12, and 17 from deployment, and at Williamstown in weeks 3, 5, 12, and 17 from deployment. During each survey, the stage and condition of each transplanted or tagged individual was noted and whether the holdfast had reattached, as well as a count of urchins within the 1-m^2 deployment area. Individuals were classified as: missing; only the holdfast remaining; stipe present but no lamina; Stage I, II or III; and holdfast attached.

To test the effects of *Treatment* and *Initial Stage* on sporophyte *Loss*, a time-to-event (i.e., to loss, maturation, or reattachment) analysis was undertaken in R (v. 4.0.0) using the survive (v. 3.1.12) package (Therneau & Grambsch 2000; R Core Team 2020; Therneau 2020). Testing of the model determined the need to include a time interaction with *Initial Stage* in order to comply with the proportional hazard assumption (Schoenfield residual $p < 0.05$), but no significant interaction between *Treatment* and *Initial Stage* was observed (Table 2).

Table 2 Summary of time-to-event models with predictor variables used. t_{start} = week of observation.

Target variable	*Model ID*	*Predictor variable(s)*
Loss	M1a	All Treatments
	M1b	InitialStage + InitialStage:t_{start}
	M1c	Fence + Fence:t_{start}
	M1d	Translocated
	M1e	Canopy
	M1f	Reattached + Matured + Reattached:t_{start}
Reattachment	M2a	All Treatments (excluding Control)
	M2b	InitialStage
	M2c	Fence
	M2d	Translocated
	M2e	Canopy
	M2f	Matured
Maturation	M3a	All Treatments (excluding Control)
	M3b	InitialStage
	M3c	Fence
	M3d	Translocated
	M3e	Canopy
	M3f	Reattached

The observational data was restructured with a time-to-event for *Loss*, *Reattachment*, and *Maturation*, and a censoring code to indicate whether each event occurred. Since there were eight separate occasions where transplants had recovered after being eroded back to the holdfast, *Loss* was defined as complete loss including the holdfast. The time unit was converted from days to weeks allowing observations at both reefs during a single week to be linked. The data was split into 1-week blocks using the Greg package (v. 1.3.3) allowing the inclusion of a time covariate where necessary (Gordon & Seifert 2020). All analyses were run separately for the two *Initial Stages*. Additional models were run to investigate the specific impacts of *Fencing*, *Translocation*, and *Canopy*, combining relevant treatments for greater power.

A time interaction with *Fencing* was required to maintain the proportional hazards assumption.

Reattachment and *Maturation* were modelled in the same way as loss; however, the *Control* was not included since no reattachment was possible and low survival in the *Control* resulted in failed model convergence for maturation. A time interaction with *Initial Stage* was required for both *Reattachment* and *Maturation*, however the time interaction with *Fence* was not required. To investigate the impact of *Reattachment* and *Maturation* on survival these observations were also included as factors. A time interaction with *Reattachment* was required. As these factors cannot be controlled, the results may be influenced by the data structure (i.e., both *Reattachment* and *Maturation* only occurred towards the end of the experiment).

Mass loss of sporophytes was observed during the study, with a gradient of loss observed from shallow to deep (see Results). This impact was most pronounced in the Background Control, which was located in shallower water to the Disturbance Control and all other treatments because of the high availability of juvenile sporophytes. This loss of shallow sporophytes led to a higher survival being observed in the Procedural Control than the Background Control, removing my capacity to determine loss due to disturbance, and further indicating the Background Control does not provide a good indication of background survival rates (at the depth of treatments). The Procedural Control was therefore adopted as the comparator in my analysis.

Results of the time-to-event analysis are presented as hazard ratio plots in Figure 4, with a value of greater than one representing an increased likelihood of loss (M1), reattachment (M2), or maturation (M3) relative to the denominator. Denominators used in the plots were selected to consider each component of the transplant method (Fig. 3); Procedural Control (a), initial stage I (b), unfenced (c), not translocated (d), no canopy (e), and not reattached or matured (f). Results are also provided in table form in the Supporting Information (Tables S1 – S3).

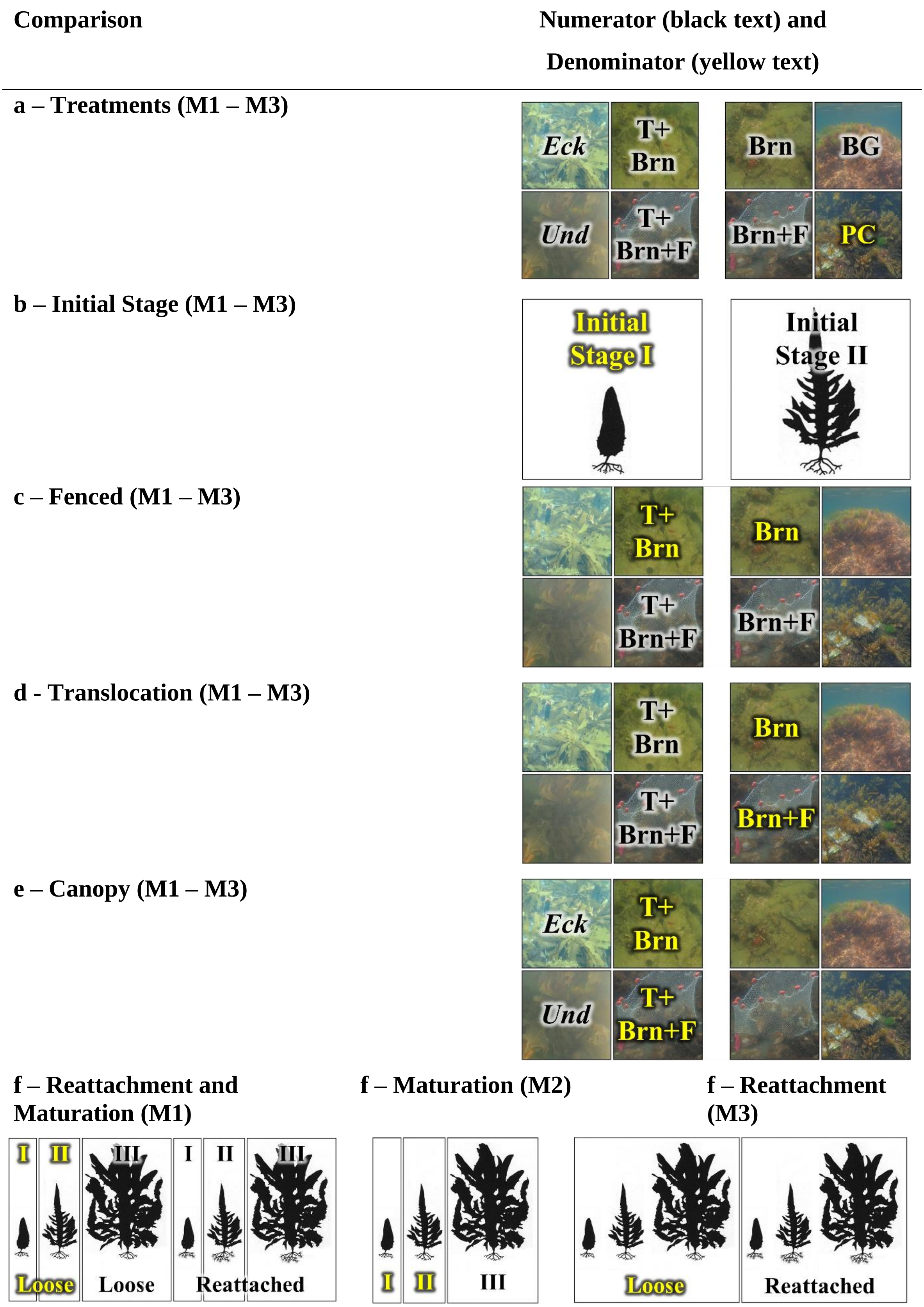

Figure 3. Symbolic illustration of numerators (black text) and denominators (yellow text) used for each comparison. Figures of stage I and stage II sporophytes adapted from Kirkman (1984). Eck = Ecklonia canopy, Und = Undaria canopy, Brn = Barren, T+ = Translocation, +F = Fenced, BG = Background Control, PC = Procedural Control.

Results

Urchins returned at various densities to the treatments after initially being removed. Urchin densities in Williamstown were generally much higher than Point Linley, ranging from 15-m^{-2} in the *Undaria Canopy* treatment down to 5-m^{-2} in the *Ecklonia Canopy* treatment. The fenced and unfenced Barren treatments in Williamstown had similar maximum densities of 14-m^{-2} and 13-m^{-2}, respectively. The corresponding treatments in Point Linley reached maximum densities of 1-m^{-2} and 7-m^{-2}, respectively, while no urchins were observed at any time in the *Control* or *Procedural Control*.

Loss of tagged sporophytes in the *Background Control* was highly dependent on depth after 12 weeks, with 25% survival at 1.2-m, 40% survival at 1.4-m, and 100% survival at 2.0-m. Loss was not significantly affected by treatments at either site (Fig. 4 M1a). Stage II transplants had significantly lower loss (0.17x) compared to stage I, however this effect decreased with time (Fig. 4 M1b).

