



Alternative stable states, demography and
intraspecific facilitation in the intertidal ecosystem
engineer *Hormosira banksii*

Ryan D Lewis

BSc Marine Biology (Honours)
Flinders University, South Australia

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Declarations

Statement of originality

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Statement of Co-Authorship

The following people and institutions contributed to the publication of work undertaken as part of this thesis:

Candidate – Ryan David Lewis, Institute of Marine and Antarctic Studies, University of Tasmania

Author 1 – Jeff T Wright, Institute of Marine and Antarctic Studies, University of Tasmania

Author 2 – Craig R Johnson, Institute of Marine and Antarctic Studies, University of Tasmania

Author 3 – James E Byers, Odum School of Ecology, University of Georgia

Author 4 – Cayne Layton, Institute of Marine and Antarctic Studies, University of Tasmania

Author 5 – Victor Shelamoff Institute of Marine and Antarctic Studies, University of Tasmania

Author 6 – Masayuki Tatsumi, Institute of Marine and Antarctic Studies, University of Tasmania

Paper 1: Located in Chapter 2

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Author Contributions:

Conceived and designed experiment: Candidate, Author 1, Author 2

Performed the experiment: Candidate, Author 1, Author 2

Provided advice and feedback on experimental design, data analysis and writing: Author 1, Author 2

Analysed the data: Candidate, Author 1

Wrote the manuscript: Candidate, Author 1, Author 2

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Author Contributions:

Conceived and designed experiment: Candidate, Author 1, Author 2

Performed the experiment: Candidate, Author 1, Author 2

Provided advice and feedback on experimental design, data analysis and writing: Author 1, Author 2

Analysed the data: Candidate, Author 2

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Author Contributions:

Conceived and designed review and meta-analysis: Candidate, Author 1, Author 2, Author 3, Author 4, Author 5, Author 6

Data collection: Candidate, Author 1, Author 2, Author 3, Author 4, Author 5, Author 6

Performed the meta-analysis and review: Candidate, Author 6

Provided advice and feedback on experimental design, data analysis and writing: Author 1, Author 3, Author 4, Author 5, Author 6

Analysed the data: Candidate, Author 1

Wrote the manuscript: Candidate, Author 1, Author 3, Author 4, Author 5, Author 6

We, the undersigned, endorse the above stated contribution of work undertaken for each of the peer-reviewed manuscripts contributing to this thesis:

Signed:

Ryan D Lewis	Jeff Wright	Catriona MacLeod
Candidate	Primary Supervisor	Head of School
IMAS	IMAS	IMAS
University of Tasmania	University of Tasmania	University of Tasmania
Date: 17/01/2019	22/01/2019	22/01/2019

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Contents

Declarations	i
Statement of originality	i
Statement of authority of access	i
Statement of Co-Authorship	ii
Acknowledgements	v
Contents	vii
List of Tables	x
List of Figures	xi
Abstract	xiv
1. Introduction	1
1.1 Ecosystem engineers	1
1.2 Alternative stable states	2
1.3 Study system	5
1.4 Thesis structure	7
2. No evidence of alternative stable states in the dynamic between the habitat-forming seaweed <i>Hormosira banksii</i> and coralline turf	9
2.1 Abstract	9
2.2 Introduction	10
2.3 Method	14
2.3.1 Study Site	14
2.3.2 Manipulation of percent cover and sampling	14
2.3.3 Statistical Analyses	15

2.4 Results	16
2.5 Discussion.....	18
3. Demography of the intertidal furoid <i>Hormosira banksii</i> : importance of variable recruitment to local abundance.....	28
3.1 Abstract.....	28
3.2 Introduction	29
3.3 Method.....	32
3.3.1 Natural history.....	32
3.3.2 Study Site	32
3.3.3 Experimental design and demographic sampling.....	33
3.3.4 Statistical Analysis	34
3.4 Results	36
3.4.1 Does recruitment vary over time and between treatments containing different amounts of <i>H. banksii</i> and turf?	36
3.4.2 Is recruitment related to local abundance?	37
3.4.3 Does post-recruitment mortality vary among cohorts?	37
3.4.4 Does growth and survivorship vary among different size classes and times?.....	37
3.4.5 Is post-recruitment mortality density-dependent or density-independent?	38
3.5 Discussion.....	39
4. Intraspecific facilitation in marine ecosystem engineers: a review.....	54
4.1 Abstract.....	54
4.2 Introduction	56
4.3 Method.....	59

4.3.1 Data Collection and Eligibility Criteria.....	59
4.3.2 Data Collection and Effect Size Calculation.....	60
4.3.3 Meta-analysis	61
4.4 Results	62
4.4.1 Effects of intraspecific facilitation on the demography of ecosystem engineers	63
4.4.2 Is intraspecific facilitation in ecosystem engineers stronger in intertidal compared subtidal systems?	64
4.4.3 Does intraspecific facilitation differ between invertebrate and macrophyte ecosystem engineers?.....	64
4.4.4 Does intraspecific facilitation differ between studies which focused on the presence vs. absence or high vs. low density of ecosystem engineers?.....	64
4.5 Discussion.....	66
5. Synthesis	74
5.1 Alternative Stable States	76
5.2 Recruitment, survivorship and growth of <i>Hormosira banksii</i>	79
5.3 Intraspecific facilitation by ecosystem engineers in marine environments.....	80
5.4 Conclusion.....	81
6. References	83

List of Tables

Table 2.1. One-way ANOVA results for the effects of ratio of <i>Hormosira banksii</i> to coralline turf before manipulation, after manipulation (T0) and after 24 months (T24). Analyses were conducted on the percentage cover of five key variables; <i>H. banksii</i> canopy, coralline turf understory, bare rock, sand, and other macroalgae (sand was not measured before manipulation). * $p \leq 0.05$, ** $p \leq 0.01$, *** $p \leq 0.001$	22
Table 2.2. PERMANOVA of the effects of Ratio and Site on the percent cover of <i>Hormosira banksii</i> and coralline turf post-manipulation (T0) (A) and after 24 months (T24) (B). *** $p \leq 0.001$	23
Table 2.3. Pairwise a posteriori comparisons of levels of the factor Ratio post-manipulation (T0) and after 24 months (T24) following the PERMANOVA for <i>H. banksii</i> and coralline turf percentage cover. Significant values ($P < 0.05$) are shown in bold.....	24
Table 3.1. Two-factor ANOVA testing the effects of treatment (ratio of <i>Hormosira banksii</i> to coralline turf) and time on <i>H. banksii</i> recruitment.....	45
Table 3.2. Relationships between the number of adult plants in each quadrat and the number of recruits three months later ($t + 3$) for cohorts recruiting in April 2015 to July 2016.....	46
Table 3.3. ANOVA testing for the differences in percentage survivorship and growth (based on transition from one size class to the next) of <i>Hormosira banksii</i> on different size classes and times. Results of Tukey's tests done within the size class \times time interactions are shown.	47
Table 4.1. Summary of the studies included in the meta-analysis.....	70

List of Figures

- Figure 2.1.** Percent cover of *Hormosira banksii* and coralline turf in September 2014 immediately after manipulation and after 24 months in September 2016. Treatments are indicated as cover of *Hormosira banksii* (H):coralline turf (C) in legend. Each point is a replicate quadrat.....25
- Figure 2.2.** Mean percent cover of *Hormosira banksii* (A), coralline turf (B), bare rock (C), sand (D) and other macroalgae (E) measured over 24 months (\pm SE) within the plots manipulated to eight different treatments of *H. banksii*:coralline turf ratios. Treatments are indicated as cover of *Hormosira banksii* (H):coralline turf (C). Shared letters for each panel indicate treatments that did not differ from one another after 24 months based on Tukey's HSD test following significant treatment effects (*H. banksii* and coralline turf).....26
- Figure 2.3.** Non-metric multidimensional (nMDS) scaling plots showing the variation in *H. banksii* and coralline turf percentage cover among treatments at (A) T0, (B) T24 and, (C) comparison between plots at T0 and T24.....27
- Figure 3.1.** Mean (\pm SE) recruitment of *Hormosira banksii* into eight treatments of different combinations of initial cover of *H. banksii* and coralline turf over 18 months (N = 4 quadrats per treatment). The mean maximum air temperature at the site is also shown.....48
- Figure 3.2.** Survivorship curves for each cohort from April 2015 through to September 2016. No recruitment occurred in July 2015 for treatments H28:C72, H57:C43 and H100:C0, October 2015 treatments H28:C72 and H0:C100 and April 2016 treatment 6. Where symbols are overlaid the same percentage of recruits survived.....49
- Figure 3.3.** Survivorship of the five *Hormosira banksii* size classes for each treatment (pooled across N = 4 quadrats) every 3 months. A) Size class 1: < 10 mm, B) size class 2: 10-29 mm, C) size class 3: 30-49 mm, D) size class 4: 50-79 mm and E) size class 5: \geq 80 cm. F)

Mean (\pm SE) survivorship of the eight treatments (pooled) for each size class every 3 months.....50

Figure 3.4. Growth based on the transition from one size class to the next for four *Hormosira banksii* size classes for each treatment (pooled across N = 4 quadrats) every 3 months. A) Size class 1: < 10 mm, B) size class 2: 10-29 mm, C) size class 3: 30-49 mm, and D) size class 4: 50-79 mm. E) Mean (\pm SE) growth of the eight treatments (pooled) for each size class every 3 months.....51

Figure 3.5. A) Percentage survivorship for each size class. B) Growth (transition to the next size class, mean \pm SE) of thalli for each of the five size classes over 18 months in April 2015 Data is pooled across treatments. Initial sample sizes for each size class: 1 (49), 2 (41), 3 (40), 4 (82) and 5 (49).....52

Figure 3.6. Relationships between (A) adult density vs. % recruit mortality, (B) recruit density vs. % recruit mortality and (C) recruitment in January 2016 vs. number that survived through to October 2016 for the January 2016 cohort. N = 32 quadrats.....53

Figure 4.1. Number of publications which focused on intraspecific facilitation per year from 1999 to 2019. Studies involved ecosystem engineers being manipulated in the field and recruitment, growth or survivorship of the engineer measured.....71

Figure 4.2. Forest plot of overall effect size of the studies included in the analysis (Hedges' $-g \pm 95\%$ CI). Three studies (Dell 2016, Layton 2019, Silliman 2015) assessed multiple demographic traits. R (recruitment), G (growth), S (survivorship).....72

Figure 4.3. Forest plots of the overall effect size (Hedges' $-g \pm 95\%$ CI) comparing intraspecific facilitation between A) different demographic traits (growth, survival, recruitment), B) intertidal vs subtidal ecosystem engineers, C) invertebrate vs. plant ecosystem engineers, and D) overall effect of ecosystem engineers in studies where presence

vs. absence and low vs. high density were tested. Numbers shown inside the y-axes indicate the number of studies for each category.....73

Abstract

In the intertidal zones of southern Australia and New Zealand, the fucoid brown macroalgae *Hormosira banksii* is often the dominant canopy-forming species. *H. banksii* is commonly found in association with an understory of red coralline turf algae. *H. banksii* is well recognised as an important habitat-forming or ‘ecosystem engineering’ species for its ability to add structure and complexity to its habitat. This important engineering species ameliorates harsh environmental variables which are common in intertidal areas such as wave activity and factors caused by prolonged exposure which include extreme temperatures and desiccation. Canopy forming species such as *H. banksii* add diversity to intertidal communities and make the environment more favourable for other species by providing complex structures which not only ameliorate the effects of environmental variables, but also provide benefits such as a refuge from predation, substrate for attachment and food source.

In intertidal habitats disturbance is common, *H. banksii* populations are impacted by a range of natural and anthropogenic disturbances, these can include; trampling by foot traffic in populated areas, storm water and sewage effluent discharge, extreme temperatures, desiccation and storms increasing the intensity of wave activity. Threats to this important ecosystem engineer are becoming more common with the increasing human populations in coastal areas and climate change increasing the intensity and frequency of extreme weather events.

Several studies have focussed on the associated assemblages, community structure and effects of disturbance events on *H. banksii*, however few have focussed on the effects of these disturbance events on canopy density and recruitment. The aims of this thesis were to determine; (i) how different gradients of disturbance intensity affected the recovery and recruitment of *Hormosira banksii* and its associated understory of coralline turf algae, (ii)

how the survivorship of *H. banksii* was influenced by, and the effects of adult density on recruitment and post-recruitment mortality, and; (iii) to explore how ecosystem engineering species facilitate their own recruitment and survivorship through positive feedbacks in marine environments.

In chapter 2, I manipulated the density of *H. banksii* canopy and coralline turf understory in a field experiment on the rocky shores of northern Tasmania. Percent cover of both canopy and understory were manipulated to eight different levels, the recovery of these plots was then monitored over the following two years. The aim of this experiment was to determine whether a threshold of disturbance exists at which the recovery of *H. banksii* was inhibited, or an alternate stable state dominated by coralline turf would competitively exclude *H. banksii* as previous studies have shown. I found that even where total removal of canopy or understory occurred, although slowly, the percentage of both cover types increased over following 24 months to densities near what was observed prior to manipulation. No change in species composition was observed regardless of the intensity of the disturbance. It could be assumed that factors which have caused alternate stable states between *H. banksii* and coralline turf and other types of furoid algae in other studies, were largely absent from this system.

In chapter 3, I followed the recruitment, growth and mortality of individual *H. banksii* plants at all growth stages over 18 months, these subplots were located within the plots that were manipulated in chapter 2. This aimed to determine the influence of the ‘adult’ population on the recruitment, growth and post-recruitment survivorship of *H. banksii*. We found that recruitment and post-recruitment survivorship were density-independent and within this system, adult populations appeared to have little influence on recruitment. Although *H. banksii* recruitment occurs all year round, we found evidence of a seasonal increase in recruitment over summer and that survivorship of recruits and adult plants was high overall.

Chapter 4 reviewed the literature surrounding intraspecific facilitation in marine ecosystem engineers incorporated a meta-analysis of studies which experimentally addressed this phenomenon. We examined the overall effects of these species on their own demographic traits, whether the effects differed between intertidal and subtidal habitats, functional groups and between different types of manipulative studies. We found that overall, published works on marine ecosystem engineers mostly revealed they facilitate their own growth, recruitment and survivorship. This effect was consistent across functional and habitat groups and demographic traits.

Overall, this study indicates that on the northern Tasmanian rocky shore, the population of *Hormosira banksii* appears to be resilient and stable, from our experiments it does not seem to be impacted by the same stressors which are causing localised decline in canopy forming furoid algae worldwide. It examines the effects of different gradients of disturbance on *H. banksii*, documents its recovery and did not find evidence of alternative stable states within this system. This study provides an insight into the demography of the ecosystem engineer *Hormosira banksii* and is one of the first to follow individual plants over a long term period and observe small scale recruitment, growth and mortality.

1. Introduction

1.1 Ecosystem engineers

Ecosystem engineers are organisms that directly or indirectly modulate the availability of resources to themselves and other species, by causing physical state changes in biotic or abiotic materials (Jones et al. 1994, Alper 1998). These species can account for key processes which are not directly trophic or competitive and, can result in the creation, modification and maintenance of habitats which are the foundation of diverse and productive ecosystems (Jones et al. 1994, 1997, Berkenbusch & Rowden 2003). Jones et al. (1994) differentiated between ‘autogenic’ and ‘allogenic’ engineering species: autogenic species (e.g. macroalgae, seagrasses, terrestrial plants/trees) modify their habitat through their own physical structures, whilst allogenic species (e.g. burrowing or bioturbating marine invertebrates, beavers building dams) modulate resources from one physical state to another via different means such as their behavior. Autogenic ecosystem engineering can be considered as having four components; the ecosystem engineer itself, structural changes, abiotic changes and biotic changes (Jones et al. 2010). The biotic change can be both other species associated with the engineer as well as the engineer itself. Consequently, four cause-effect relationships can explain how ecosystem engineers alter their environment: 1. An engineer causes structural change; 2. Structural change causes abiotic change; 3. Structural and abiotic change cause biotic change (in other species); 4. Structural, abiotic and biotic change all feedback to the engineer itself (its demographic rates, density etc. Jones et al. 2010).

Importantly, ecosystem engineering species can positively or negatively affect other species and conspecifics via multiple mechanisms which can often have broad-reaching effects on entire communities (Jones et al. 1994, 1997, Daleo et al. 2006, Hastings et al. 2007, Jones et al. 2010, Wright et al. 2014). Their ability to change physical and chemical factors within an ecosystem and exert significant control over resource availability for other biota often allows

them to become invasive and compete with other species for resources (Wright et al. 2014, Guy-Haim et al. 2018). Conversely, because engineering species often have cascading facilitative effects (Thomsen et al. 2010), they can also be used to restore ecological systems (Byers et al. 2006).

Ecosystem engineers causing structural change to their environment can positively influence their own demography. A well known example of this phenomena is beavers building dams, which in turn reduces movement costs and predation on beavers themselves (Jones et al. 1994, 1997, Jones et al. 2010). These demographic feedbacks occur when an activity or density is influenced by the engineered structural, abiotic or biotic states. For these to occur, any of the following three conditions need to happen: an engineers activity is sensitive to the engineered structural, abiotic or biotic states; activity is affected by density and density is altered by demographic feedbacks arising from engineer-induced structural, abiotic or biotic change (changes in recruitment, mortality or survivorship); or density is altered by demographic feedbacks (Jones et al. 2010). In marine environments, positive demographic feedbacks or intraspecific facilitation are associated with ecosystem engineers. Examples of these species include tube-building polychaetes (*Lanice conchilega*) affecting sediment dynamics, drag and turbulence which in turn affects their population density (Rabaut et al. 2007, Borsje et al. 2014, Alves et al. 2017a, Alves et al. 2017b) and the physical structure of seagrasses affecting flow, light and sediment accretion which in turn influences their recruitment, self-organisation and survivorship (van der Heide et al. 2010, Yang et al. 2016). Overall however, much less is known about intraspecific facilitation in ecosystem engineers compared to our understanding of interspecific facilitation.

1.2 Alternative stable states

The theory that natural ecosystems can exist in more than one stable state was first proposed by Lewontin (1969) and since then ecologists have been gathering empirical evidence for the occurrence of these states (Beisner et al. 2003). Alternative stable states can be described as a change in state variables or environmental parameters, causing an abrupt change to community composition (Beisner et al. 2003). Experimental evidence for alternative stable states requires the demonstration of stability of greater than one state in an ecosystem without continued manipulation (Petraitis & Latham 1999, Beisner et al. 2003, Petraitis 2013). Alternative stable states theory is often used to explain why different community assemblages can occur in close proximity, under seemingly the same environmental variables (Noy-Meir 1975, May 1977). According to theory, these alternative community states arise from either different starting conditions, or perturbations that move species densities from one point of equilibrium to another (Lewontin 1969, Noy-Meir 1975, May 1977, Knowlton 1992).

Gathering experimental evidence for alternative stable states can be difficult as it is not always clear whether different community compositions can be considered alternative stable states (Connell & Sousa 1983, Sousa & Connell 1985). In order to test for the existence of alternate stable states, experiments must fulfil four criteria: alternate states must be shown to occur in the same environment; manipulation must occur in a pulse perturbation that initiates a switch from one state to another; the experiment must be conducted over a sufficient time period and large enough area to ensure that the state can persist (Connell & Sousa 1983, Knowlton 1992, Petraitis & Dudgeon 2004). Peterson (1984) suggested that proof of the existence of alternative stable states could be done solely by showing that the same site could be dominated by different species.

Alternative stable states have been identified in a number of marine communities. For example, intertidal reefs in the Gulf of Maine, USA were one of the first marine communities to be identified as having alternative stable states (Petraitis & Dudgeon 2004, Petraitis et al.

2009). In this system, ice-scour removes macroalgal (*Ascophyllum nodosum* and *Fucus vesiculosus*) canopies, which are replaced with *Mytilus edulis* beds, which persist as long as predators are absent. On south eastern Australian intertidal rocky shores, it was suggested that the macroalgae *Hormosira banksii* and coralline turf could exist as alternative stable states. *H. banksii* was typically dominant but its abundance decreased at sites with high levels of nutrients from sewage effluent. At these high-nutrient sites the abundance of coralline turf was higher and when a threshold abundance of coralline turf was reached, *H. banksii* recruitment was lower (Bellgrove et al. 2010). This finding suggests *H. banksii* and coralline turf may exist as alternative stable states but in the absence of experimental evidence this remains inconclusive. Intertidal marine communities provide ideal systems for experimental tests for alternate stable states as they are often more easily manipulated than terrestrial or aquatic ecosystems (Petraitis & Latham 1999, Petraitis & Dudgeon 2004).

Facilitation can contribute to the maintenance of alternative stable states, where the conditions which favour one species over another are maintained (Baskett & Salomon 2010, Bozec et al. 2013, Bulleri et al. 2016). This was observed on a coral reef where coral or macroalgae dominated depending on the level of grazing by parrot fish. Although a high cover of macroalgae inhibited coral growth, coral creates a favourable habitat for parrot fish which graze on the macroalgae and enhance coral growth. The facilitative effects of coral on parrot fish maintains the coral state over the macroalgal state (Bozec et al. 2013). A decline in parrotfish populations could initiate a switch back to the alternative stable state of macroalgae due to a reduction in grazing pressure (Bozec et al. 2013).

Alternative stable states can often be attributed to ecosystem engineering species changing biotic and/or abiotic conditions to favour their own demography (Knowlton 2004). Petraitis and Latham (1999) found that when large clearings are made in *Ascophyllum* canopy, recruitment was reduced because of the vulnerability of germlings to more stressful abiotic

conditions such as increasing temperature, desiccation and water movement as well as limited dispersal capabilities of gametes. In addition, *Ascophyllum* fronds scour the substrate and provide shelter for predators of invertebrates such as mussels and in the absence of a canopy, the recruitment of mussels can increase and an alternative mussel-dominated stable state can be maintained (Petraitis & Latham 1999, Knowlton 2004). Similarly, in subtidal habitats where the loss of sea urchin predators leads to an increase in grazing on kelp, a kelp dominated system can change to a sea urchin dominated barrens. The sea urchins inhibit recruitment of kelp through grazing and maintain the barrens state until other factors such as the return of sea urchin predators or disease can allow a shift back to a kelp dominated state (Ling et al. 2009, Johnson et al. 2011, Filbee-Dexter & Scheibling 2014).

1.3 Study system

Marine macroalgae are important autogenic ecosystem engineers in temperate marine environments worldwide (Thompson et al. 2002, Bellgrove et al. 2010, Pocklington et al. 2017, Layton et al. 2019). On intertidal shores, their physical structure changes conditions beneath the canopy, which can ameliorate abiotic stress by reducing desiccation and/or temperature, provide a refuge from predation and create favorable conditions for marine invertebrates and other seaweed (Kelaher 2002, Kelaher 2003, Daleo et al. 2006, Wright et al. 2014).