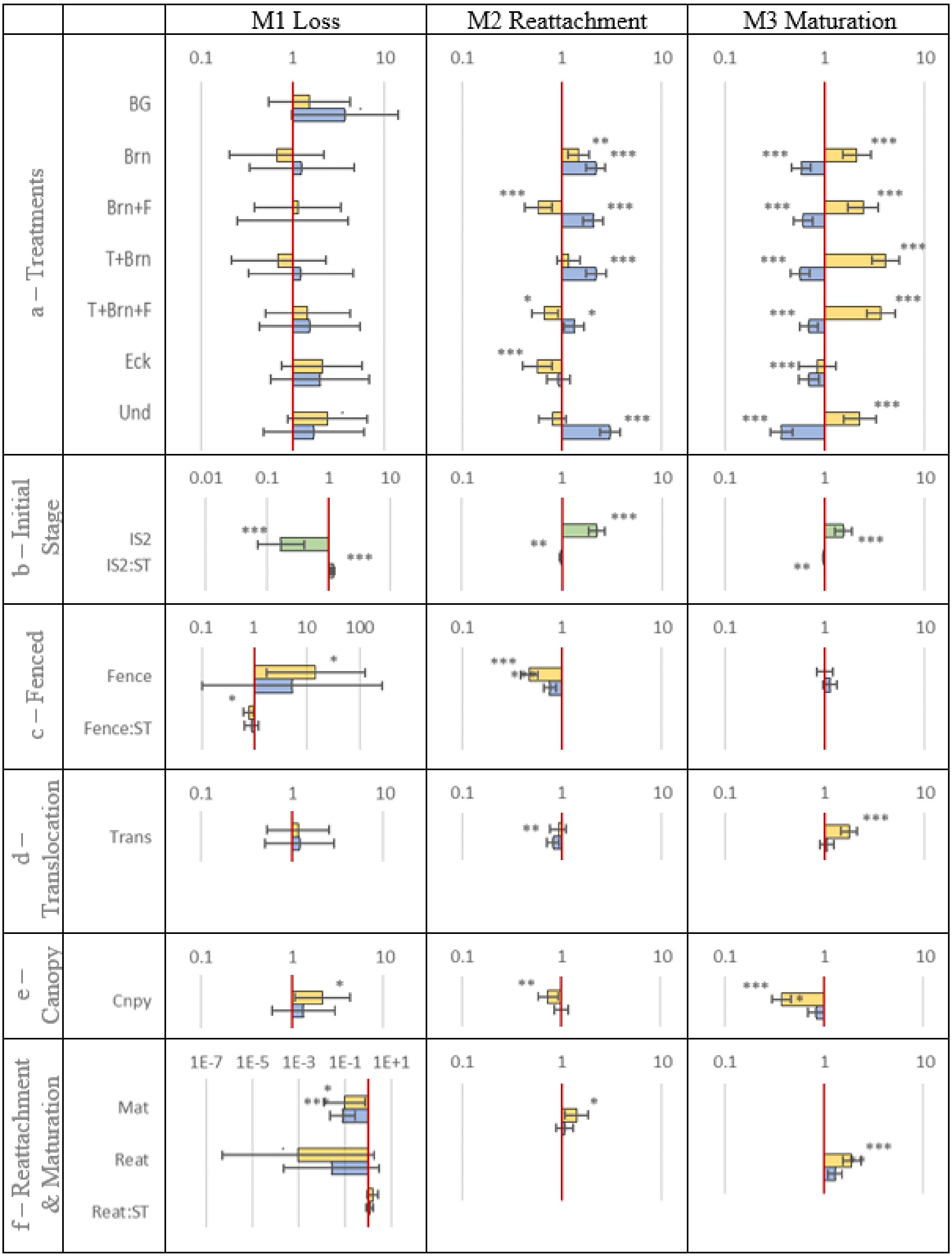

*Figure 4. Hazard ratio plots for loss, reattachment, and maturation (+/- 95% CI). In the top panel each treatment (numerator) is compared against the Procedural Control (denominator). Thus, hazard ratios greater than 1 indicate an increased hazard (i.e., increased loss, reattachment, and maturation). Initial stage I (yellow bars) and stage II (blue bars) were modeled separately, except when testing the effect of Initial Stage (green bars). BG = Background Control, Brn = Barren, F = Fence, T = Translocated, Eck = Ecklonia, Und = Undaria, IS2 = Initial stage II, ST = Start time (week), Trans = Translocated, Cnpy = Canopy, Mat = Maturation, Reat = Reattachment. Asterisks denote significance at different alpha levels: * <0.05; ** <0.01; *** <0.001.*

While the fences did not exclude urchins as intended, their presence resulted in significantly increased loss of stage I (15x) and non-significantly increased loss of stage II (5x) (Fig. 4 M1c). The effect on stage I transplants decreased significantly through time (Fig. 4 M1c). Translocation across the Bay had minimal impact on loss (Fig. 4 M1d). The provision of a canopy resulted in significantly increased loss of stage I (2x), while having little impact on the survival of stage II transplants (Fig. 4 M1e).

Reattachment was significantly enhanced for stage II transplants across all treatments except *Ecklonia Canopy*, while the impact on stage I transplants was mixed (Fig. 4 M2a). Stage II transplants were significantly more likely to reattach (2x), however the effect decreased significantly with time (Fig. 4 M2b). Translocation across the Bay, fencing, and presence of a canopy all significantly reduced reattachment of stage I transplants (Fig. 4 M2c,d,e). Provision of an *Undaria* canopy compared to *Ecklonia* canopy resulted in a significantly higher likelihood of reattachment (3x). *Maturation* significantly increased reattachment for stage I transplants but had little effect on the reattachment of stage II transplants (Fig. 4 M2f).

All treatments except *Ecklonia Canopy* resulted in significantly increased maturation of stage I transplants, but significantly reduced maturation of stage II transplants, compared to the *Procedural Control* (Fig. 4 M3a). Stage II transplants were significantly more likely to fully mature but the difference between initial stages reduced over time (Fig. 4 M3b). Fencing had little impact on maturation for either stage (Fig. 4 M3c). Translocation across the Bay resulted in significantly greater maturation of stage I transplants while having almost no effect on stage II transplants (Fig. 4 M3d). Provision of a canopy significantly reduced maturation of both stage I and II transplants (Fig. 4 M3e). *Reattachment* significantly increased maturation of both stage I and II transplants (Fig. 4 M3f).

Discussion

In undertaking this *Ecklonia radiata* transplant experiment in the Bay and monitoring the fate of transplants over a 17-week period, I have been able to assess the likely factors contributing to loss (disturbance, placement in a barren, and translocation across the Bay) and whether additional interventions (urchin exclusion fence and canopy provision) are necessary to increase survival. Encouragingly, the survival of stage I and II individuals across all transplant treatments were the same as procedural controls. Methodological factors independent of treatment (e.g., loss from failure of the initial attachment method), likely contributed to the observed high variability in loss rates, and hence the lack of statistical significance. As maturation and reattachment rates are based only on individuals that were not lost, these data were not impacted by this issue. As the undisturbed control had significantly lower survival rates than the procedural control, this suggests that these shallow-water boulder habitats could serve as a sustainable source of juvenile sporophyte transplants in the Bay. Urchin densities were unrelated to transplant losses, with greater losses observed under canopy treatments, which were expected to protect transplants from urchin herbivory. Translocation across the Bay, as well as the canopy type, had little impact on loss rates. Stage II transplants had a significantly lower loss rate and higher rates of reattachment and maturation than stage I transplants. Many of these results can be explained by the impact of shading. These findings add to the growing evidence that kelps, including *Macrocystis spp.* (Hernández-Carmona et al. 2000; Westermeier et al. 2016), *Lessonia spp.* (Westermeier et al. 2016), and *Ecklonia spp.* (Reeves 2017; Layton et al. 2021) can be successfully transplanted.

Tracking of undisturbed individuals on the donor reef (control) revealed a potential sink population (Pulliam 1988), as juvenile sporophytes on this boulder habitat are unlikely to survive to maturity. Although previous experiments tracking survival of transplants and undisturbed controls for kelp and Fucales have found little loss due to disturbance (Campbell et al. 2014; Reeves 2017), I observed the highest loss in the undisturbed control. The choice of background population (control) in this study was driven by the availability of juvenile sporophytes, which were concentrated towards the shallow top of the boulders, which were void of adult kelp. These juvenile sporophytes experienced high loss (75%), especially of stage II individuals, which was depth dependent. These observations are consistent with increased drag forces from larger fronds resulting in increased wave-induced detachment from the boulder, which may have been exacerbated by settlement on to a potentially unstable substrate (i.e., the mussel bed which was also lost), as mussels can experience detachment in forces as little as 5-N (Witman & Suchanek 1984; Thomsen et al. 2004). The presence of a sink population of juvenile *E. radiata* sporophytes, if found to recur each year, indicates a potential source with minimal impact on the donor reef, an important consideration in active restoration (Carney et al. 2005; Morris et al. 2020). Further investigation of the mechanisms leading to poor survival to maturation and subsequent mapping can assist in identifying areas suitable for sourcing juvenile sporophytes and for the placing of artificial substrates for kelp recruitment, as well as areas unsuitable for restoration via transplantation.

The advantages observed in this study of transplanting stage II rather than stage I sporophytes, including increased survival (6x), reattachment (2.2x), and maturation (1.5x), likely outweighing the benefits of greater developmental plasticity (Fowler-Walker et al. 2005) and increased availability of stage I sporophytes for transplantation. The observed increase in survival was pronounced compared to a recent transplant experiment with the same kelp within the Bay that found stage II survival was only 1.12x greater than stage I (Reeves 2017), where juvenile sporophytes were transplanted with the rock they were attached to. The increased survival of transplants means less sporophytes are required to achieve target densities. Stage II transplants reached maturity (stage III) slightly faster than stage I transplants (90 and 98 days, respectively), rates consistent with previous observations (Kirkman 1981; Schiel 1988). The 8-day difference in maturation date in the context of seasonality in spore release cycles suggests either stage transplant would provide similar contributions to the next spore release and protection for new recruits from solar insolation, both important positive feedback mechanisms in kelp restoration (Reeves 2017). The significantly increased likelihood of reattachment may, however, lead to additional service provision such as habitat for invertebrates (Hauser et al. 2006).

The reduced maturation of juvenile sporophytes transplanted under an adult canopy was consistent with previous observations of arrested development within kelp beds allowing rapid recovery following canopy disturbance (Toohey & Kendrick 2007). Potential explanations for this, and the coincident low survival, may include reduced light, reduced water movement, potential scouring of fronds, or changes in water chemistry (Miller et al. 2011; Britton et al. 2016). Of the transplants in the procedural control that survived to the end of the experiment, 83% of stage IIs matured to stage III, while only 30% of stage Is did. This suggests that conditions of the procedural control, including more light in the shallower water, may have facilitated faster growth of the stage II sporophytes which subsequently shaded the smaller stage Is. This prediction is consistent with what I observed in the experimental treatments, where the provision of a canopy significantly reduced maturation compared to treatments without canopy algae. The timing of this experiment made full use of the vegetative phase of *Undaria pinnatifida*, which reached full size around the end of August and lasted until the end of November. The timing of this phase (winter/spring) coincides with periods of lower solar insolation (Lee et al. 1995). Running the same experiment in summer might result in a reversal of effects with shading improving survival of juvenile sporophytes, which would be consistent with what has been observed in other studies (Layton et al. 2019). This suggests that while co-transplanting with adults or using surrogate canopies may improve transplant success in summer, it may be deleterious when transplanting in winter. It is therefore important to consider the potential seasonal effects of treatments when planning a restoration project, and future research should explicitly explore when transplantation is likely to be most successful and require the least intervention.

The urchin exclusion fences were also ineffective at reducing urchin numbers, with urchin densities similar inside and outside the fences at Williamstown. This was presumably due to the challenges of ensuring 100% removal and exclusion on a topographically complex reef, noting only one urchin was observed inside the fence at Point Linley. The increased difficulty in applying urchin exclusion devices in complex habitats may mean these habitats will incur greater maintenance and financial costs to restore (Bennett et al. 2017). The fences also became heavily fouled with filamentous algae, likely resulting in shading and presumably reduced water flow inside the fences (Miller & Gaylord 2007; Bennett et al. 2017), both of which could have contributed to the increased loss in fenced treatments. Enhancing this effect was the fence length to area ratio (4-m/m^2) which is far higher than would occur in a larger restoration effort. For example, restoring a 10 x 10-m patch of reef with a fence around it would have a length to area ratio of 0.4-m/m^2.

Despite very high urchin densities returning to treatments at Williamstown in all except the *E. radiata* treatment, juvenile sporophyte transplant loss rates were unrelated to urchin density. The lowest and highest urchin densities at Williamstown occurred in the canopy treatments of *E. radiata* and *U. pinnatifida*, respectively, supporting the idea that *E. radiata* canopy provides a deterrence function, while survival in these treatments was very similar. As there was abundant kelp on the reefs in the vicinity of the experimental plots, it is possible that food (specifically drift algae) was not a limiting food source (Kriegisch et al. 2019). With urchins grazing drift rather than transplanted kelp, the effect of urchin deterrence by the *E. radiata* canopy may have been masked. In other restoration contexts with less drift available, urchin grazing may pose a much greater hazard to transplants.

The transplanting method discussed here could be easily adapted for restoration of kelp beds at various transplant densities by spacing the tiles and could be upscaled to deploy around 140 tiles in a 6-hour day, sufficient for 140-m^2 at a density of 8.3 sporophytes/m^2. The costs associated with this method at scale (Eger et al. 2020) are comparable to other restoration projects such as *Saccharina latissima* green gravel where transplants were cultured in the laboratory (Fredriksen et al. 2020) and adult crayweed, *Phyllospora comosa*, transplanted on mesh mats (Layton et al. 2020). The table has now been moved to the Supporting Information (Table S4).