Hormosira banksii (Turner) Decaisne is a perennial intertidal brown macroalgae which is abundant throughout the southern temperate waters of Australia and New Zealand (Macinnis-Ng et al. 2005, Schiel & Lilley 2007, Bellgrove et al. 2010, Schiel & Lilley 2011, Kain 2015, Bellgrove et al. 2017b, Mueller et al. 2018). *H. banksii* is characterised by its distinctive structure of branched chains of spherical vesicles although its morphology is highly variable (Osborn 1948, Womersley 1987, Bishop et al. 2009b). It is distributed from Albany in

Western Australia to Lennox Head in New South Wales, Tasmania, North and South Islands of New Zealand and smaller islands (Osborn 1948, Bellgrove et al. 2017b), is dioecious with conceptacles occurring beneath the surface of mature vesicles, and is fertile all year round with gametes released at low tide (Kain 2015, Mueller et al. 2018). *H. banksii* can also exist as a ‘free-living’ form in wave-protected bays, estuaries, lagoons and mangrove forests, which tend to have a larger morphology than coastal *H. banksii* (Ralph et al. 1998, Bishop et al. 2009b, Mueller et al. 2015, Bellgrove et al. 2017b, Gemelli et al. 2019). *H. banksii* forms a dense canopy and can have a standing biomass of up to 8 kg/m² (Schiel & Lilley 2007) which ameliorates harsh abiotic conditions and provides habitat for many invertebrates and macroalgal species (Keough & Quinn 1998a, Underwood 1999, Lilley & Schiel 2006, Schiel & Lilley 2007, Bishop et al. 2009b). An understory of turf or encrusting coralline algae commonly occurs with *H. banksii* (Osborn 1948, Keough & Quinn 1998a, Schiel & Taylor 1999) and it has been proposed that alternative stable states of *H. banksii* and coralline turf may exist (Bellgrove et al. 2010).

Intertidal macroalgae, including *H. banksii* are susceptible to a range of natural and anthropogenic disturbances including urbanisation and climate change (Bendetti-Cecchi et al. 2001, Airoidi & Beck 2007, Bertocci et al. 2010, Wernberg et al. 2013), trampling by foot traffic (Beauchamp & Gowing 1982, Povey & Keough 1991, Brosnan & Crumrine 1994, Keough & Quinn 1998a, Brown & Taylor 1999, Schiel & Taylor 1999, Milazzo et al. 2004), increased nutrients due to effluent discharge (Doblin & Clayton 1995, Bellgrove et al. 2010, Bellgrove et al. 2017a), storms and increased wave activity (Underwood 1998, 1999, Bertocci et al. 2010) and sediment scouring (Lilley & Schiel 2006).

The structure of intertidal communities is strongly influenced by physical disturbances and the subsequent recovery of species post-disturbance (Dayton 1971, Arrontes & Underwood 1991, Underwood 1999) (Sousa 1979a). Disturbance events can be considered as either a

‘pulse’ or ‘press’, where a pulse disturbance is short-term, easily delineated and often high intensity, whilst a press disturbance is ongoing and continues at a constant intensity (Bender et al. 1984). Experimental manipulations aiming to determine the presence of alternative stable states should generally use a pulse perturbation, which can initiate positive feedback mechanisms and result in a change of state, press perturbations are more likely to only maintain different outcomes (Petraitis & Latham 1999).

1.4 Thesis structure

This thesis examines the effects of disturbance on the important intertidal ecosystem engineer, *Hormosira banksii*, whether a threshold *H. banksii* cover exists below which the system switches to a coralline turf state, the relative importance of demographic processes in contributing to its post-disturbance recovery and the importance of self-facilitation in marine ecosystem engineers. Chapter 2-4 were prepared as stand-alone manuscripts formatted for publication with chapters 2 and 3 based around long-term field experiments.

Chapter 2 describes a field experiment manipulating the cover of both *H. banksii* and understory coralline turf to determine whether different intensities of disturbance to either species caused a switch to an alternative stable state. This experiment ran for two years to track the recovery of both species and to assess whether there was a threshold cover below which either species did not recover.

Chapter 3 determined whether the demography of *H. banksii* was influenced by different intensities of disturbance. Individual recruits were identified every 3 months and followed for up to 18 months to determine whether patterns of recruitment, growth and post-recruitment survivorship varied as a function of disturbance and time and, whether the post-recruitment mortality of *H. banksii* was density-dependent or independent.

Chapter 4 is a meta-analysis reviewing the literature on intraspecific facilitation by ecosystem engineers in marine environments. This chapter explores the extent to which intra-specific facilitation by ecosystem engineers is described in literature, the overall effect on the engineer's demography (recruitment, survivorship and growth) and examines which species and in which ecosystems intra-specific facilitation has been documented.

The final chapter is a synthesis of this research and draws together the outcomes and concepts investigated in this thesis. It discusses the current knowledge base of ecosystem engineering and alternative stable state theory, limitations and links to demographic traits of these species and how they can influence and maintain states. This chapter also discusses how this research can be applied to management of disturbance in intertidal seaweed communities and builds on knowledge of how these communities will respond to increases in natural and anthropogenic disturbance events.

2. No evidence of alternative stable states in the dynamic between the habitat-forming seaweed *Hormosira banksii* and coralline turf

Ryan D. Lewis, Craig R. Johnson, Jeffrey T. Wright

Institute for Marine and Antarctic Studies, Tasmania

2.1 Abstract

Coastal marine ecosystems are among the most ecologically and socio-economically important on the planet. The ecosystem engineer *Hormosira banksii* is often the dominant species in the temperate intertidal of southern Australia, where it is commonly associated with an understory of coralline turf. Where *H. banksii* forms a dense canopy, it facilitates other species by ameliorating the harsh effects of abiotic factors such as temperature and desiccation. Disturbances are common in intertidal areas and climate-driven increases in storm intensity and temperature are exerting increased pressure on these important ecosystems. Previous studies have shown that removal of canopy-forming macroalgae can lead to replacement by turf-forming algae, suggesting the possibility of alternative stable states and hysteresis in the dynamic. In this study, we manipulated cover of the *H. banksii* canopy and understory coralline turf in a pulse perturbation on an intertidal rocky reef on the northern coast of Tasmania. The manipulated plots contained eight treatments ranging from 100% removal of *H. banksii* to 100% removal of the understory coralline turf. We then followed the trajectory of both *H. banksii* and coralline turf for 24 months, to determine whether there was a threshold density for both species above which they maintained dominance, thus indicating the possibility of discontinuous phase shift. Overall, the results

indicate that rather than a shift between these dominant species indicating alternative stable states under identical environmental conditions, both species appeared to slowly return to coexist in quasi equilibrium within the experimental plots, irrespective of the manipulation treatment.

2.2 Introduction

Theory and observation indicate that natural multi-species assemblages of plants and animals can possess several different equilibrium points (May 1977). Communities can persist in the environment over considerable timescales, even when subjected to multiple natural or anthropogenic disturbances (Cesar 2014). At the same time, communities can be susceptible to catastrophic change and shift from one state to another (Scheffer et al. 2001, Scheffer & Carpenter 2003, Petraitis 2013). Alternative, or multiple stable states occur when more than one type of community can stably persist in a single environmental regime (Knowlton 2004), and they arise in dynamical systems with more than one equilibrium point (Petraitis & Dudgeon 2004). Theoretical ecologists describe two ways that a community can move between stable states; a large perturbation applied directly to the state variables (such as population density) or a change in the parameters which determine a state variable (recruitment or mortality) (Beisner et al. 2003). Reversal of these changes in state can be difficult due to hysteresis effects: for a reversal to occur, the environmental parameters which initiated a change in state need to be moved back somehow beyond the threshold where the change occurred in the first place (Petraitis & Latham 1999, Scheffer et al. 2001, Scheffer & Carpenter 2003, Petraitis & Dudgeon 2004, Petraitis et al. 2009, Petraitis & Hoffman 2010, Fung et al. 2011, Petraitis 2013).

There has been robust discussion of the criteria needed to demonstrate alternative stable states exist within an ecosystem (Petraitis 2013, Menge et al. 2017). Connell and Sousa (1983) and Peterson (1984) gave four requirements that must be fulfilled in order to experimentally test for multiple stable states including: the experiment must be conducted in a single environment (same site); the site is shown to have the potential to be occupied by two or more distinct communities; the communities tested are self-replicating; and the experimental manipulations must be pulse perturbations that mimic a natural event. Schröder et al. (2005) added to these requirements that the existence of alternative stable states must be demonstrated experimentally and that the state must persist for more than one generation.

Marine ecosystems were the first to provide potential examples of multiple stable states (Knowlton 2004). Changes between states, sometimes sudden, have been observed in many marine ecosystems including; shifts from corals to macroalgae in tropical systems (Mumby et al. 2007a, Mumby et al. 2007b, Fung et al. 2011, Burkepile et al. 2013), and from macroalgae to barrens (Filbee-Dexter & Scheibling 2014, Ling et al. 2015) or mussel beds in temperate systems (Petraitis & Hoffman 2010). The transition from a kelp bed to sea urchin barrens is a well-known example of a discontinuous phase shift in marine systems (Ling & Johnson 2009, Marzloff et al. 2013, Filbee-Dexter & Scheibling 2014, Steneck & Johnson 2014, Ling et al. 2015, Marzloff et al. 2016). Phase shifts have also been described on intertidal rocky shores. For example, Menge et al. (2017) found that removal of the *Ascophyllum nodosum* canopy resulted in replacement by *Fucus* spp. which has remained the dominant species in cleared patches after 35 years despite multiple pulse perturbations and changes in the system due to the effects of climate change. Although experiments testing the hypotheses that alternative stable states exist in the marine intertidal are rare, this research demonstrates that it is possible to meet the criteria necessary to test for alternative stable states. Interestingly, these result differ to the findings of Petraitis and Latham (1999) who found that *A. nodosum* and

Fucus vesiculosus formed one state and that cover of the mussel *Mytilus edulis* was the alternative state. In general, the detection of alternative stable states has been successfully demonstrated in relatively few field studies (Schröder et al. 2005).

Temperate rocky intertidal reefs are often dominated by a canopy of furoid algae (Schiel & Foster 2006, Bellgrove et al. 2010). In southern temperate waters of Australia and New Zealand, *Hormosira banksii* (Turner) Decaisne is often the dominant species on the mid and lower intertidal shores (Schiel & Lilley 2007). *H. banksii* forms a dense monotypic canopy with a standing biomass of up to 8 kg/m² and can attain densities of several hundred plants per square metre (Schiel 2006). As an ecosystem engineer (*sensu* Jones et al. (1997)), *H. banksii* directly influences the presence of other algae and invertebrates through the amelioration of environmental stressors such as desiccation, heat and wave action (Keough & Quinn 1998a, Schiel & Lilley 2007, Bishop et al. 2009b). The *H. banksii* canopy also provides habitat and protection against predation for many invertebrate species (Keough & Quinn 1998a, Lilley & Schiel 2006, Schiel & Lilley 2007, Bishop et al. 2009b, Schiel & Lilley 2011) and their larvae (Moreno 1995). *H. banksii* and coralline algal turf are commonly associated in mid to low intertidal rocky shores (Osborn 1948, Schiel et al. 2006, Alestra & Schiel 2014), with the turf algae usually in an understory beneath the *H. banksii* canopy. The coralline turf algae mainly consists of *Corallina officinalis* but can also be comprised of numerous other species of tightly packed erect filaments (Gorgula & Connell 2004).

Natural and anthropogenic disturbances to *H. banksii* range from small-scale impacts such as rocks turning over in waves that remove a few individual plants, to larger scale events such as storms that can remove entire canopies (Underwood 1998, Schiel & Lilley 2007). A reduction in the cover of *H. banksii* can have large effects on associated invertebrate communities (Povey & Keough 1991, Keough & Quinn 1998a, Schiel & Taylor 1999, Schiel

& Foster 2006, Schiel & Lilley 2007). *H. banksii* is susceptible to anthropogenic disturbances such as trampling which directly removes the canopy (Keough & Quinn 1998a, Schiel & Taylor 1999) and increased nutrients (Bellgrove et al. 2010). Increased nutrient loads in the water column can indirectly affect *H. banksii* populations through increasing the growth of turf algae potentially leading to competitive exclusion (Gorgula & Connell 2004, Bellgrove et al. 2010, Alestra & Schiel 2014, Alestra et al. 2014). On human dominated coasts where there are increased nutrients and sediment loads from effluent release and runoff, coralline turf algae can dominate where there have been perturbations to the *H. banksii* canopy (Bellgrove et al. 2010). Indeed, the change from a *H. banksii*-dominated state to one dominated by coralline turf has been suggested as a phase shift to an alternative stable state (Bellgrove et al. 2010) but there is no experimental evidence to support that hypothesis. This increase in turf may lead to a decrease in recruitment of *H. banksii* as seen in other fucoids (Benedetti-Cecchi & Cinelli 1992b, Bulleri et al. 2002) and kelp (Kennelly 1987, Airolidi & Cinelli 1997, Strain et al. 2014, Reeves et al. 2018).

In this study we use an experimental approach to determine whether alternative stable states exist between *Hormosira banksii* and coralline turf on the rocky shores of northern Tasmania, Australia. We tested this hypothesis by manipulating both the *H. banksii* canopy and the understory coralline turf in a pulse perturbation to establish different ratios of canopy to understory turf and followed these manipulations for two years to determine whether a threshold cover exists for either species above which the other species did not recover, hence that this system had the ability to exist in multiple states. This design meets the requirements set by Connell and Sousa (1983) and Peterson (1984) to test for alternative stable states.

2.3 Method

2.3.1 Study Site

The study was undertaken at a site (Beechford) on the north coast of Tasmania (41°01'14.4"S, 146°57'02.2"E) which consists of a north-west facing sandy beach with a series of eight reefs of various shapes and sizes along 2 kilometres of coast. The reef selected for the study site was ~ 400 metres long and ~ 80 metres wide. It consists of numerous small to medium basalt boulders up to 0.25 m² on a base of solid basalt bedrock. The lower intertidal zones on these reefs are dominated by a canopy of *Hormosira banksii* with an understory of coralline turf as well as other less common perennial macroalgae (e.g. several *Cystophora* species) and seasonal ephemeral algae. The north coast of Tasmania has relatively low wave exposure and a semi-diurnal tidal regime, which often leaves species exposed to air twice a day (Mueller et al. 2015). *Hormosira* on the north coast has a small bushy morphology, with individuals often packed closely together forming 100% canopy cover in many places (Mueller et al. 2015).

2.3.2 Manipulation of percent cover and sampling

In September 2014, we set up four replicate 1 m² plots of each of eight treatments. The plots were placed haphazardly across the reef where there was at least 80% canopy of *H. banksii* and the corners of each plot were marked with marine epoxy resin. Photos were used as reference for correctly locating the quadrat, landmarks such as larger rocks and clear patches in photos as well as the epoxy markers ensured that each plot location was easily identified. The percentage cover of *H. banksii* canopy and coralline turf was then manipulated into eight different treatments in a pulse perturbation. The eight treatments ranged from 100% *H. banksii* and 0% coralline turf, through to 0% *H. banksii* and 100% coralline turf with even intervals in between (H0:C100, H14:C86, H28:C72, H43:C57, H57:C43, H72:C28, H86:C14, H100:C0) (Fig. 1). Two replicates were located on each side of the reef, these were

considered separate sites (East and West). Manipulation of *H. banksii* was conducted by removing entire thalli including the holdfast while the manipulation of the coralline turf was done using a paint scraper with care taken to ensure no damage was to any *H. banksii* thalli in the plots.

The percentage cover of *H. banksia*, coralline turf, other macroalgae (primarily *Cystophora* and *Cystoseira spp.*), bare rock and sand was determined before manipulation, post-manipulation (T0) and every three months for two years from September 2014 through to September 2016 (T24) using an *in situ* point intercept method. The point intercept measurements were conducted using a 500 x 500 mm clear Perspex board with a 10 x 10 grid of drilled holes at 40 mm intervals. The board was supported by 250 mm legs to hold it above the substratum. Once the board was positioned in a plot, a metal pin was dropped into a randomly selected hole in the grid and the substratum the pin landed on, and any understory and canopy species through which the pin passed was recorded. The point intercept board was randomly positioned twice within each 1 m² plot and 40 measurements taken at each position.

2.3.3 Statistical Analyses

Differences in the percentage cover of *H. banksia*, coralline turf, other macroalgae, bare rock and sand among ratio treatments was determined prior to manipulation, immediately post-manipulation (T0) and two years after manipulation (T24) with a single Factor Analysis of Variance (ANOVA). Normality and homogeneity of variance were checked using Box-Cox plots and residuals. No data transformation was necessary. Post-hoc analyses were then conducted using Tukey's Honest Significant Difference test. A 2-factor Permutational Analysis of Variance (PERMANOVA, Site x Ratio treatment) based on Bray Curtis similarity using 9999 permutations was also conducted to examine the combined effects of *H.*

banksii and coralline turf percentage cover between treatments, and was followed by pairwise tests. Non-metric multidimensional scaling (nMDS) was used to visualise the differences between treatments at T0 and T24 and also across all treatments between T0 and T24. ANOVA and Tukey HSD were both conducted using R version 3.3.2 and the PERMANOVA and nMDS results were analysed using PRIMER+ PERMANOVA version 6.

2.4 Results

Prior to manipulation there were no significant differences among ratio treatments in the cover of any variables (Table 1) with mean (\pm SE) percentage cover for *H. banksii* 80.8 ± 1.42 % (maximum of 96 %), coralline turf of 60.6 ± 1.45 % (maximum of 76 %) and bare rock 10.4 ± 0.96 % (maximum of 23 %). Cover of other macroalgae was minimal in plots with a mean (\pm SE) cover of 1 ± 0.39 % and a maximum of 11 %. Sand cover was not included as a variable until observed post-manipulation. Although we had intended to have up to 100% cover of both *H. banksii* and coralline turf in some treatments, complete covers did not occur across entire plots. Consequently, in treatments in which the initial cover was intended as 72, 86 or 100%, the initial cover was often set by the actual cover in the plot (Fig. 1).

Post manipulation (T0) there was a highly significant difference between treatments for *H. banksii* canopy, coralline turf, and bare rock but not for sand and other macroalgae (Table 1). This higher cover of rock was a result of the removal of the canopy and understory (up to 30% where the entire cover of *H. banksii* had been removed). Tukey's HSD pairwise comparisons indicated that each treatment was significantly different from all others for the percentage cover of *H. banksii* and coralline turf ($P < 0.05$; Figs. 2A, 2B).

After 24 months (T24), all treatments had trended towards a similar cover for each alga (Figs. 1, 2) although there were still significant differences among treatments in the cover of *H. banksii*, coralline turf and other macroalgae (Table 1). Initially, the cover of *H. banksii* in treatments with a high cover declined, so that no treatment had a mean cover > 50 % after 3 months, but after 24 months the mean final percentage cover of *H. banksii* ranged between 21 – 58 % for all treatments. For *H. banksii*, Tukey's tests at T24 showed the H100:C0 and H85:C14 treatments had significantly higher cover than all other treatments except H72:C28; the H72:C28 treatment differed to the H0:C100 and H14:C86 treatments; while all other treatments did not differ (Fig. 2A). After 24 months the percentage cover of coralline turf in all treatments ranged between 17 – 58 % and similar to *H. banksii*, Tukey's tests revealed three distinct groups which could be described as high, medium and low percentage cover. The H14:C86 and H28:C72 treatments differed from all other treatments except the H0:C100 treatment; the H0:C100 treatment differed from the H100:C0 and H86:C14 treatments; while other treatments did not differ from one another (Fig. 2B). After 24 months the cover of bare rock (all treatments $\leq 15\%$) and sand (all treatments $< 6\%$) was low with no significant differences between treatments (Table 1, Fig. 2C). The cover of other macroalgae was also low (all treatments $< 5\%$) but H16:C84 differed from all other treatments (Table 1, Fig. 2D).

PERMANOVA examining the combined effects of *Hormosira banksii* and coralline turf revealed a significant difference between ratio treatments post-manipulation (Table 2A) and after 24 months (Table 2B). Pairwise *a posteriori* comparisons indicate that at T0 the majority of ratio treatments were significantly different from one another, except for the treatments H45:C57 vs. H57:C43; H57:C43 vs. H72:C28; and H72:C28 vs. H86:C14 (Table 3, Fig. 3A). After 24 months (T24) only half of the comparisons were significantly different, with most differences between treatments that were manipulated to opposite levels of percent cover (i.e. comparisons involving the H100:C0, H86:C14 or H72:C28 treatments, Table 3,

Fig. 3B). The factor of site was included in the multivariate analysis to assess whether the two sites (East and West sides of the reef) differed in composition: post-manipulation (T0) the two sites were significantly different, however after 24 months there was no significant difference (Table 2). Finally, a comparison of the communities at T0 vs. T24 indicated convergence of communities at T24 compared to T0 (Fig. 3C). Overall, the multivariate analysis supports the univariate analyses whereby treatments that were initially different appear to be moving towards a similar relative abundance of both *H. banksii* and coralline turf.

2.5 Discussion

This study aimed to determine whether alternative stable states existed in the dynamic between *Hormosira banksii* and coralline turf within the intertidal rocky reefs of northern Tasmania. The results after two years do not show strong evidence that either species was showing dominance above any level of initial manipulated cover and thus, no evidence to suggest the existence of alternative stable states. Initially the plots seemed to respond to the disturbance, high cover treatments of both species lost 5-10% of cover within the first three months, while the low cover treatments appeared to gain cover within the same period. The treatments all moved towards 30-60 percent cover of both *H. banksii* and coralline turf, then began to gradually follow the same trajectory of increasing cover. Twenty-four months after the disturbance the composition in the plots still differed significantly, however for both species they formed distinct groups of similarity that could be considered as low, mid and high percentage cover for both *H. banksii* and coralline turf. Nonetheless, after 24 months the gradual increase of both species in treatments where they were initially manipulated to low levels suggested that the treatments were returning to their pre-manipulation 'natural' state.

Bellgrove et al. (2010) suggested that a threshold of coralline turf cover at greater than 40 percent may result in the canopy cover of *H. banksii* barely reaching 20 percent, and that this could represent a shift to an alternative state. Alternative stable states between furoid algae (dominated by *Cystoseira* sp.) and coralline turf was also suggested by Benedetti-Cecchi and Cinelli (1992a) when initial canopy removal lead to competitive exclusion of *Cystoseira* sp. by articulated coralline turf. In both studies it was suggested that an anthropogenic pulse disturbance lead to the alternative coralline state being maintained. Similarly, it was proposed that a state dominated by furoid algae (*Ascophyllum nodosum* and *Fucus vesiculosus*) could change to a state dominated by mussels (*Mytilus edulis*), as a result of a pulse disturbance from ice scour in New England (Petraitis & Latham 1999). Menge et al. (2017) manipulated *A. nodosum* canopy in the same system and found it to be quickly out competed by *F. vesiculosus*, which persisted for more than 35 years suggesting multiple stable states. One of the best studied examples of alternative stable states comes from freshwater lakes, where macrophytes and clear water are replaced by suspended microalgae, increasing turbidity and reduced light to the benthos, thought initially to be due to high nutrients being introduced by anthropogenic activity (Scheffer et al. 2001).

The majority of studies that have suggested the existence of alternative stable states have noted a large scale, natural or anthropogenic disturbance at the site (Scheffer et al. 2001, Petraitis et al. 2009, Bellgrove et al. 2010). The site at which this study was conducted was largely absent of factors that have been found to initiate a change in state in other systems. Several studies have suggested that waves moving boulders can negatively affect intertidal communities (Sousa 1979a, Shanks & Wright 1986). Beechford is on the northern coast of Tasmania, a region that is relatively protected from large waves and mostly subject to wind-driven swell and only moderate wave activity (Short 2006). It is also somewhat protected by a headland to the west of the site. Moreover, boulders at this site are relatively large which

are less likely to be moved by waves than small boulders. During the experiment, there were only five occasions when boulders moved within a plot. The disturbed boulders were able to be moved back into place (with aid of reference photos) at the next sampling time and there appeared to be minimal disturbance to the plots. Human trampling is another well-known cause of disturbance to intertidal macroalgal communities including *H. banksii* (Addessi 1994, Brosnan & Crumrine 1994, Keough & Quinn 1998a, Schiel & Taylor 1999). However, this was also likely to be relatively low at our site due to the low population in the area, the distance of the site from the beach (~500 metres) and the relatively short exposure time at low tide. Additionally, although the Curries River runs onto the beach near our site, it passes through a catchment of relatively low-impact agriculture and forestry and typically had a low flow. Thus, it appears unlikely to have provided significant nutrient input.