Underlying all restoration efforts is an understanding that the restored habitat would have greater value than the existing condition. Along with the costing in the supporting information online, available ecological service values have been included. It should be noted that this includes only a very limited number of quantified services, and the services have been explicitly stated to be non-spatially homogenous (Gaylard et al. 2020) so they should not be simply multiplied by the area being considered. Ecosystem services considered include waste treatment, abalone and rock lobster, wild catch fisheries, aquaculture, and tourism and recreation while services not assessed include cultural values, biodiversity, carbon storage, coastal protection, and food provision. Justification of restoration efforts would be aided by more comprehensive ecological service valuations at high resolution that account for differences among reef states and qualities.

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Conflict of Interest

The authors have no conflicts of interest with the publication of this article.

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Supplementary

Table S1 **Results from time-to-event analysis on kelp loss (M1) presented as hazard ratios (+/- 95% CI). The source represents the numerator, with the alternative state as the denominator (i.e., a = Procedural Control, b = Initial Stage I, c = Unfenced, d = Not Transported, e = No Canopy, f = Not Reattached, and Not Matured). IS = Initial stage. Ctrl = Control, Brn = Barren, F = Fence, T = Transport, Eck = *Ecklonia*, Und = *Undaria*, IS2 = Initial stage II, ST = Start time (week), Trans = Transported, Cnpy = Canopy, Mat = Maturation, Reat = Reattachment. Asterisks denote significance at different alpha levels: * <0.05; ** <0.01; *** <0.001.**

M1a	**Source**	**exp(coef)**	**lower 0.95**	**upper 0.95**	***z***	***p***	**Significance**
(IS = I)	Ctrl	1.506	0.544	4.167	0.788	4.31E-01	
	Brn	0.672	0.205	2.202	-0.656	5.12E-01	
	Brn + F	1.142	0.384	3.398	0.238	8.12E-01	
	T + Brn	0.698	0.213	2.286	-0.595	5.52E-01	
	T + Brn + F	1.446	0.501	4.167	0.682	4.95E-01	
	Eck	2.088	0.758	5.748	1.425	1.54E-01	
	Und	2.377	0.877	6.437	1.703	8.86E-02	.

M1a	**Source**	**exp(coef)**	**lower 0.95**	**upper 0.95**	***z***	***p***	
(IS = II)	Ctrl	3.709	0.967	14.232	1.911	5.61E-02	.
	Brn	1.251	0.336	4.660	0.334	7.38E-01	
	Brn + F	1.000	0.250	3.998	0.000	1.00E+00	
	T + Brn	1.215	0.326	4.527	0.291	7.71E-01	
	T + Brn + F	1.526	0.431	5.409	0.655	5.13E-01	
	Eck	1.978	0.579	6.758	1.088	2.77E-01	
	Und	1.693	0.478	5.998	0.815	4.15E-01	

M1b	**Source**	**exp(coef)**	**lower 0.95**	**upper 0.95**	***z***	***p***	
	IS2	0.167	0.070	0.396	-4.062	4.86E-05	***
	IS2 x ST	1.157	1.259	1.063	-3.373	7.43E-04	***

M1c	**Source**	**exp(coef)**	**lower 0.95**	**upper 0.95**	***z***	***p***	
(IS = I)	Fence	14.542	1.694	124.844	2.440	1.47E-02	*
	Fence x ST	0.785	0.976	0.632	2.179	2.93E-02	*

M1c	**Source**	**exp(coef)**	**lower 0.95**	**upper 0.95**	***z***	***p***	
(IS = II)	Fence	5.149	0.101	261.516	0.818	4.13E-01	
	Fence x ST	0.883	1.185	0.658	0.829	4.07E-01	

M1d	**Source**	**exp(coef)**	**lower 0.95**	**upper 0.95**	***z***	***p***	
(IS = I)	Trans	1.167	0.532	2.559	0.386	6.99E-01	

M1d	**Source**	**exp(coef)**	**lower 0.95**	**upper 0.95**	***z***	***p***	
(IS = II)	Trans	1.210	0.501	2.920	0.424	6.72E-01	

M1e	**Source**	**exp(coef)**	**lower 0.95**	**upper 0.95**	***z***	***p***	
(IS = I)	Cnpy	2.154	1.076	4.309	2.168	3.02E-02	*

M1e	**Source**	**exp(coef)**	**lower 0.95**	**upper 0.95**	***z***	***p***	
(IS = II)	Cnpy	1.334	0.598	2.979	0.704	4.82E-01	

M1f	**Source**	**exp(coef)**	**lower 0.95**	**upper 0.95**	***z***	***p***	
(IS = I)	Reat	0.001	0.000	1.774	-1.811	7.01E-02	.
	Mat	0.095	0.012	0.741	-2.247	2.47E-02	*
	Reat x ST	1.536	0.888	2.657	1.536	1.25E-01	

M1f	**Source**	**exp(coef)**	**lower 0.95**	**upper 0.95**	***z***	***p***	
(IS = II)	Reat	0.026	0.000	3.125	-1.493	1.36E-01	
	Mat	0.078	0.023	0.262	-4.130	3.63E-05	***
	Reat x ST	1.167	0.841	1.620	0.923	3.56E-01	

Table S2 Results from time-to-event analysis on kelp reattachment (M2) presented as hazard ratios (+/- 95% CI). The source represents the numerator, with the alternative state as the denominator (i.e., a = Procedural Control, b = Initial Stage I, c = Unfenced, d = Not Transported, e = No Canopy, f = Not Reattached, and Not Matured). IS = Initial stage. Ctrl = Control, Brn = Barren, F = Fence, T = Transport, Eck = *Ecklonia*, Und = *Undaria*, IS2 = Initial stage II, ST = Start time (week), Trans = Transported, Cnpy = Canopy, Mat = Maturation, Reat = Reattachment. Asterisks denote significance at different alpha levels: * <0.05; ** <0.01; * <0.001.**

M2a	**Source**	**exp(coef)**	**lower 0.95**	**upper 0.95**	***z***	***p***	**Significance**
(IS = I)	Brn	1.463	1.144	1.870	3.031	2.44E-03	**
	Brn + F	0.579	0.426	0.787	-3.492	4.80E-04	***
	T + Brn	1.162	0.899	1.503	1.146	2.52E-01	
	T + Brn + F	0.672	0.494	0.913	-2.540	1.11E-02	*
	Eck	0.562	0.402	0.787	-3.356	7.91E-04	***
	Und	0.807	0.589	1.105	-1.336	1.81E-01	

M2a	**Source**	**exp(coef)**	**lower 0.95**	**upper 0.95**	***z***	***p***	
(IS = II)	Brn	2.180	1.736	2.737	6.711	1.93E-11	***
	Brn + F	2.051	1.629	2.582	6.117	9.55E-10	***
	T + Brn	2.197	1.752	2.756	6.810	9.78E-12	***
	T + Brn + F	1.319	1.037	1.680	2.251	2.44E-02	*
	Eck	0.914	0.702	1.191	-0.666	5.06E-01	
	Und	3.027	2.411	3.801	9.538	1.45E-21	***

M2b	**Source**	**exp(coef)**	**lower 0.95**	**upper 0.95**	***z***	***p***	
	IS2	2.209	1.841	2.651	8.515	1.66E-17	***
	IS2 x ST	0.970	0.989	0.951	1.463	2.23E-03	**

M2c	**Source**	**exp(coef)**	**lower 0.95**	**upper 0.95**	***z***	***p***	
(IS = I)	Fence	0.471	0.384	0.577	-7.276	3.43E-13	***

M2c	**Source**	**exp(coef)**	**lower 0.95**	**upper 0.95**	***z***	***p***	
(IS = II)	Fence	0.754	0.652	0.872	-3.808	1.40E-04	***

M2d	**Source**	**exp(coef)**	**lower 0.95**	**upper 0.95**	***z***	***p***	
(IS = I)	Trans	0.918	0.761	1.107	-0.896	3.71E-01	

M2d	**Source**	**exp(coef)**	**lower 0.95**	**upper 0.95**	***z***	***p***	
(IS = II)	Trans	0.814	0.704	0.941	-2.788	5.30E-03	**

M2e	**Source**	**exp(coef)**	**lower 0.95**	**upper 0.95**	***z***	***p***	
(IS = I)	Cnpy	0.735	0.584	0.925	-2.625	8.66E-03	**

M2e	**Source**	**exp(coef)**	**lower 0.95**	**upper 0.95**	***z***	***p***	
(IS = II)	Cnpy	0.997	0.855	1.162	-0.040	9.68E-01	

M2f	**Source**	**exp(coef)**	**lower 0.95**	**upper 0.95**	***z***	***p***	
(IS = I)	Mat	1.402	1.072	1.834	2.465	1.37E-02	*

M2f	**Source**	**exp(coef)**	**lower 0.95**	**upper 0.95**	***z***	***p***	
(IS = II)	Mat	1.065	0.875	1.298	0.631	5.28E-01	

Table S3 **Results from time-to-event analysis on kelp maturation (M3) presented as hazard ratios (+/- 95% CI). The source represents the numerator, with the alternative state as the denominator (i.e., a = Procedural Control, b = Initial Stage I, c = Unfenced, d = Not Transported, e = No Canopy, f = Not Reattached, and Not Matured). IS = Initial stage. Ctrl = Control, Brn = Barren, F = Fence, T = Transport, Eck = *Ecklonia*, Und = *Undaria*, IS2 = Initial stage II, ST = Start time (week), Trans = Transported, Cnpy = Canopy, Mat = Maturation, Reat = Reattachment. Asterisks denote significance at different alpha levels: * <0.05; ** <0.01; *** <0.001.**

M3a	**Source**	**exp(coef)**	**lower 0.95**	**upper 0.95**	***z***	***p***	**Significance**
(IS = I)	Brn	2.087	1.503	2.898	4.394	1.11E-05	***
	Brn + F	2.411	1.722	3.376	5.125	2.98E-07	***
	T + Brn	4.064	2.968	5.566	8.743	2.27E-18	***
	T + Brn + F	3.659	2.633	5.086	7.721	1.15E-14	***
	Eck	0.844	0.547	1.303	-0.763	4.45E-01	
	Und	2.244	1.558	3.232	4.343	1.40E-05	***

M3a	**Source**	**exp(coef)**	**lower 0.95**	**upper 0.95**	***z***	***p***	
(IS = II)	Brn	0.581	0.466	0.725	-4.808	1.53E-06	***
	Brn + F	0.604	0.484	0.753	-4.470	7.81E-06	***
	T + Brn	0.562	0.451	0.701	-5.105	3.32E-07	***
	T + Brn + F	0.692	0.558	0.856	-3.380	7.24E-04	***
	Eck	0.689	0.553	0.860	-3.300	9.68E-04	***
	Und	0.368	0.285	0.476	-7.620	2.53E-14	***

M3b	**Source**	**exp(coef)**	**lower 0.95**	**upper 0.95**	***z***	***p***	
	IS2	1.536	1.272	1.856	4.458	8.28E-06	***
	IS2 x ST	0.972	0.992	0.953	1.553	5.97E-03	**

M3c	**Source**	**exp(coef)**	**lower 0.95**	**upper 0.95**	***z***	***p***	
(IS = I)	Fence	0.998	0.837	1.191	-0.017	9.86E-01	