For *H. banksii* and coralline turf to exist as alternative stable states we would expect the two species to form almost monospecific patches where the other species was excluded, but this did not occur. Rather, it appeared that the two species coexisted and it is possible that *H. banksii* facilitates coralline turf as when the canopy was completely removed, the understory coralline turf often appeared bleached and damaged. This response has also been observed in New Zealand with the same species (Schiel & Lilley 2007). However, in a later study Schiel and Lilley (2011) found that when fucoid algae was removed via disturbance, coralline turf increased in density and had a negative impact on the recovery and recruitment of the *H. banksii*. Schiel and Lilley (2011) suggested that to understand the feedbacks between fucoids and coralline turf, non-trophic interactions must be better understood.

A range of processes including intraspecific and interspecific interactions, ecosystem engineering of abiotic factors and possible demographic feedbacks, as well as the intensity and scale of disturbance and external environmental factors are all likely to contribute to

when an alternative stable state is possible or likely to occur. A multitude of studies have aimed to determine where alternative stable states occur in marine ecosystems (Petraitis & Dudgeon 2004, Petraitis 2013) and many have highlighted difficulties in conducting field experiments to achieve this aim. A review of alternate stable states conducted in 2005 found 13 experiments which directly demonstrated the presence of alternative stable states, eight where they were absent and 14 which did not fulfil the requirements to unequivocally determine alternative stable states, with most not being run for a sufficient amount of time to demonstrate the persistence of the alternative state (Schröder et al. (2005). We believe our experiment has indicated that *Hormosira banksii* and coralline turf do not represent alternative stable states at this site. However, if conditions that affect factors like the recruitment, mortality and competition change, so too could this outcome. More research is needed to identify which factors might drive changes in state and allow ‘new’ states to persist.

Table 2.1. One-way ANOVA results for the effects of ratio of *Hormosira banksii* to coralline turf before manipulation, after manipulation (T0) and after 24 months (T24). Analyses were conducted on the percentage cover of five key variables; *H. banksii* canopy, coralline turf understory, bare rock, sand, and other macroalgae (sand was not measured before manipulation). * $p \leq 0.05$, ** $p \leq 0.01$, *** $p \leq 0.001$.

Source of Variation	df	<i>Hormosira banksii</i>		Coralline turf		Bare rock		Sand		Other	
		MS	F	MS	F	MS	F	MS	F	MS	F
Before manipulation											
Ratio	7	66.17	1.031	66.27	0.976	27.77	0.914	-	-	4.214	0.812
error	24	64.18		67.92		30.40		-		5.188	
Post-manipulation (T0)											
Ratio	7	2307.6	103.6***	1505.1	47.28***	218.5	4.497***	30.98	2.724*	2.554	0.745
error	24	22.3		31.8		48.58		11.38		4.208	
24 months post-manipulation (T24)											
Ratio	7	204.5	8.815***	334.6	13.98***	27.96	0.943	19.70	1.51	10.246	3.122**
error	24	23.2		23.9		29.66		13.04		3.281	

Table 2.2. PERMANOVA of the effects of Ratio and Site on the percent cover of *Hormosira banksii* and Coralline turf post-manipulation (T0) (A) and after 24 months (T24) (B). *** $p \leq 0.001$

A. PERMANOVA post-manipulation (T0)

Source	df	MS	F	P (perm)
Site	1	331.03	10.758	0.0001***
Ratio	7	3266.10	106.14	0.0001***
Site x Ratio	7	3.5913	0.11671	0.9648
Residual	16	30.771		
Total	31			

B. PERMANOVA after 24 months (T24)

Source	df	MS	F	P (perm)
Site	1	113.67	3.5883	0.0527
Ratio	7	363.47	11.474	0.0001***
Site x Ratio	7	21.982	0.69392	0.7126
Residual	16	31.677		
Total	31			

Table 2.3. Pairwise a posteriori comparisons of levels of the factor Ratio post-manipulation (T0) and after 24 months (T24) following the PERMANOVA for *H. banksii* and coralline turf percentage cover. Significant values ($P < 0.05$) are shown in bold.

Ratios	T0		T24	
	t	P(perm)	t	P(perm)
0:100, 14:86	4.5848	0.0312	1.6976	0.1698
0:100, 28:72	7.7644	0.0292	1.2273	0.3047
0:100, 43:57	9.6221	0.0295	1.6326	0.1512
0:100, 57:43	12.542	0.0276	1.4926	0.1534
0:100, 72:28	13.509	0.0274	3.4192	0.0303
0:100, 86:14	15.046	0.0258	3.3635	0.0281
0:100, 100:0	19.138	0.0316	4.5039	0.0295
14:86, 28:72	4.5713	0.0290	1.4654	0.1720
14:86, 43:57	6.876	0.0256	2.9134	0.0500
14:86, 57:43	11.304	0.0184	2.4456	0.0882
14:86, 72:28	11.711	0.0268	6.5209	0.0303
14:86, 86:14	13.416	0.0247	4.4688	0.0284
14:86, 100:0	19.008	0.0288	6.9549	0.0310
28:72, 43:57	3.7965	0.0308	1.5486	0.1905
28:72, 57:43	8.2964	0.0295	1.1924	0.2921
28:72, 72:28	8.9554	0.0271	5.6049	0.0269
28:72, 86:14	10.754	0.0272	3.8513	0.0295
28:72, 100:0	17.025	0.0271	6.2589	0.0293
43:57, 57:43	1.4032	0.2466	-	-
43:57, 72:28	3.3247	0.0410	4.2467	0.0273
43:57, 86:14	4.7024	0.0255	2.9992	0.0485
43:57, 100:0	8.3397	0.0266	5.1447	0.0313
57:43, 72:28	2.8026	0.0680	3.6488	0.0344
57:43, 86:14	4.4957	0.0258	2.8852	0.05598
57:43, 100:0	9.6738	0.0279	4.7577	0.0336
72:28, 86:14	1.4659	0.2170	0.7266	0.6080
72:28, 100:0	5.0175	0.0294	1.8755	0.1256
86:14, 100:0	3.3328	0.0295	0.6044	0.615

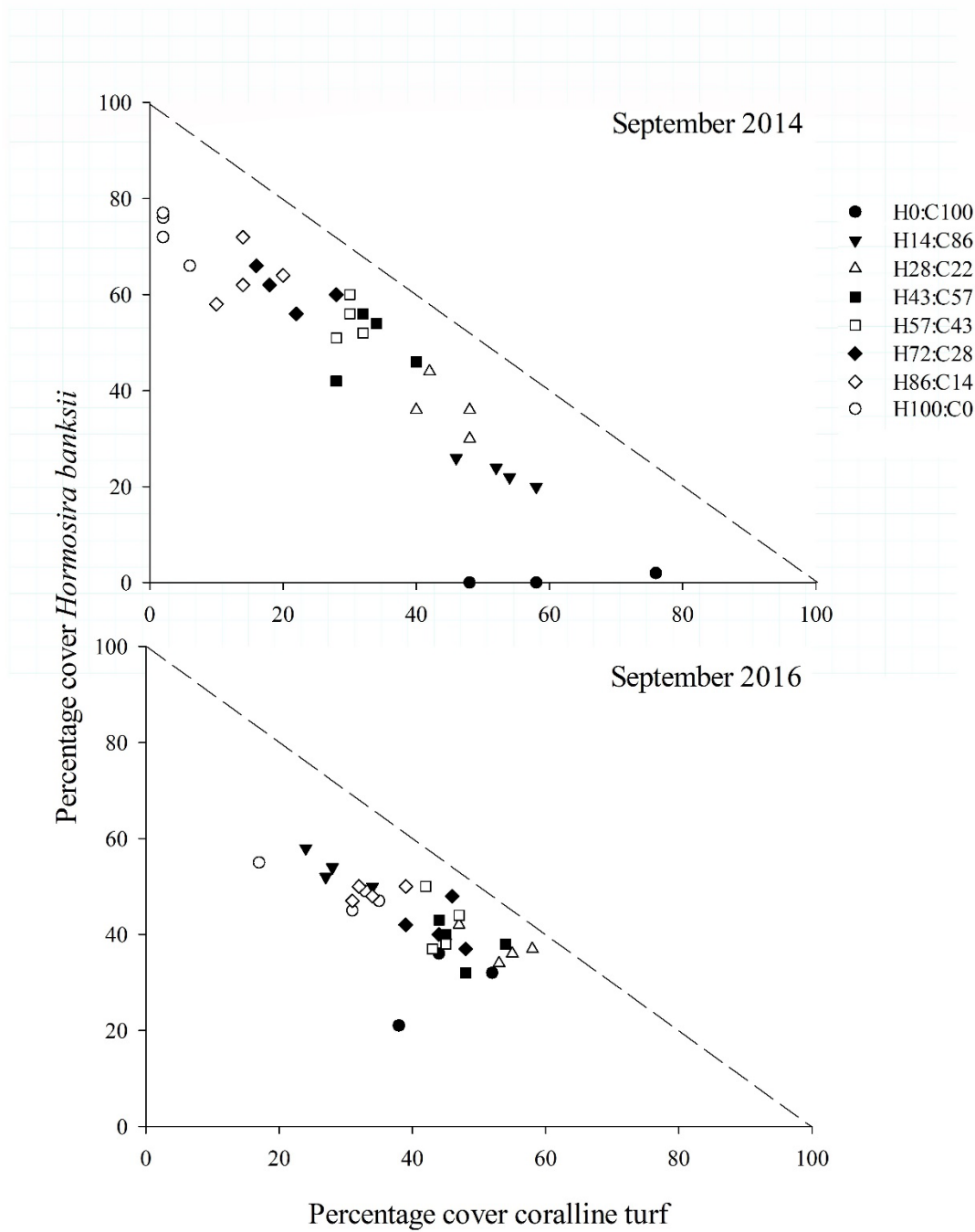


Figure 2.1. Percent cover of *Hormosira banksii* and coralline turf in September 2014 immediately after manipulation and after 24 months in September 2016. Treatments are indicated as cover of *Hormosira banksii* (H):coralline turf (C) in legend. Each point is a replicate quadrat.

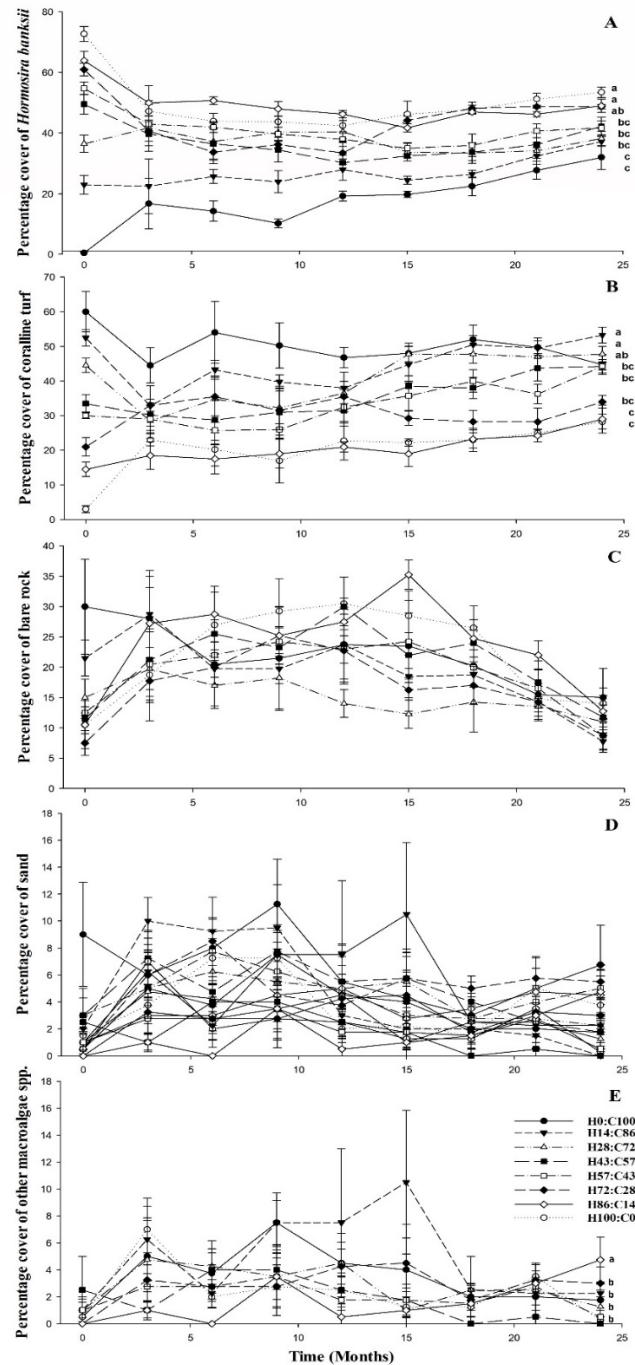


Figure 2.2. Mean percent cover of *Hormosira banksii* (A), coralline turf (B), bare rock (C), sand (D) and other macroalgae (E) measured over 24 months (\pm SE) within the plots manipulated to eight different treatments of *H. banksii*:coralline turf ratios. Treatments are indicated as cover of *Hormosira banksii* (H):coralline turf (C). Shared letters for each panel indicate treatments that did not differ from one another after 24 months based on Tukey's test following significant treatment effects (*H. banksii* and coralline turf).