M3c	**Source**	**exp(coef)**	**lower 0.95**	**upper 0.95**	***z***	***p***	
(IS = II)	Fence	1.130	0.958	1.334	1.452	1.47E-01	

M3d	**Source**	**exp(coef)**	**lower 0.95**	**upper 0.95**	***z***	***p***	
(IS = I)	Trans	1.745	1.463	2.082	6.179	6.46E-10	***

M3d	**Source**	**exp(coef)**	**lower 0.95**	**upper 0.95**	***z***	***p***	
(IS = II)	Trans	1.053	0.892	1.243	0.613	5.40E-01	

M3e	**Source**	**exp(coef)**	**lower 0.95**	**upper 0.95**	***z***	***p***	
(IS = I)	Cnpy	0.371	0.296	0.466	-8.531	1.46E-17	***

M3e	**Source**	**exp(coef)**	**lower 0.95**	**upper 0.95**	***z***	***p***	
(IS = II)	Cnpy	0.831	0.697	0.990	-2.075	3.80E-02	*

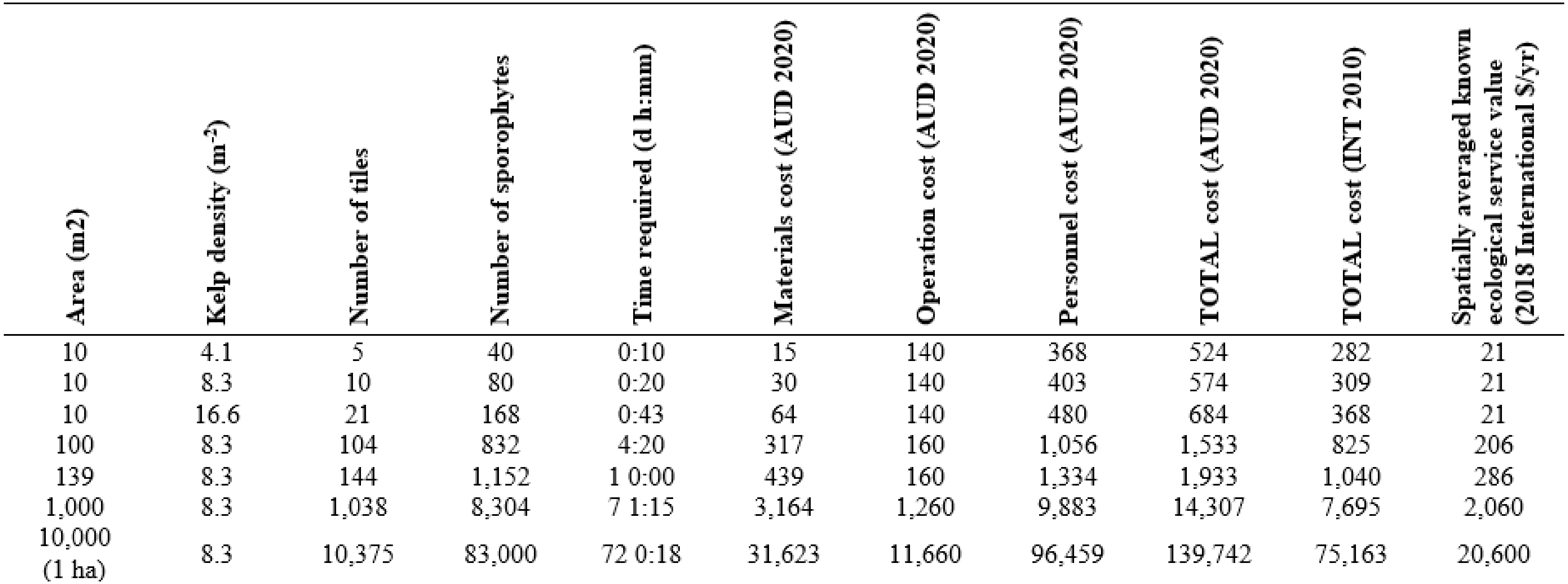
M3f	**Source**	**exp(coef)**	**lower 0.95**	**upper 0.95**	***z***	***p***	
(IS = I)	Reat	1.898	1.543	2.333	6.073	1.25E-09	***

M3f	**Source**	**exp(coef)**	**lower 0.95**	**upper 0.95**	***z***	***p***	
(IS = II)	Reat	1.291	1.107	1.506	3.248	1.16E-03	**

Table S4 Number of urchins observed across treatments during the experiment. Grayed cells indicate timesteps where the treatment was not maintained (i.e., fence was removed at week 12).

Week	Control	Disturbance Control	Barren	Barren + Fence	Transport + Barren	Transport + Barren + Fence	*Ecklonia* Canopy	*Undaria* Canopy
2	0	0	0	0	-	-	-	-
3	0	0	3	1	8	6	5	18
4	0	0	1	1	-	-	-	-
5	0	0	0	0	7	2	4	20
12	0	0	7	0	13	14	0	20
17	0	0	5	1	12	15	4	24

Table S4 **Example of costs for various possible restoration scenarios. Cost conversion from AUD 2020 to INT 2010 by Eger et al. (2020). Known ecological service values from Gaylard et al. (2020).**



Area (m2)	Kelp density (m^{-2})	Number of tiles	Number of sporophytes	Time required (d h:mm)	Materials cost (AUD 2020)	Operation cost (AUD 2020)	Personnel cost (AUD 2020)	TOTAL cost (AUD 2020)	TOTAL cost (INT 2010)	Spatially averaged known ecological service value (2018 International $/yr)
10	4.1	5	40	0:10	15	140	368	524	282	21
10	8.3	10	80	0:20	30	140	403	574	309	21
10	16.6	21	168	0:43	64	140	480	684	368	21
100	8.3	104	832	4:20	317	160	1,056	1,533	825	206
139	8.3	144	1,152	1 0:00	439	160	1,334	1,933	1,040	286
1,000	8.3	1,038	8,304	7 1:15	3,164	1,260	9,883	14,307	7,695	2,060
10,000 (1 ha)	8.3	10,375	83,000	72 0:18	31,623	11,660	96,459	139,742	75,163	20,600

CHAPTER 6 - GENERAL DISCUSSION

Since I began work on this thesis 5 years ago, the number of journal articles about kelp restoration has more than doubled (see Figure 11 in Supplementary). This increased research effort has been motivated by a growing appreciation for the scale of kelp forest degradation globally, along with the ecosystem services they provide. It coincides with a broader move towards ecosystem restoration, highlighted by the UN's "decade on restoration (UNDoR)", which aims to stop and reverse degradation of ecosystems worldwide, calling for hundreds of millions of hectares to be restored. Over 75% of the current committed area for restoration is explicitly terrestrial, with coastal areas clearly neglected (Sewell et al., 2020; Feehan et al., 2021).

Kelp forest restoration has been practiced since the 1700s, but to date it has been carried out mostly at small scales (Eger et al., 2022). The global cover of kelp and kelp-like species has been estimated at around 1.5 million km^2 globally (Duarte et al., 2022), but kelp forests have declined in many areas in recent years in response to a range of factors (e.g., Butler et al., 2020; McPherson et al., 2021; Coleman et al., 2022; Young et al., 2022). Upscaling restoration to the scale of kelp forest degradation is complicated by a lack of scalability in techniques used at small scale, high failure rates, insufficient funding or support due to a perception that it is too costly, as well as political issues (McAfee et al., 2022). Efforts to improve the condition of kelp forest ecosystems must consider the local context including current distributions, connectivity, species interactions, stressors, and potential ecosystem service values (Lester et al., 2020). A spatial management tool can be useful for systematically considering these factors.

A spatial management plan for degraded kelp forest ecosystems of Port Phillip Bay

Spatial management planning in the context of marine ecosystems refers to a strategic approach to understand and interact with marine ecosystems to support their ecological, social, and economic values (Ehler & Douvere, 2009). It has the potential to improve rollout of management actions aimed at improving the condition or resilience of ecosystems by increasing the likelihood of success, better targeting of co-benefits, and allowing a more wholistic appreciation for the context of individual interventions. Marine spatial planning aims to manage current and future uses of marine resources in a sustainable way, protecting their ecological, social, and economic values (DELWP, 2020). Spatial planning for marine ecosystem restoration has often focussed on identifying the most ideal conditions for the target ecosystem, with its persistence, or that of a particular species, as the primary measure of success (Lester et al., 2020). Such an approach risks restoring to a small range of environmental conditions, which in turn could make the restored habitat more vulnerable to complete loss from a single driver (Lamy et al., 2019). For example, areas with sheltered wave climate may provide insurance populations in the case of a severe storm despite high wave exposure normally benefitting kelp (Rattray et al., 2015). An important component of this approach, however, is the exclusion of unsuitable sites, which can be extended through consideration of specific details at a particular site (e.g., Layton et al., 2020). Targeting ecosystem service values may help spread restoration effort across gradients of environmental or social factors, make trade-offs more explicit (Lester et al., 2020), and provide greater return on investment (Gilby et al., 2020). While spatial management planning is in its infancy for marine ecosystems, there are already been some examples of how it can help (e.g., Pirrotta et al., 2014).

The management plan outlined below incorporates aspects from several sources, most notably from Pressey and Bottrill (2009), Lester et al. (2020), and Ehler and Douvere (2009). It aims to: (1) maximize impact through identification of appropriate management action based on existing conditions, (2) make use of all available information while recognizing limits and uncertainties, and (3) provide transparency to the process including what ecosystem services are being targeted and who the beneficiaries of those services would be. The 10 proposed steps are listed in Table 1 along with a brief description. I provide two example implementations of this plan to demonstrate its use with varying objectives and resources. I note that while this plan is focussed on the technical aspects of kelp forest ecosystem management relevant to Port Phillip Bay, drawing on work in this thesis, it should be embedded within a comprehensive framework. The framework should also integrate social, cultural, legal, and economic factors. For example, community consultations are essential for the project's long-term success and legitimacy. Likewise, legal vetting would be necessary to ensure compliance.

Table 1 Overview of steps in spatial management plan for kelp and urchin management.

Step	*Description*
1 | Identify assets	Define the extents of rocky reefs suitable for kelp forests across the study area. These may need to be clustered or divided to produce assets of a suitable size for management actions.
2 | Collect asset information	Collect relevant information on kelp and urchin management from across the study area. This is likely to include data at various spatial and temporal scales. It is important to note uncertainties or assumptions (e.g., observations from previous years that are likely to have changed, or inferences from studies of other species). Some examples include: ***Spatial:*** *Geometry, rugosity, depth.* ***Biotope:*** *Wave exposure, substrate, historic kelp extents.* ***Stressors:*** *Turbidity, nutrients, temperature.* ***Management overlays:*** *Marine protected areas, commercial fishing grounds, navigation channels.* ***Ecosystem services:*** *Nutrient concentrations or sources, access points, connectivity.* ***Fishery:*** *Catch, effort, diver observations.* ***Current status:*** *Species distributions and density, connectivity, condition.*
3 | Categorize by management action	Identify specific management actions appropriate for each asset where data is available. Importantly, this should identify areas where no action is required, and where further specific data are required.
4 | Define management priorities	The management priorities can help prioritize identified management actions and also inform how the work is carried out. This may include engagement with specific stakeholders, protection of specific areas, testing of techniques, or targeting specific ecosystem services.
5 | Identify available resources	This step allows feasibility assessment of the identified management actions. Resources may vary by action as well, especially where additional stakeholders can be engaged who can contribute to the work.
6 | Select locations and management actions	Based on the priorities and available resources, identified management actions are selected for implementation. This includes selection of scale for the intervention, which may be smaller than a defined asset, or include multiple assets.
7 | Local context and logistics	Given the complexity of the marine ecosystems being restored, implications of site-specific attributes should be considered, as well as the generality of assumptions being made. Some examples include *site access, wave and current exposure, local reef material, and context of studies informing expected response.*
8 | Set objectives and expectations	Quantitative objectives aligning with defined management priorities should be used where possible. Qualitative objectives should also be included where relevant, likely aligning with ecosystem services that are hard to quantify (e.g., cultural connection, education, &c.).
9 | Document and report	The decision-making process and implementation should be documented and reported to ensure transparency and inform future work. Changes to the design should be noted, including reasons for the changes.
10 | Monitor and review	A monitoring program should be included in the budgeting which provides required data for assessment against quantitative objectives. The entire process should be reviewed to identify necessary changes, for example additional data collection.

Example Restoration

The identification of assets, collection of asset information, and categorization by management option (steps 1-3) were completed in Chapter 2 of this thesis and are summarized in Table 2. The categorization tree, observed reef state, urchin density and roe quality, and proposed management actions determined in Chapter 2 are again illustrated here for reference in Figures 1-3. Note that subsites may be categorized as C, D, or E with canopy algae dominant or not, which will likely have implications for management. Following urchin removal these would end up as either A (no action required) or F or G (potentially requiring further actions). Two example scenarios of management priorities and available resources are considered, then specific locations, logistics, and objectives flowing from these are described in Table 3 and Table 4.

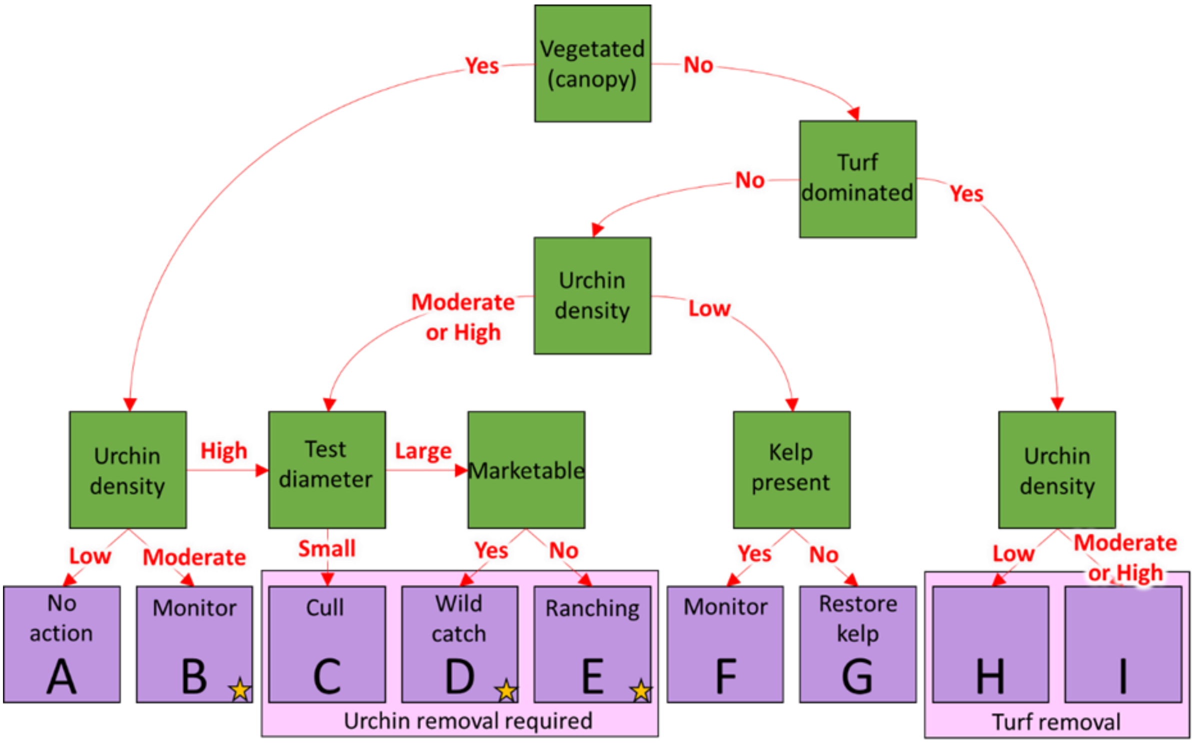
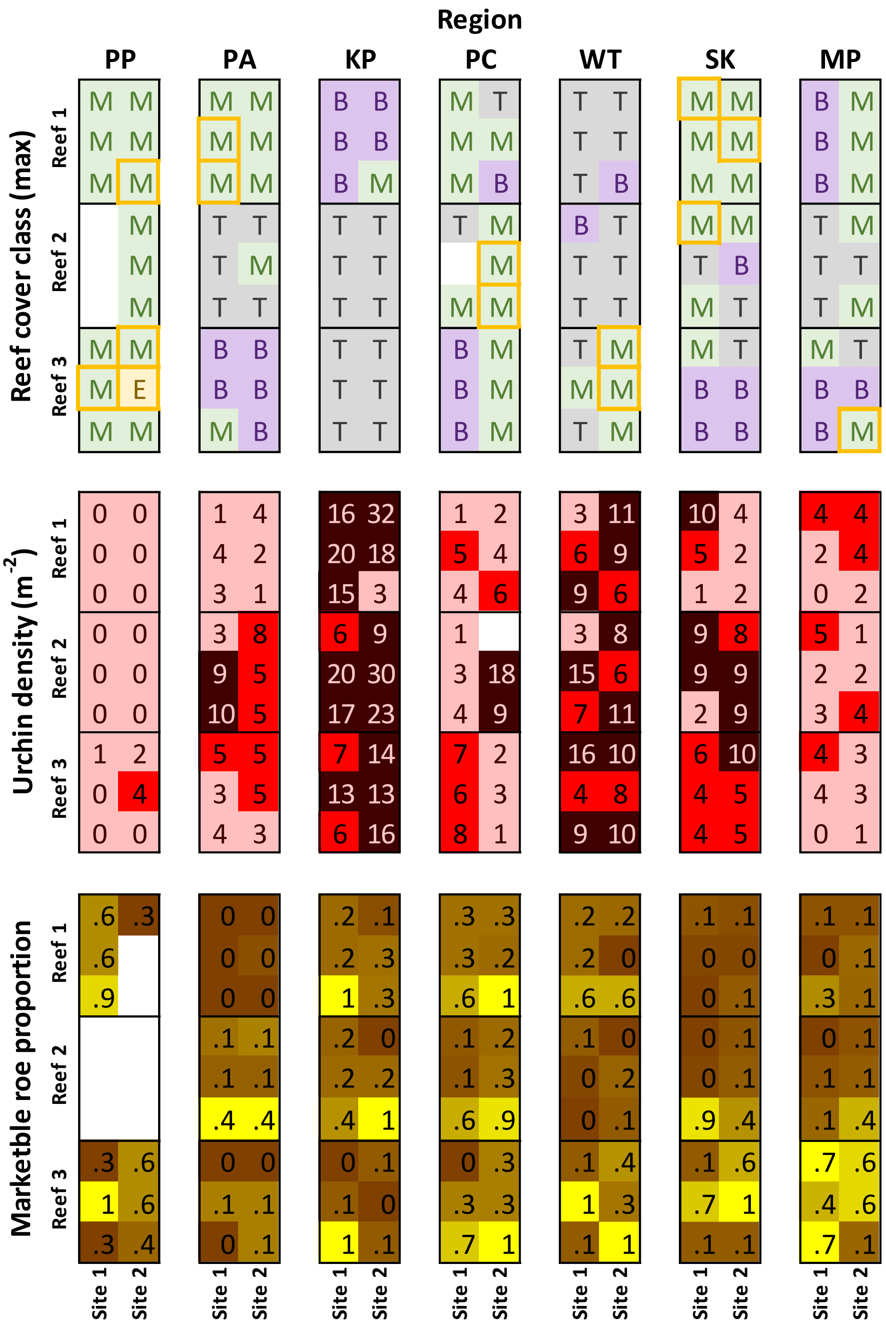


Figure 1 Categorization tree for reef management actions. Green boxes contain questions, red text the responses, and purple boxes the resulting actions. Stars indicate priority actions with greatest return for effort.



Reef cover class (max)	PP Site 1	PP Site 2	PA Site 1	PA Site 2	KP Site 1	KP Site 2	PC Site 1	PC Site 2	WT Site 1	WT Site 2	SK Site 1	SK Site 2	MP Site 1	MP Site 2
Reef 1	M	M	M	M	B	B	M	T	T	T	M	M	B	M
	M	M	M	M	B	B	M	M	T	T	M	M	B	M
	M	M	M	M	B	M	M	B	T	B	M	M	B	M
Reef 2		M	T	T	T	T	T	M	B	T	M	M	T	M
		M	T	M	T	T		M	T	T	T	B	T	T
		M	T	T	T	T	M	M	T	T	M	T	T	M
Reef 3	M	M	B	B	T	T	B	M	T	M	M	T	M	T
	M	E	B	B	T	T	B	M	M	M	B	B	B	B
	M	M	M	B	T	T	B	M	T	M	B	B	B	M

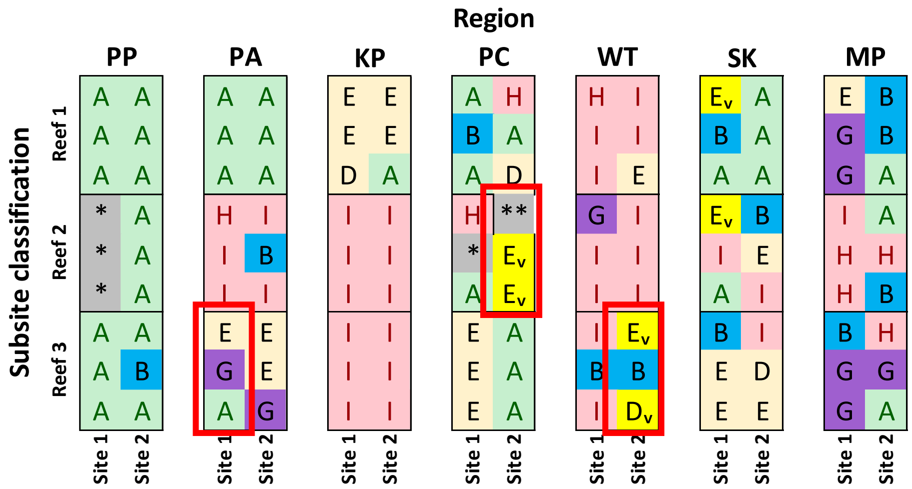
Urchin density (m^{-2})	PP Site 1	PP Site 2	PA Site 1	PA Site 2	KP Site 1	KP Site 2	PC Site 1	PC Site 2	WT Site 1	WT Site 2	SK Site 1	SK Site 2	MP Site 1	MP Site 2
Reef 1	0	0	1	4	16	32	1	2	3	11	10	4	4	4
	0	0	4	2	20	18	5	4	6	9	5	2	2	4
	0	0	3	1	15	3	4	6	9	6	1	2	0	2
Reef 2	0	0	3	8	6	9	1		3	8	9	8	5	1
	0	0	9	5	20	30	3	18	15	6	9	9	2	2
	0	0	10	5	17	23	4	9	7	11	2	9	3	4
Reef 3	1	2	5	5	7	14	7	2	16	10	6	10	4	3
	0	4	3	5	13	13	6	3	4	8	4	5	4	3
	0	0	4	3	6	16	8	1	9	10	4	5	0	1