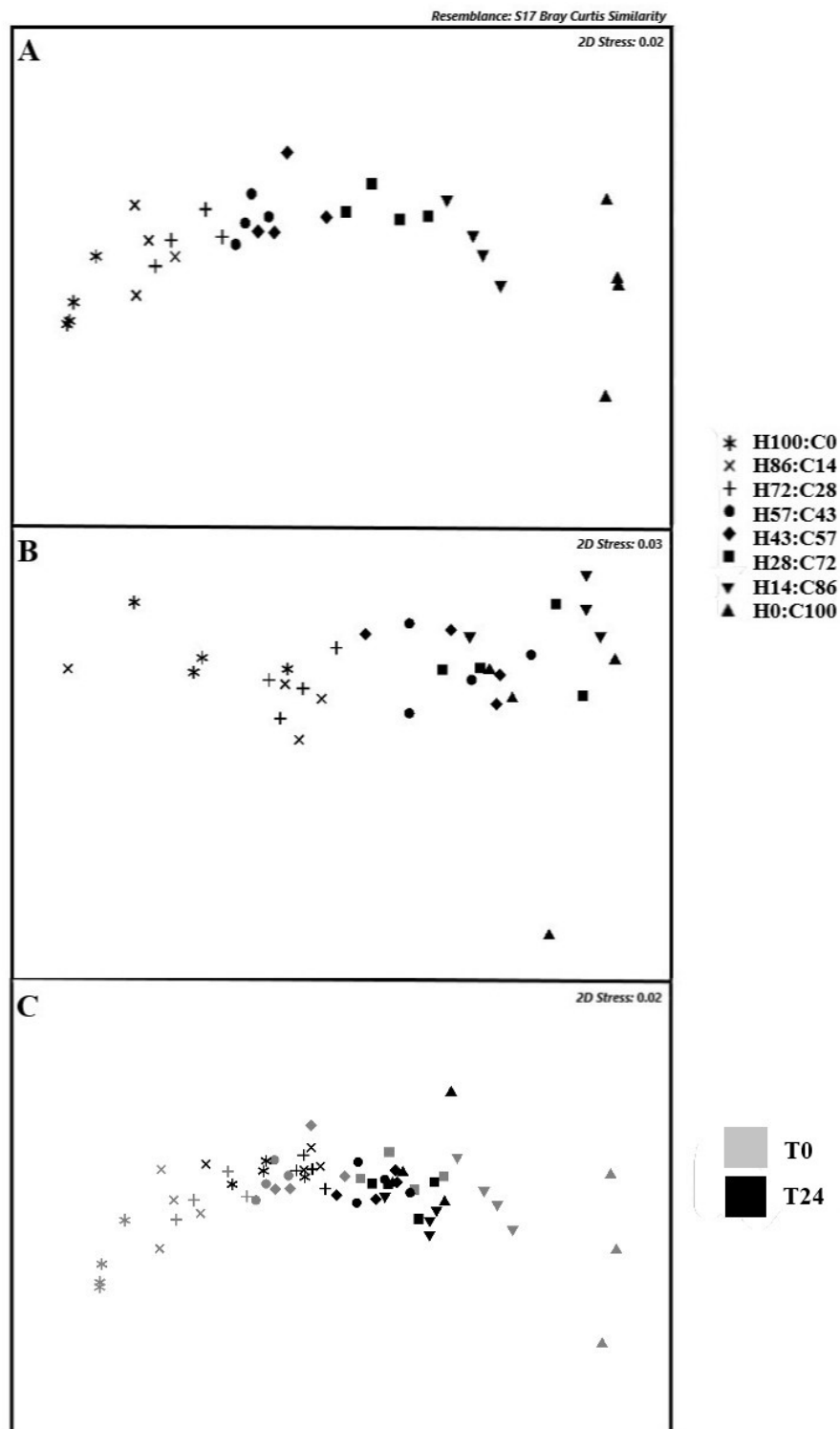


Figure 2.3. Non-metric multidimensional (nMDS) scaling plots showing the variation in *H. banksii* and coralline turf percentage cover among treatments at (A) T0, (B) T24 and, (C) comparison between plots at T0 and T24.

3. Demography of the intertidal fucoid *Hormosira banksii*: importance of variable recruitment to local abundance

Ryan D. Lewis, Craig R. Johnson, Jeffrey T. Wright

Institute for Marine and Antarctic Studies, Tasmania

3.1 Abstract

Canopy-forming macroalgae form the basis of diverse coastal ecosystems globally. The fucoid, *Hormosira banksii*, is often the dominant canopy-forming macroalga in the temperate intertidal of southern Australia and New Zealand, where it is commonly associated with an understory of coralline turf. *H. banksii* is susceptible to both natural and anthropogenic disturbance and despite its abundance, few studies have examined the demography of this important species. This study determined the demographic response of *H. banksii* to different gradients of disturbance to both its canopy and to the understory coralline turf. We established plots in which the density of *H. banksii* and/or understory coralline turf were manipulated in a pulse perturbation to simulate a disturbance event. The manipulated plots contained eight treatments ranging from 100% removal of *H. banksii* to 100% removal of the understory coralline turf. We then measured recruitment and followed individual recruits for up to 18 months to determine growth and survivorship. We found that *H. banksii* recruitment was seasonally variable throughout the experiment and highest over summer, survivorship of recruits was generally high and the species was slow-growing and long-lived. Moreover, the level of disturbance did not seem to affect recruitment, growth or survivorship and post-recruitment mortality was independent of *H. banksii* density. In this system, it appears that *H. banksii* is a relatively long-lived perennial species whose demography is density-independent which appears to allow recovery from disturbance.

3.2 Introduction

Local population abundance of most marine species is determined by the combined effects of recruitment and the mortality or loss of residents (Caley et al. 1996, Wright & Steinberg 2001). The relative importance of variation in recruitment and post-recruitment processes (density-dependent and density-independent) in determining the dynamics of marine populations has been the focus of many studies in fishes and invertebrates (Underwood & Fairweather 1989, Caley et al. 1996). For example, when post-recruitment mortality is density-independent, local abundance will largely reflect recruitment (Sutherland 1990, Doherty & Fowler 1994), but when post-recruitment mortality is density-dependent local abundance is typically regulated by post-recruitment processes (Carr & Hixon 1997, Steele 1997, Menge 2000).

For seaweed, there is still limited information of the relative importance of recruitment and post-recruitment processes in determining local abundance (Capdevila et al. 2015). Many seaweeds recruit at relatively high densities in nearly monospecific stands, where intraspecific competition is predicted to be strong (Reed 1990) and a number of studies have shown density-dependent effects on seaweed recruitment (Capdevila et al. 2015) and post-recruitment mortality (Black 1974, Chapman 1984, Schiel 1985, Johnson & Mann 1988, Ang Jr & De Wreede 1992, Flukes et al. 2014). Density-dependent mortality often depends on the stage of development and as thalli increase in size, mortality can shift between density-dependence and density-independence (Ang Jr & De Wreede 1992, Capdevila et al. 2015). Density-independent mortality due to factors such as storms, heatwaves, ice scour and herbivory (Dayton et al. 1984, Aberg 1992b, a, Dayton et al. 1992, Wright & Steinberg 2001, Wernberg et al. 2016) can also have profound impacts on local abundance of seaweed. Because most seaweeds have very limited capacity for dispersal (Santelices 1990, Kendrick & Walker 1991, Norton 1992), and recruitment varies greatly in space and time (Reed et al.

1988, Bennett & Wernberg 2014), variation in recruitment might be predicted to be crucial in determining population abundance of many species. To identify a link between recruitment and subsequent abundance, individual recruits or cohorts need to be followed through time to determine patterns of post-recruitment mortality (density-dependent or density-independent, Caley et al. 1996). For example, post-recruitment mortality in the red alga *Delisea pulchra* was density independent, although variation in recruitment did not always explain subsequent adult abundance due to high mortality at some sites (Wright & Steinberg 2001).

Temperate intertidal rocky reefs are often dominated by canopies of furoid algae including *Fucus* spp., *Ascophyllum nodosum* and *Pelvetia canaliculata* in the northern Hemisphere (Brawley & Johnson 1991, Aberg 1992b, a, Wright et al. 2004) and *Hormosira banksii* and *Durvillaea* spp. in the southern hemisphere (Cheshire & Hallam 1988, Keough & Quinn 1998a, Schiel & Lilley 2007, Bellgrove et al. 2010). In temperate Australasia, *H. banksii* (Turner) Decaisne is often the dominant habitat-forming species in the mid-low intertidal zones (Schiel & Lilley 2007, Kain 2015). As an ecosystem engineer, *H. banksii* directly influences the presence of other algae and invertebrates through the amelioration of environmental variables such as temperature and desiccation (Keough & Quinn 1998a, Schiel & Lilley 2007, Bishop et al. 2009a) and it can tolerate a wide temperature range (Kain 2015). The *H. banksii* canopy also provides habitat and protection against predation for many invertebrate species (Bishop et al. 2009a) and their larvae (Moreno 1995). In many places, *H. banksii* and coralline turf coexist (Osborn 1948, Bellgrove et al. 2010), with the coralline turf occurring as an understory beneath the *H. banksii* canopy. Coralline turf consists mainly of *Corallina officinalis* but can also be comprised of several other species of red algae consisting as a mat of tightly packed erect filaments (Gorgula & Connell 2004).

Many canopy forming macroalgal populations are in decline worldwide (Johnson et al. 2011, Wernberg et al. 2013, Krumhansl et al. 2016) due to impacts from climate change (increased

air and water temperatures and wave intensity) and other anthropogenic stressors including habitat destruction, overfishing, pollution and increased sedimentation (Underwood 1998, Jackson et al. 2001, Thompson 2002, Airolidi 2003, Ling et al. 2008, Krumhansl et al. 2016, Wernberg et al. 2016). *H. banksii* is sensitive to anthropological disturbances such as trampling (Povey & Keough 1991, Keough & Quinn 1998a, Schiel & Taylor 1999) and increased nutrients via sewage discharge (Fairweather 1990, Bellgrove et al. 2010). The ability to recover from a disturbance will depend on the amount of recruitment and patterns of post-recruitment mortality. Despite a number of studies examining the recovery of *H. banksii* following disturbance, relatively few studies have quantified recruit densities in the field (although see Bellgrove et al. 2004, Alestra et al. 2014) and to our knowledge, none have followed those recruits over time to determine the extent to which recruitment explains subsequent abundance. Generally, studies quantify changes in the percentage cover of *H. banksii* following disturbance which have revealed that canopy cover recovered fastest when only fronds were removed rather than complete plants, and recovered fastest from pulse disturbances compared to press disturbances (Keough & Quinn 1998b, Underwood 1998, Schiel & Lilley 2007). However, recovery varied depending on the seasonal timing of the disturbance, and among years and/or between locations (Keough and Quinn 1998, Schiel and Taylor 1999, Underwood 1999, Schiel & Lilley 2007, Schiel & Lilley 2011).