Marketble roe proportion	PP Site 1	PP Site 2	PA Site 1	PA Site 2	KP Site 1	KP Site 2	PC Site 1	PC Site 2	WT Site 1	WT Site 2	SK Site 1	SK Site 2	MP Site 1	MP Site 2
Reef 1	.6	.3	0	0	.2	.1	.3	.3	.2	.2	.1	.1	.1	.1
	.6		0	0	.2	.3	.3	.2	.2	0	0	0	0	.1
	.9		0	0	1	.3	.6	1	.6	.6	0	.1	.3	.1
Reef 2			.1	.1	.2	0	.1	.2	.1	0	0	.1	0	.1
			.1	.1	.2	.2	.1	.3	0	.2	0	.1	.1	.1
			.4	.4	.4	1	.6	.9	0	.1	.9	.4	.1	.4
Reef 3	.3	.6	0	0	0	.1	0	.3	.1	.4	.1	.6	.7	.6
	1	.6	.1	.1	.1	0	.3	.3	1	.3	.7	1	.4	.6
	.3	.4	0	.1	1	.1	.7	1	.1	1	.1	.1	.7	.1

Figure 2 Subsite classification by highest percentage cover (top), urchin density (middle), and proportion of marketable roe (bottom)). Subsite initials: E = Ecklonia radiata, M = mixed macroalgae, B = bare, T = turf. Orange outlines indicate presence of E. radiata detected. Urchin densities coloured as high >8 (dark red), moderate (red), and low <4 (pink). Region initials: PP = Port Phillip Heads, PA = Portarlington, KP = Kirk Point, PC = Point Cooke, WT = Williamstown, SK = Saint Kilda, MP = Martha Point. White cells indicate missing data.

Table 2 Example implementation, steps 1-3 undertaken in Chapter 2.

Step	*Description*
1 | Identify assets	Biotope mapping of Port Phillip Bay that identifies rocky subtidal reefs already exists, based largely on work by (Ball & Blake, 2007). In Chapter 2 the Bay's reefs were divided at various spatial scales starting with 7 regions (200 ha) and extending down to subsites on the order of 1 ha. This finer resolution seems appropriate for management units.
2 | Collect asset information	Geometry and bathymetric derivatives (e.g., depth, slope, aspect, curvature, ruggedness) of the subtidal reefs across the Bay are readily available from the Victorian coastal DEM (Allemand et al., 2017). The bathymetric data is unlikely to vary significantly over time across the rocky reefs. Reef geometries may vary slightly due to detection methods used, particularly deeper reefs if aerial imagery was used to detect them. Spatial data layers for Marine Park boundaries and navigation channels, are available online (DEECA, 2022). Biotope mapping (Mazor et al., 2023) provides further information including reef state, underlying geology, and reef geometry. Much of this information is likely useful for future use, but specific biotope classifications, species presence/absence, or percentage cover are likely to change over time. Wave climate information was made available from a coupled hydrodynamic-spectral wave model of the Bay (Tran, 2020). While the wave climate may be changing with sea level rise and climate change, the model results are expected to be suitable at the scale of the model. As illustrated in Chapter 3, however, higher resolution hydrodynamics, including variations with depth, are likely to play important roles in kelp spore dispersal, as well as impact on sediment accumulation, turf development, and urchin activity. The survey in Chapter 2 provided current reef state, urchin density, and roe quality. The timing of collection for this data is critical. Roe quality can only be determined during the harvest period, and can change drastically year to year with, for example, changes in drift algae supply. This highlights the importance of collaboration with the urchin fishery, and having these plans in place so they can be actioned within days or weeks of data collection. Ecosystem services relevant to kelp beds in the Bay are limited and have not yet been evaluated at a sub-Bay level. The main service identified in a recent cost-benefit analysis was nutrient uptake (Whiteoak et al., 2020), which could be assumed to be greatest around the Western Treatment Plant, Altona River, and south-east of the Yarra River mouths, as the three main sources of nutrients from wastewater, market gardens, and urban runoff. Next was recreational and commercial fishing, which are likely concentrated around subtidal reefs, and areas with access and supporting facilities such as boat ramps, fishing platforms, and cleaning stations.
3 | Categorize by management action	In Chapter 2 I presented a categorization tree for management options. In that chapter I showed that interpolation of reef state and urchin density based on lower resolution averages resulted in incorrect management action categorization. This means management actions could not be determined outside of the targeted subsites and highlights the importance of high-resolution observation data. No action was required at 37 subsites, and another 39 subsites had turf, for which no management action is currently determined, and 5 had insufficient data to classify. There were 6 vegetated subsites at risk of collapse due to high urchin densities, and another 19 requiring urchin removal. Of the subsites requiring urchin removal, 4 had 100% marketable roe and would be ideal targets for commercial wild catch.



		Region													
		PP		PA		KP		PC		WT		SK		MP	
		Site 1	Site 2	Site 1	Site 2	Site 1	Site 2	Site 1	Site 2	Site 1	Site 2	Site 1	Site 2	Site 1	Site 2
Subsite classification	Reef 1	A	A	A	A	E	E	A	H	H	I	E_v	A	E	B
		A	A	A	A	E	E	B	A	I	I	B	A	G	B
		A	A	A	A	D	A	A	D	I	E	A	A	G	A
	Reef 2	*	A	H	I	I	I	H	**	G	I	E_v	B	I	A
		*	A	I	B	I	I	*	E_v	I	I	I	E	H	H
		*	A	I	I	I	I	A	E_v	I	I	A	I	H	B
	Reef 3	A	A	E	E	I	I	E	A	I	E_v	B	I	B	H
		A	B	G	E	I	I	E	A	B	B	E	D	G	G
		A	A	A	G	I	I	E	A	I	D_v	E	E	G	A

*Figure 3 Subsite management category based on categorization tree. A = no action required, B = monitor, C = cull, D = wild catch, E = ranching, F = monitor, G = restore kelp, H = turf removal, I = turf removal. The subscript $_V$ indicates vegetated reefs. * = A, F, G, or H; ** = A, B, or E. Red boxes indicate sites selected in the example applications.*

Table 3 Example implementation 1 – Protecting existing vegetated reefs and engaging partners.

Step	*Description*
4 | Define management priorities	• Protect existing vegetated reef. • Engage with partners (e.g., Urchin fishers, Parks Vic, community groups). • Promote recreational fishing of urchins.
5 | Identify available resources	• Funding to support 10 days on the water with a boat and dive team. • Urchin fishers – boats, divers (preferably with wild catch). • Parks Victoria support – boat, divers, volunteer network (for work inside Parks).
6 | Select locations and management actions	Two sites are of particular interest as they each contain three vegetated subsites, two of which are at risk of collapse due to overabundance of urchins. In addition to this, *E. radiata* was observed at four of the subsites. The first site is Point Cooke Reef 2 Site 2 (PC22A-C). Two of these subsites require urchin removal, while the third (PC22A) doesn't currently have urchin density data but may require urchin removal, monitoring, or no action. The second site is Williamstown Reef 3 Site 2 (WT32A-C). Here one subsite only requires monitoring as urchin densities are already below the threshold 8.m^{-2}. The other two require urchin removal, one of which (WT32C) has 100% marketable roe suitable for wild catch.
7 | Local context and logistics	PC22A-C is just inside Point Cooke Marine Sanctuary's eastern boundary. Working here gives the opportunity to fill a data gap, and also to work closely with Parks Victoria. While at least two of the subsites require urchin removal, this would require Parks permits, which are likely to exclude removal for commercial profit. The incentive for commercial fishers to help with the removal would therefore be lost. Parks Victoria themselves, however, may be able to contribute resources for both the initial urchin removal and ongoing monitoring. The reef (PC2) has a total area of 263 ha which includes healthy vegetated areas (e.g., PC21C), and areas dominated by turf (e.g., PC21A). The neighbouring reefs are 1.5 km to the north (PC3) which is vegetated, and 1.9 km to the south-west (PC1) which is mostly vegetated, with some barren (e.g., PC12C) and some turf dominated reef (e.g., PC21A). Urchin densities on both neighbouring reefs is low to moderate. The site (PC22) is close to popular fishing areas immediately outside the sanctuary, but is not commonly visited by divers or snorkelers, and fishing is strictly prohibited. The sandy

	area between this reef and the reef to the north supports a large sea grass meadow, which likely benefits from drift algae supply from the neighbouring reefs. WT32A-C is located south-east of Williamstown Beach. It is exposed so south-westerly, southerly, and south-easterly wind waves. The reef at Williamstown (WT3) has an area of 5 ha, and includes areas dominated by turf (e.g., WT31A and WT31C). There is a neighbouring reef 250 m to the west which was not included in the survey of Chapter 2. The next reef to the east is 5 km away on the other side of the Yarra River channel with an *E. radiata* connectivity strength of less than 5%, and *H. erythrogramma* connectivity strength of less than 10% (Johnson et al., 2015). The area is popular with boaters, fishers, swimmers, snorkelers, and beach goers. WT32C had 100% marketable urchins. It is the shoreward subsite, with an average depth of around 1 m. This would make commercial harvesting using traditional hookah setups difficult but may be particularly suited to collection by shore divers / snorkellers. This would be a great opportunity to promote recreational harvesting of urchins. WT32A is the deepest subsite with an average depth of around 5.6 m. Only 40% of urchins were marketable from this subsite, so urchins would likely need to be ranched prior to sale. Commercial urchin fishers may be able to be included in the collection of urchins from the shallow subsite. Aerial imagery of the reef suggests the reef geometry may underestimate the total extent. A consistent dark area extends into deeper water across all years of imagery observed suggesting the reef area may be double the current estimate. This is an opportunity to validate the extents of the reef and update the input layers if required.
8 | Set objectives and expectations	• Prevent the formation of barrens across the two sites. • Document urchin densities and reef state following urchin removal, and at the monitoring subsite (WT32B). • Maintain urchin densities below the $8.m^{-2}$ threshold. • Maintain engagement of partners throughout the year. Learn from the relationships to improve future engagements including identification of co-benefits. • 100 recreational urchin fishing trips through the year following initial removal. • Validate the extents of the Williamstown reef and update data layers if necessary.
9 | Document and report	All planning decisions and on-ground actions will be documented. Reports will be prepared for both technical and administrative (research and government stakeholders) as well as in more appropriate formats for recreational and commercial fishing partners.
10 | Monitor and review	Ongoing monitoring across all 6 subsites will be undertaken quarterly through to the following harvest season at which time a report will be prepared to explain findings from the first year. Asset information will be updated for the following season, and the process adjusted if required.

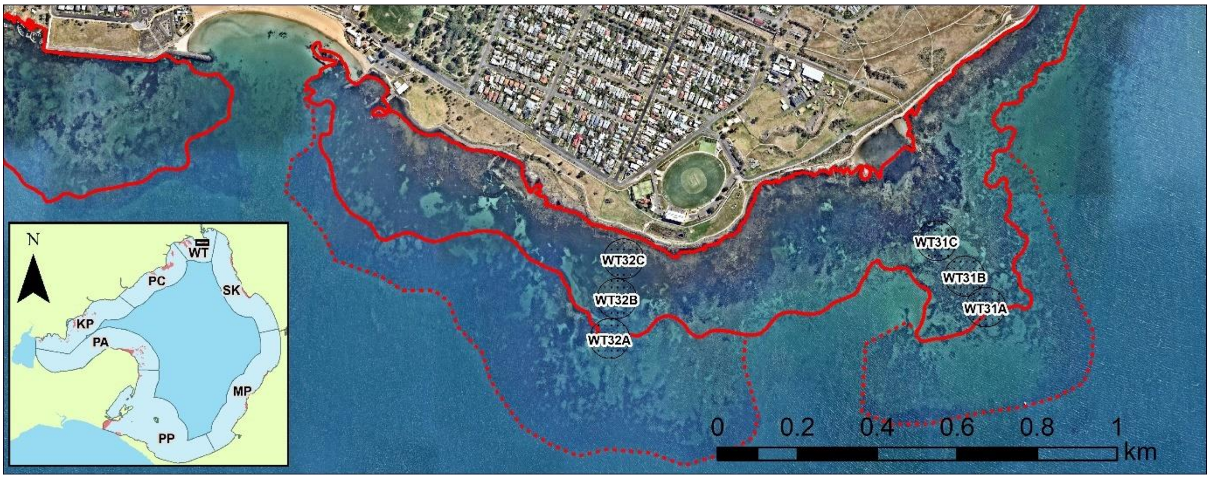


Figure 4 Williamstown Reef 3 with subsites marked as black circles. Red lines indicate reef extent from current biotope mapping, while imagery shows a darker colouring out to deeper water suggesting the reef may extend further.

Table 4 Example implementation 2 – Trialling transplanting and ranching.

Step	*Description*
4 | Define management priorities	• Full scale trial of transplanting method. • Trial urchin ranching at scale. • Work at a less accessible site to avoid too much public exposure for a risky project. Risky considering the chance of different outcomes in different conditions, and scale effects (e.g. Chapters 3 and 5).
5 | Identify available resources	• Partner with an aquaculture facility. • Research partners with dive team experienced in transplanting kelp. • Several tonnes of bluestone blocks. • Funding to support 10 days on the water with a boat and dive team.
6 | Select locations and management actions	PA31A-C is selected as a site requiring both urchin removal (not marketable quality; PA31A) and active restoration (transplanting; PA31B). The third subsite (PA31C) is vegetated with low urchin density so requires no action.
7 | Local context and logistics	This site is located off Portarlington and attracts relatively few divers despite only being 3 to 5 m deep. The reef has an area of 33 ha and is surrounded on all sides by smaller reefs which were not included in the Chapter 2 survey. The area is exposed to wind waves from the north, east, and south, and experiences relatively strong tidal currents. Connectivity plots suggest weak delivery of kelp propagules and urchin larvae from the Port Phillip Heads region which has healthy reefs with generally very low urchin densities. The nearest observed kelp in the survey was at two subsites 1.5 km north. To the west of that kelp bed on the same reef is a bathymetric feature similar to the bommies at Pt Linley where a potential sink for kelp sporophytes was identified in Chapter 5. Here the reef suddenly rises from 5 m to less than 2 m. This should be investigated as a potential source of juvenile sporophytes for transplanting. Within PA31B, the highest rugosity lies in the north-east across an area of approximately 140 m^2 (Figure 5 right panel). Increased ruggedness suggests higher likelihood of vertical surfaces which I established in Chapter 4 see higher recruitment of juvenile kelp. Applying the transplant method from Chapter 5 the whole 140 m^2 could be revegetated in a single day at an average sporophyte density of around 8 m^{-2}. Based on current literature this should be a sufficient density and patch size to see high survival and recruitment (Layton, Shelamoff, et al., 2019). Alternatively, transplants could be deployed to several

	areas within the subsite, maintaining sufficient patch sizes to promote survival, growth, and recruitment, noting the largest patch size considered by Layton, Shelamoff, et al. (2019) was under 8 m^2. The basalt blocks available are thicker and heavier than the tiles used in Chapter 5 so would require additional deck space but should anchor well despite the higher current speeds. Collection of urchins from PA31A could yield over 7,500 urchins, with lower density across the rest of the site. The area in the north-west of the subsite also has relatively high rugosity, so it could be either targeted for transplants as well or monitored to detect recruitment from the transplants 50 m to the west. Having three different starting conditions and interventions on a single reef provides a great opportunity to learn about the natural progression of reef states as well as the effectiveness of my interventions. Reef outlines from biotope mapping appear to be offset to the south-west about 50 m. This work could be an opportunity to validate the reef extents and also get collect reef state and urchin density information for the small reefs around the site. It is quite possible that some of these contain kelp beds.
8 | Set objectives and expectations	• Maintain a kelp density across restored area of 8 m^{-2}. • Observe recruitment within and outside the extents of transplant area. • Collect time series of changes in urchin densities and reef state across the site. Expansion of the kelp bed is expected to be slow (see Chapter 4). There is an opportunity here to test the possible impact of stronger tidal currents on dispersal and recruitment. • Kelp transplanting should take place as soon as recruits, preferably stage II, are available in winter to avoid photodamage (Graham et al., 2021). The urchin removal for ranching would more likely be suited to early summer when water is a bit warmer. • Develop relationship with partners for urchin ranching and demonstrate return on investment for ranching at scale. • Establish an ongoing market for ranched urchins. • Validate existence of sink population(s) if kelp is present. • Validate reef extents and collect reef state and urchin density data from neighbouring reefs.
9 | Document and report	All planning decisions and on-ground actions will be documented. Reports will be prepared for both technical and administrative (research and government stakeholders). Results from the ranching will also be documented, and promotional material developed to assist the brand.
10 | Monitor and review	Ongoing monitoring across all 6 subsites will be undertaken quarterly through to the following harvest season at which time a report will be prepared to explain findings from the first year. Asset information will be updated for the following season, and the process adjusted if required.

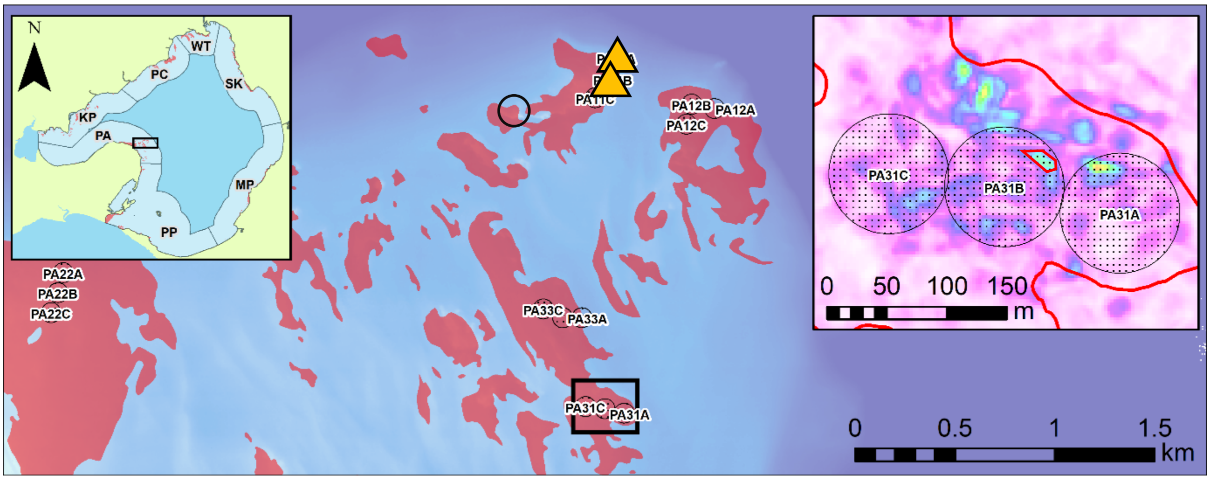


Figure 5   Portarlington reefs discussed in implementation 2. Red shading shows subtidal rocky reef. Yellow triangles: subsites with observed kelp. Black circle: Potential sink for kelp recruits. [Left inset] Port Phillip Bay with extent indicator for main figure. [Right inset] Proposed site for implementation 2 (PA31) with rugosity map in the background. Red polygon in PA31B is the proposed location for transplant deployment.

Future Directions

Kelp restoration research is growing fast with some exciting initiatives emerging, but there remain many research gaps. The rapid pace of kelp forest degradation necessitates optimized solutions and research effort, including open sharing of knowledge across the restoration community. Restoration attempts themselves are important data sources, whether successful or not (Waltham et al., 2021; Eger et al., 2022). The recent formation of the Kelp Forest Alliance[1] is a good example of a tool to promote collaboration and sharing of knowledge.

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[1] https://kelpforestalliance.com/

My work on this thesis has highlighted five areas that demand further attention:

1. Exploring approaches to understand and mediate negative effects of turf algae;
2. Defining kelp dispersal kernels and recruitment patterns;
3. Quantifying kelp ecosystem services;
4. Partnering with relevant stakeholders; and
5. Expanding understanding of kelp-urchin metacommunity dynamics.

Approaches to understand and mediate negative effects of turf algae

Turfing algae are typically fast growing, opportunistic algae lacking the seascape structure of kelps and fucoids, and able to trap sediments to form a turf-sediment matrix (Filbee-Dexter & Wernberg, 2018). Turf dominated systems have been identified as an alternate stable state to kelp dominated states on temperate rocky reefs, increasing in spatial prevalence along with the decline of macroalgal beds (Munda, 1993; Airoldi, 2007). They can prevent successful recruitment of other algae to the underlying substrate (Layton, Cameron, et al., 2019; Harvey et al., 2021) and provide an insecure substrate for direct recruitment (Burek et al., 2018). While urchin barrens may form due to excessive herbivore pressure, and may be managed with urchin removal or predator protection, the development of algal turfs may indicate less suitable environmental conditions for kelp, such as higher temperature, lower pH, and/or higher nutrient loads (Filbee-Dexter & Wernberg, 2018). Addressing these underlying stressors is an important preliminary step in the management of such reefs, to provide a more suitable environment for the kelp ecosystem, and reduce the need for ongoing maintenance.

The management actions required following removal of background stressors is not yet clearly understood. Urchins may modify their diet to consume turf algae (Miller et al., 2022) which may facilitate reef rehabilitation, conversely, the turf may restrict urchin movement or grazing (O'Brien & Scheibling, 2018), or promote dislodgement of urchins (Kawamata, 2010). Consequently, understanding urchin – turf – kelp dynamics is essential to inform management. Several management actions have been applied to mediate these interactions with mixed outcomes. While mechanical removal of turf has been used in field experiments, it is generally considered infeasible at large scale. Green gravel is a recent innovation that involves seeding gravel with kelp sporophytes before distributing the gravel on a reef for restoration (Fredriksen et al., 2020). An initial trial with *Saccharina latissima* showed similar survival, increased growth, and higher retention of seeded green gravel in turf compared to bare reef (Fredriksen et al., 2020). The low attachment rate of sporophytes to the substrate under turf (~1.6%) is a major concern, as dislodgement could result in loss from storms, or with the increased drag associated with frond growth. Consequently, successfully seeding at reef scale would require deploying gravel at 65 times the desired final sporophyte density (4.9 kg.m^{-2} for 7 sporophytes.m^{-2}), making it more like an artificial reef. One potential solution to this was observed during testing of the cultivation stage for *E. radiata*, where detached gametophytes reattached to substrate (Alsuwaiyan et al., 2022). Adult sporophytes grown using this method may remove the turf locally through mechanical action of the fronds, and therefore provide clear substrate for subsequent recruitment. However, infilling rates may still be reduced in the presence of turf at certain densities. Transplanting of juvenile sporophytes on tiles (Chapter 5; Graham et al., 2021) may also prove useful for turf removal, with the tiles anchoring the sporophytes to maturity, allowing sweeping and recruitment, then potentially redeployment of the tiles elsewhere. Removal of turf to facilitate kelp recovery will be difficult, especially if the underlying causes of turf dominance such as eutrophication are not directly addressed. Given the plethora of work to be done in this space, the management actions presented in Chapter 2 did not expand on actions for turf dominated reefs.