Despite its abundance and ecological importance, the demography of *H. banksii* is still not well described. This study determined the demographic response (recruitment, post-recruitment growth and survivorship) of *H. banksii* subject to different levels of disturbance to its canopy and coralline turf algae over 24 months. We manipulated the *H. banksii* canopy and understory coralline turf to eight different combinations of percentage cover ranging from total canopy loss through to total understory loss and then identified and followed individual recruits for up to 18 months. We asked the following questions: 1) Does

recruitment vary significantly over time and between treatments containing different amounts of *H. banksii* and turf? 2) Is recruitment related to local adult abundance (density-dependent)? 3) Does post-recruitment mortality of cohorts vary over time? 4) Does growth and survivorship differ among different size classes and times? 5) Is post-recruitment mortality density-dependent or density-independent?

3.3 Method

3.3.1 Natural history

Hormosira banksii (Turner) Decaisne is a perennial fucoid alga which dominates much of the rocky intertidal coastline of temperate Australian and New Zealand (Schiel & Taylor 1999, Bellgrove et al. 2010, Schiel & Lilley 2011, Bellgrove et al. 2017b). It inhabits the mid to low intertidal zone and often forms a dense monotypic canopy with a standing biomass of up to 8 kg/m² and densities of several hundred plants per square metre (Schiel 2006). It is a slow growing perennial, dioecious species (Alestra & Schiel 2014) which is fertile all year round and releases gametes at low tide (Levring 1949, Womersley 1967). *H. banksii* shows large morphological variation depending on environmental conditions (Osborn 1948, Ralph et al. 1998, Macinnis-Ng et al. 2005, Bishop et al. 2009a, Mueller et al. 2015). *H. banksii* on the north coast of Tasmania has a small bushy morphology, with individuals having many small vesicles and short fronds that rarely exceed 150 mm in length, and thalli are often packed close together forming 100 % canopy cover (Mueller et al. 2015, Gemelli et al. 2018).

3.3.2 Study Site

The study was undertaken on the northern coast of Tasmania near the township of Beechford (41°01'14.4"S, 146°57'02.2"E), at a site consisting of a north-west facing sandy beach with a series of eight reefs of various shapes and sizes along two kilometres of coast. The reef selected for the study site was ~ 400 metres long and ~ 80 metres wide. It consisted of numerous small to medium basalt boulders up to 0.25 m² surface area on a base of solid basalt bedrock. The lower intertidal zones (≤ 0.5 MLLW) on these reefs are dominated by a canopy of *H. banksii* with an understory of coralline turf as well as other less common perennial macroalgae (e.g. several *Cystophora* species) and seasonally ephemeral algae. The north coast of Tasmania has relatively low wave exposure and a semi-diurnal tidal regime (Mueller et al. 2015), which often exposes the reef and its inhabitants to air twice daily.

3.3.3 Experimental design and demographic sampling

Sampling of recruitment, post-recruitment growth and mortality of *H. banksii* was done in 0.0625 m² (250 x 250 mm) quadrats placed in the centre of the 1 m² plots. The plots were placed haphazardly across the reef where there was at least 80% canopy of *H. banksii* and the corners of each plot were marked with marine epoxy resin. Photos were used as a reference to correctly locate each quadrat, using landmarks such as larger rocks and clear patches as well as the epoxy markers, which ensured that each plot location was easily identified. The percentage cover of *H. banksii* canopy and coralline turf was then manipulated into eight different treatments ($N = 4$ quadrats/treatment) in a pulse perturbation in September 2014. These eight treatments consisted of different ratios of *H. banksii* : coralline turf percentage cover manipulated to the following levels (H0:C100%, H14:C86%, H28:C72%, H43:C57%, H57:C43%, H72:C28%, H86:C14%, H100:C0%). These different ratios of *H. banksii* aimed to simulate varying intensities of disturbance in this system, natural disturbance on this reef were variable but generally low.

In April 2015 we mapped the location of each *H. banksii* individual within the 0.25 x 0.25 m² quadrats (N = 811 plants in 32 quadrats). The size of each individual was recorded into one of five size classes; 1: < 10 mm, 2: 10-29 mm, 3: 30-49 mm, 4: 50-79 mm and 5: ≥ 80 mm. These size classes were determined based on a pilot study that measured the size distribution of *H. banksii* at this site (N = 145 thalli) and resulted in approximately equal numbers of plants in each of the five categories. Every three months for 18 months we returned to each quadrat and the presence or absence of each mapped individual and their size class was recorded and new recruits identified and mapped. Recruits were defined as individuals which were in the size category 1 (< 10 mm) that were not present in quadrats at the previous count (Wright & Steinberg 2001). Plants that were absent were considered to have died. This sampling allowed us to track recruitment, post-recruitment growth and mortality of each individual over time within the quadrats.

To relate patterns of recruitment to temperature we obtained mean maximum monthly air temperature was obtained from the Australian Bureau of Meteorology Low Head station (091 293) which is 14.1 km from our study site.

3.3.4 Statistical Analysis

Does recruitment vary over time and between treatments containing different amounts of H. banksii and turf? Variation in recruitment was analysed using a two-factor Analysis of Variance (ANOVAs: Time x Treatment, both fixed). To improve normality recruitment data were $\ln(x + 1)$ transformed as determined by a Box-Cox analysis. Post hoc analyses were conducted using a Tukey's HSD.

Is recruitment related to local abundance? To explicitly test whether the total *H. banksii* abundance (pooled across size classes 2-5) correlated with recruitment, we ran regressions

between total density at time t and recruitment three months (time $t + 3$ months) later for each recruit cohort using each quadrat as a replicate (pooled across all treatments). We pooled across treatments as there were no significant treatment effects on recruitment (see results).

Does post-recruitment mortality vary among cohorts? Variation in early post-recruitment mortality (percentage mortality in the first three months) was not analysed due to low recruitment in many treatments in most months. However, we assessed variation in post-recruitment survivorship by generating survivorship curves for each annual recruit cohort.

Does growth and survivorship vary among different size classes and times? Given there were often no individuals of some size classes in individual quadrats at certain times, and there was no obvious effect of treatment, we pooled across quadrats within treatments at each time to determine survivorship and growth for each size class each time. Qualitatively, growth and survivorship appeared to vary among size classes and so to enable analyses we considered the pooled data for each treatment as the unit of replication for each size class at each time. We ran two-factor ANOVAs (size class x time, both fixed factors, N=8 replicates) for both survivorship (all five size classes) and growth (defined as the transition from one size class to the next, only for size classes 1-4) over each 3-month time period. Post hoc analyses were conducted using Tukey's HSD tests. We also plotted 18-month survivorship curves and growth trajectories (based on transition from one size class to the next) for all five size classes from the April 2015 cohort to examine long-term trends.

Is post-recruitment mortality density-dependent or density-independent? We examined whether post-recruitment mortality was density-dependent in three ways focusing only on the January 2016 cohort. We focused on this cohort as it had significant recruitment in most plots whereas the other cohorts had much lower recruitment with many plots having no recruitment or only 1-2 recruits. Firstly, to test whether total abundance explained post-recruitment

mortality we ran a regression analysis between total *H. banksii* density (size classes 2-5) at time t and the percentage mortality of recruits in the first three months (time $t + 3$ months). Examining for density-dependence as a function of total density, rather than cohort density often makes sense for species with discrete recruit pulses (e.g. Schmitt and Holbrook (1999) & Wright and Steinberg (2001)). However, we also ran a regression analysis between recruit density at time t and percentage mortality of recruits in the first three months (time $t + 3$ months). Because there were no obvious treatment effects, both of these relationships were examined using each quadrat as a replicate (pooled across treatments). Finally, to determine whether variation in recruitment explained subsequent variation in the abundance of the cohort, we performed a regression analysis of the number of plants after 9 months (October 2016) as a function of initial recruit density in January 2016. If abundance after 9 months is positively related to initial recruit density then this is consistent with density-independence and recruitment limitation (Caley et al. 1996).

Data was analysed using R Studio and Sigmaplot Version 12.

3.4 Results

3.4.1 Does recruitment vary over time and between treatments containing different amounts of *H. banksii* and turf?

Recruitment of *H. banksii* was extremely variable over the 18 months of the experiment with significantly higher recruitment occurring during November 2015-January 2016 compared to all other times, which did not differ from each other (Fig. 1, Table 1). The very high recruitment between November 2015 to January 2016 (up to 900 recruits m^{-2}) coincided with warmest air temperatures, suggesting a seasonal increase in recruitment over summer. There was no significant difference in recruitment between treatments throughout the experiment

(Table 1) indicating that disturbance and the cover of *H. banksii* and coralline turf did not influence *H. banksii* recruitment at this site.

3.4.2 Is recruitment related to local abundance?

There were no significant relationships between adult density and recruitment three months later for any cohort (Table 2).

3.4.3 Does post-recruitment mortality vary among cohorts?

All cohorts had relatively high post-recruitment survivorship and there was no evidence of any differences among treatments. No cohort had less than 60% survivorship during the 18 months of the study. For example, the April 2015 cohort had an average of 80% survivorship after 18 months and the July 2015 cohort had 100% survivorship in every treatment over 15 months (Fig. 2).

3.4.4 Does growth and survivorship vary among different size classes and times?

Survivorship varied significantly with size class and time (Table 3). This reflected relatively low survivorship of the smallest size class between February 2015-April 2016 (78%) and August 2016-October 2016 (74%) compared to between August 2015-October 2015 (95%) and November 2015-January 2016 (97%, Fig. 3, Table 3). Survivorship of size classes 2-5 rarely dropped below 90% and did not differ among times although the largest size class had a trend for lower survivorship in May 2015-July 2015 (86%) and August 2015-October 2015 (87%, Fig. 3). Size class 1 had lower survivorship than all other size classes in February 2016-April 2016 and August 2016-October 2016 and lower survivorship compared to size classes 2 and 3 in May 2015-July 2015 (Table 3, Fig 3).

Growth also varied with size class and time (Table 3). The two smaller size classes both had the highest growth between November 2015-January 2016 (Fig. 4, Table 3). Notably, 85% of size class one grew into size class 2 from November 2015-January 2016 and this was higher growth compared to all other times. For size class 2, 57% grew into size class 3 in November 2015-January 2016 and this was higher growth compared to May 2016-July 2016, August 2016-October 2016 and May 2015-July 2015 (Table 3, Fig 4). In contrast, size class 3 had higher growth between February 2016-April 2016 (43% grew) compared to August 2016-October 2016 and May 2015-July 2015. Size class 1 had higher growth than size class 4 between May 2015-July 2015, and compared to size classes 3 and 4 between November 2015-January 2016 but not at any other times. Size class 2 also had higher growth than size classes 3 and 4 in November 2015-January 2016 while size class 3 had higher growth than size class 1 in February 2016-April 2016.

Survivorship of the plants initially mapped in April 2015 was high over the study. After 18 months, size classes 2 (90%) and 3 (85%) had the highest survivorship while size class 1 had the lowest (61%) with size class 5 having 69% (Fig. 5A). The growth of the April 2015 cohort was slow. On average, after 18 months size class 1 individuals grew into size class 3, with only one of 49 plants growing to size class 5 in that time (Fig. 5B). The growth of the other size classes was similarly slow and overall, these results suggest it would take approximately five years for a plant in size class 1 to reach size class 5.

3.4.5 Is post-recruitment mortality density-dependent or density-independent?

Post-recruitment mortality of *H. banksii* was independent of density. The relationships between post-recruitment mortality for the January 2016 cohort vs. the number of adult plants (size classes 2-5) ($r^2=0.080$ $P=0.202$, Fig. 6A) and vs. the number of recruits ($r^2=0.120$ $P=0.114$, Fig. 6B) were both non-significant. However, there was a significant positive

relationship between the number of recruits per plot and abundance 9 months later ($r^2=0.982$, $P<0.001$, Fig. 6C).