Defining kelp dispersal kernels and recruitment patterns

To maximise the efficiency and efficacy of restoration, managers should make full use of natural recruitment including infilling. This requires an understanding of both the: 1) expected spore density, which is a function of distance, size, density, and adult reproductive output of source beds as well as their location relative to dispersal processes; and 2) the expected sporophyte recruitment rate for given environmental conditions, which requires development and reproduction of gametophytes followed by development of embryonic sporophytes. If suitable environmental conditions (e.g., bare substrate with limited grazing pressure and sufficient nutrients) can be provided within an area with sufficient natural propagule supply, or propagules can be provided to an area with suitable conditions for recruitment, more intensive active restoration activities may be avoided. This is desirable as passive restoration techniques are more cost effective allowing them to be applied at much larger scales.

Estimating expected spore densities requires an understanding of the magnitude and timing of spore production and dispersal. This evaluation requires a metapopulation approach, as multiple source beds may have overlapping dispersal distributions. Thus, we require spatial information on patch size, density, and reproductive effort (Layton, Shelamoff, et al., 2019). Interactions can also exist within these factors, such as varying population fecundity with density (Reed, 1990). Currents may assist spore dispersal, with studies of *M. pyrifera* suggesting sufficient current speed, forest size, and gamete viability could support dispersal more than 1 km (Gaylord et al., 2006). High current speeds, however, also risk over-diluting spores leaving gametophytes too far apart to allow successful fertilization (Lüning & Müller, 1978; Gaylord et al., 2006; Tatsumi, 2018). As a result, variations in population fecundity can also lead to changes in spatial connectivity (Castorani et al., 2017). The dispersal of *E. radiata* spores is thought to be distance limited (Coleman et al., 2009) with most travelling only on the order of meters. The survey presented in Chapter 4 showed a decline in recruitment with distance from the kelp bed, but no correlation with current directions and speeds, suggesting either finer scale hydrodynamics such as wave turbulence, mixing, and effects from bed and vegetation may play an important role, or perhaps the receiving environment played a more important role (Reed, 2004).

Following settlement of spores and successful fertilization, recruitment of the sporophyte form is dependent on a range of environmental conditions. Light, nutrient, and sediment conditions need to be within suitable ranges (Reed et al., 2006). They can be challenged by inter and intra specific competition and threatened by grazing. Understanding the role of each factor in the recruitment is made more difficult by the microscopic size these early life stages. Monitoring the spatial distribution of kelp beds, their spore production, microscopic and macroscopic recruitment, and currents, along with manipulative experiments, can help to determine whether recruitment is limited by adult reproduction, proximity of source populations, or subsequent development of early life stages.

Evaluating kelp ecosystem services

The evaluation of ecosystem services provided by kelp is important for stimulating preservation and restoration efforts and can also be used at a local scale to inform restoration actions. In arguing for an identity for the *Great Southern Reef*, Bennett et al. (2016) pointed out the limited funding temperate reefs attract relative to their tropical counterparts, noting studies on coral reef services led to a 42 fold increase in their estimated value (Costanza et al., 2014). Likewise, the slowing of saltmarsh loss has been attributed to work on understanding their ecosystem service value (zu Ermgassen et al., 2021). Services that provide tangible economic values such as increased commercial fish stocks can drive political and commercial interest and other services that can be assigned a dollar value can be useful for providing economic incentives (Costanza et al., 2014). While quantifying the dollar value of most ecosystem services can be challenging, it is still important for providing transparency in decision making where trade-offs are made (Costanza et al., 2014), including who the beneficiaries are. Framing restoration work in terms of ecosystem service provision can help to broaden its appeal (Matzek & Wilson, 2021).

Coastal habitats are at particular risk from human impacts and are areas of concentrated ecological service value (McAfee et al., 2021; Butler et al., 2022). The spatial distribution of these services can inform prioritization of management actions, as well as their execution. For example, in the case of two similar restoration sites being considered, if one has better access (for recreation, study, or spiritual connection) it may be prioritized, and additional community involvement could be included.

Few ecosystem services for *E. radiata* have been evaluated to date, and those that have are mostly at a large spatial scale (e.g., Great Southern Reef) and were not therefore able to be used to prioritise sites at smaller spatial scales (e.g., within Port Phillip Bay). Further work is required to adapt estimates to the local context, and inferences drawn from local observations (e.g., known nutrient sources, or popular diving sites) should be formally tested.

A recent cost benefit analysis reviewed published literature on kelp ecosystem service valuation and applied it to Port Phillip Bay (Whiteoak et al., 2020). They proposed a conservative estimate of \$58,000.ha^{-1} for nitrogen retention by combining estimates of nitrogen accumulation in kelp with an offset value defined by the local catchment authority (Melbourne Water, 2021). Further refinement may be possible considering known point sources of nitrogen, where concentrations are locally much higher (Harris et al., 1996), however, such cases may represent acute stressors to kelp forests as they may promote turf algal production. The provisioning service of seafood production in the Bay, in response to restored kelp habitat on bare reef, was estimated at around \$1,400.ha^{-1}.yr^{-1} including commercial finfish and shellfish, and recreational fishing (Whiteoak et al., 2020). Again, this estimate could be further refined with localized data such as locations of boat ramps and other fishing infrastructure, and areas most suited to shellfish production. The Whiteoak et al. (2020) cost-benefit analysis didn’t evaluate ecosystem services with less direct economic benefit. The recreational value of kelp beds beyond fishing is also important, with some popular diving and snorkelling sites around the Bay. These benefits are likely to be concentrated in areas that are accessible, and perhaps have supporting amenities nearby. These services are not solely dependent on kelp beds, and, therefore, care should be taken in assigning ecosystem service values to kelp beds. For example, mixed macroalgal or fucoid beds may provide similar ecosystem services. Further work could define these ecosystem values spatially across the Bay informing prioritization of sites for restoration.

Cooperation with other stakeholders

Urchin herbivory has been identified as a proximate cause of kelp forest degradation and lack of recovery in Port Phillip Bay. Chapter 2 of this thesis highlighted a benefit of cooperation between restoration ecologists and urchin fishers, with targeted harvesting providing a commercial product and improving conditions for kelp recovery. On the east coast of Tasmania, a commercial fishery for barren forming *Centrostephanus rodgersii* has developed, assisted by regionally defined economic incentives for fishers, aiming to stop the spread of the urchins and to protect kelp beds from barren formation through targeted harvest (Cresswell et al., 2022). In this scenario, coupling targeted harvest with the finer spatial scale described in Chapter

2, allows for ecologically relevant density thresholds to be targeted to avoid barren formation. Additionally, acquiring the necessary data to inform these management decisions may be facilitated by citizen scientist programs, which are useful in collecting large quantities of data on temperate reefs (Edgar et al., 2020). In collaboration with commercial fishers these assessments could provide highly relevant, high-resolution data on reef state, urchin density, and roe quality, and allow rapid implementation of targeted urchin removal following management decisions. Cooperation with the broader community may also promote ecosystem cultural services such as knowledge, education, recreation, and spiritual connections (Department of the Environment, 2009).

Understanding kelp-urchin metacommunity dynamics

Kelp-urchin dynamics can exhibit local variability from both local factors and outside connections, requiring different management interventions. However, the complexity of ecosystems has meant most studies occur in relative isolation to reduce “noise”. This approach is useful for understanding individual processes but removes us from the broader context where external interactions are often very important.

The density of urchins a kelp bed can support without collapsing may vary with environmental conditions as they impact on either the urchin grazing rates or the kelps resilience. For example, high wave or current exposure, or availability of alternate food sources, may reduce the grazing pressure from urchins (Vanderklift, 2009; Kawamata, 2010). Alternatively, high turbidity in the Bay's north, or excessive epiphytic growth from high nutrient levels or low exposure in the north-west may reduce the production rate of kelp and its ability to withstand grazing (Luening, 2003; Pedersen, 2012). In the Mediterranean a complex interaction has been observed between nutrients, kelp, urchins, and limpets. High nutrients allow higher productivity of kelp, providing a buffer to grazing pressure, while low nutrients lead to increased grazing by limpets following barren formation (Illa-Lopez et al., 2023) (Boada, 2017).

Even when local conditions are well understood, reefs are connected to one another at a larger scale through the dispersal of larvae, propagules, and wrack. Where urchin recruitment is driven by external larval supply, the current urchin density may not be a good indicator of future grazing pressure. Urchin densities may recover much quicker after removal if surrounding reefs have high urchin densities. Likewise, an influx of drift algae to a barren may lead to a spike in urchin roe development and subsequent recruitment to nearby reefs. Effective management of kelp beds and urchins requires a wholistic approach which takes into consideration these larger-scale dynamics.

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Supplementary

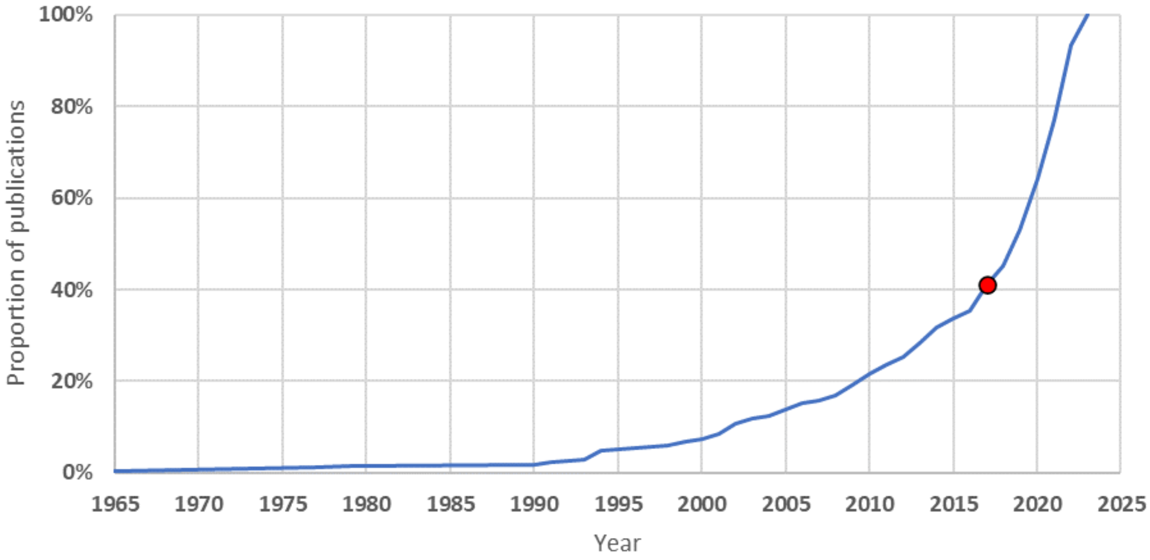

Figure 11 Cumulative proportion of publications to March 2023 returned from Web of Science search for "kelp restoration" (total = 268). Red dot indicates the year I started the thesis 2017, to which point there were 110 publications (41%).