3.5 Discussion

This study has highlighted spatial and temporal variation in *Hormosira banksii* demography but no evidence that different levels of disturbance to either its canopy or the cover of understory coralline turf algae affects these demographic metrics. We found that *H. banksii* demography is typified by year-round recruitment but with a seasonal peak in summer. Growth is relatively slow with recruits (< 10 mm in size) taking 4-5 years to grow into the largest adult size class (> 80 mm in size) and survivorship of all size classes including recruits is relatively high; new recruits always had > 74% survivorship over any three month period. Importantly, the positive relationship between recruitment and abundance nine months later suggests *H. banksii* is recruitment limited.

H. banksii is fertile all year round, similar to other fucoids (Wright et al. 2004), and this was reflected in the year-round recruitment which has been described previously in Victoria and New South Wales (Bellgrove et al. 2004, Kain 2015). The higher recruitment we observed during summer is similar for *H. banksii* in New Zealand, although this was measured as percentage cover (Schiel & Taylor 1999), but differs to findings for recruitment in rock pools in New South Wales which did not differ between seasons (Kain 2015) and on a rocky shore in Victoria where recruitment was highest in April and lowest in February and October (Bellgrove et al. 2004). Higher recruitment during summer has been described previously in other temperate intertidal brown and red algae (Sousa 1979b, Schiel & Taylor 1999).

Seasonal differences in *H. banksii* recruitment at our site reflect variable gamete production and settlement or post-settlement survivorship of embryos. Gamete release in fucoids is often

restricted to calm days (Ladah et al. 2008) and the peak in recruitment in *H. banksii* during summer could reflect lower wave activity between October 2016 through to January 2016 allowing for increased gamete release. Post settlement survivorship of furoid embryos is typically low (Schiel & Foster 2006) and a range of factors strongly influence post-settlement survivorship of *H. banksii* and other furoid embryos. Water movement and subsequent dislodgement by waves reduces the attachment and survival of *H. banksii*, *Cystophora torulosa* and *Durvillaea antarctica* zygotes (Vadas Sr et al. 1992, Taylor & Schiel 2003, Taylor et al. 2010). For example, only 24% of *H. banksii* zygotes settled for 1 hour survived after exposure to a single wave although, survivorship varied depending on the time zygotes had been settled and level of wave exposure (Taylor & Schiel 2003).

Intertidal rocky shores where *H. banksii* occurs are subjected to high temperatures with summer temperatures on northern Tasmanian rocky shores typically exceeding 25-30°C during low tide (Wright & Gribben 2017) which can be exacerbated by canopy loss due to factors such as sun burn of fronds (Bellgrove 2013). Furoid embryos are thought to survive better in cooler, moist environments such as beneath a canopy formed by adult thalli (Brawley & Johnson 1991, 1993) although we found no relationship between recruitment and the *H. banksii* canopy cover here. In New Zealand, *H. banksii* recruits are negatively affected by both sedimentation and the presence of coralline turfs (Schiel et al. 2006, Alestra et al. 2014) which can operate synergistically - turfs tend to accumulate sediment. Other algae can also compete with *H. banksii* zygotes reducing their survivorship (Alestra & Schiel 2014). Finally, micrograzers such as copepods can both remove *H. banksii* embryos and recruits (Bellgrove et al. 2014) but some grazers can remove competitors and indirectly benefit *H. banksii* embryos (Alestra & Schiel 2014). Overall, it is clear that multiple abiotic and biotic factors influence the post-settlement survival of *H. banksii* and, even if gamete production varied over time, these factors may have contributed to the observed patterns of recruitment

in *H. banksii* in this study. Further research would be required to determine the mechanisms behind these factors.

The finding that the *H. banksii* canopy and coralline turf percentage cover did not affect *H. banksii* recruitment was surprising given the protective capacity of the *H. banksii* canopy in reducing temperature (Lewis unpublished data) and the negative effects of turf in increasing sedimentation (Schiel et al. 2006, Alestra et al. 2014). A higher *H. banksii* canopy is also likely to provide a greater supply of gametes for settlement but there was no evidence for positive correlation between adult abundance and recruitment. Furoid algae such as *H. banksii* generally have short range dispersal, with propagules often settling close to parents (Mueller et al. 2018). This would suggest that recruitment might increase as the abundance of reproductive individuals increases, however we found no relationship between the abundance of size classes 2-5 (of which the majority would be of reproductive age, see Kain (2015)) and number of recruits three months later. High mortality is common in the early life stages of macroalgae; in other furoids < 5% of embryos settling survive to the macroscopic juvenile stage in the field (Schiel & Foster 2006). Thus, it is likely that by the time new *H. banksii* recruits were visible in the field their densities have been significantly impacted. Dunmore (2006) found natural recruit densities of *H. banksii* onto experimental panels reached 500 cm⁻² per week⁻¹, much higher than the densities observed here; although that study focused on the embryonic life-cycle stage and is not directly comparable to our data. Kain (2015) also found much lower numbers than Dunmore (2006) when measuring macroscopic recruitment in the field.

Both natural and anthropogenic disturbances such as trampling, high nutrients, pollution and storms reduce the *H. banksii* canopy cover (Doblin & Clayton 1995, Keough & Quinn 1998a, Schiel & Taylor 1999, Lilley & Schiel 2006, Schiel et al. 2006, Schiel & Lilley 2007, Bellgrove et al. 2010, Schiel & Lilley 2011, Kain 2015) but remnant holdfasts may remain

following disturbance. If small amounts of *H. banksii* holdfasts remain post-disturbance, recovery tends to be relatively quick, however if no holdfast remains, recovery can be slow (Underwood 1998). Here it is possible that some holdfasts were not effectively removed during establishment of the treatments, aiding the recovery of adult populations within the plots and possibly influencing some of the observed patterns. Similarly, Speidel et al. (2001) followed the recovery of *Fucus gardneri* and found that as long as some *Fucus* remained in the plots following experimental disturbance, that time to canopy closure and cover after 1 year showed no consistent trends with the initial disturbance.

All 3-month cohorts had high survivorship with no cohort having less than 60 percent survivorship over the 18 months of the study and there were no obvious differences in survivorship between treatments of different cover of *H. banksii* and coralline turf (Fig. 2). Three-monthly survivorship varied between size classes and over time but was also typically high (Fig. 3). Whilst survivorship of the larger size classes rarely dropped below 90% and did not differ over time, size class 1, which we categorised as new recruits, had lower survivorship between January-April 2016 and July-October 2016, (i.e. in late summer and winter). It is possible that these small individuals are more susceptible to high temperatures and sunburn while exposed over summer (Schoenwaelder 2002, McKenzie & Bellgrove 2008, Bellgrove 2013), and because they were smaller they may not have been able to regenerate from holdfasts (Kain 2015). Survivorship of small size classes may be lower in winter because of increased wave action and scour from sediment and other plants (Underwood 1998, 1999, Vaselli et al. 2008). Larger thalli also had a trend for lower survivorship during winter (April-July 2015 and July-October 2015) although this was non-significant.

Growth was slow but varied over time and between size classes and in general the two smaller size classes had higher relative growth. On average over 18 months, the smallest size

class grew approximately 50 mm into size class 3. Furoids are characterised by slow growth and *H. banksii* is relatively slow growing compared to other furoid alga (Dunmore 2006, Kain 2015). We found that growth occurred all year round but increased during spring and summer (November-January 16 & January-April 16), likely due to warmer conditions and increased light (Dunmore 2006).

To assess the extent to which recruitment translated into population abundance, we used the cohort with the largest recruitment event (January 2016) and followed this cohort through to October 2016. This data suggested that the post-recruitment survivorship was density-independent with a very strong relationship observed between recruitment and abundance after nine months which is consistent with population abundance of *H. banksii* largely being determined by recruitment of size class 1 individuals. Similarly, the post-recruitment mortality of the red alga *Delisea pulchra* was density-independent although recruitment did not always translate into high population abundance due to high mortality from grazing sea urchins (Wright & Steinberg 2001). The lack of a significant relationship between the density of size classes 2-5 thalli and the percentage of recruit mortality and between the number of recruits and the percent recruit mortality for the January 2016 cohort, further highlighted that recruit mortality is independent of adult density (Fig. 6A, B). The lack of density-dependence in *H. banksii* was surprising considering the dense *H. banksii* canopy and potential for density-dependent mortality in other species (Roughgarden et al. 1985, Carlon 2001) but highlights the importance of density-independent factors such as waves, temperature and desiccation in affecting the demography of intertidal algae.

This study was the first to follow individual recruits of *H. banksii* over time and provides an important insight into its demography in Tasmania. It suggests that the *H. banksii* population are slow growing and long-lived with individuals taking approximately five years to grow from recruits to the largest size class. The lack of canopy effects on recruitment and the

strong relationship between recruitment and future population abundance suggests a strong degree of resilience to disturbance as long as recruitment occurs.

Table 3.1. Two-factor ANOVA testing the effects of treatment (ratio of *Hormosira banksii* to coralline turf) and time on *H. banksii* recruitment.

Source of Variation	df	MS	F	P
Time	6	466.973	10.459	<0.001
Treatment	7	22.576	0.506	0.829
Time x Treatment	42	13.104	0.294	1.000
Residual	168	44.647		
Total	223	49.377		

Table 3.2. Relationships between the number of adult plants in each quadrat and the number of recruits three months later ($t + 3$) for cohorts recruiting in April 2015 to July 2016.

Cohort	β	R^2	P
April 2015	0.0192	0.00717	0.645
July 2015	0.2670	0.00392	0.733
October 2015	0.0047	0.00003	0.978
January 2016	0.1030	0.01780	0.466
April 2016	0.0159	0.00632	0.665
July 2016	0.0062	0.00145	0.836

Table 3.3. ANOVA testing for the differences in percentage survivorship and growth (based on transition from one size class to the next) of *Hormosira banksii* on different size classes and times. Results of Tukey's tests done within the size class \times time interactions are shown.

Dependent variable	Source	df	SS	MS	F	Pr(>F)
Survivorship	Size class	4	0.489	0.122	18.297	< 0.001
	Time	5	0.107	0.021	3.194	< 0.001
	Size class \times Time	20	0.463	0.023	3.473	< 0.001
	Residuals	203	1.356	0.007		

Tukey's tests:

Between times for each size class. **Size class 1:** Aug 15-Oct 15 = Nov 15-Jan 16 > Feb 16-Apr 16 = Aug 16-Oct 16, all other times NS. **Size classes 2 – 5:** all times NS.

Between size classes for each time. **May 15-July 15:** size class 2=3>1, all others NS, **Aug 15-Oct 15:** all NS, **Nov 15-Jan 16:** all NS, **Feb 16-Apr 16:** size class 2=3=4=5>1, **May 16-Jul 16:** all NS, **Aug 16-Oct 16:** size class 2=3=4=5>1.

Growth	Size class	3	1.141	0.380	12.881	< 0.001
	Time	5	1.792	0.3538	12.139	< 0.001
	Size class \times Time	15	3.229	0.215	7.293	< 0.001
	Residuals	168	4.959	0.030		

Tukey's tests:

Between times for each size class. **Size class 1:** Nov 15-Jan 16 > all other times NS. **Size class 2:** Nov 15-Jan 16 > May 16-Jul 16 = Aug 16-Oct 16 = May 15-Jul 15, all other times NS, **Size class 3:** Feb 16-Apr 16 > Aug 16-Oct 16 = May 15-July 15, all other times NS, **Size class 4:** all times NS.

Between size classes for each time. **May 15-July 15:** size class 1>4, all others NS, **Aug 15-Oct 15:** all NS, **Nov 15-Jan 16:** size class 1=2>3=4, **Feb 16-Apr 16:** size class 3>1, all others NS, **May 16-Jul 16:** all NS, **Aug 16-Oct 16:** all NS.

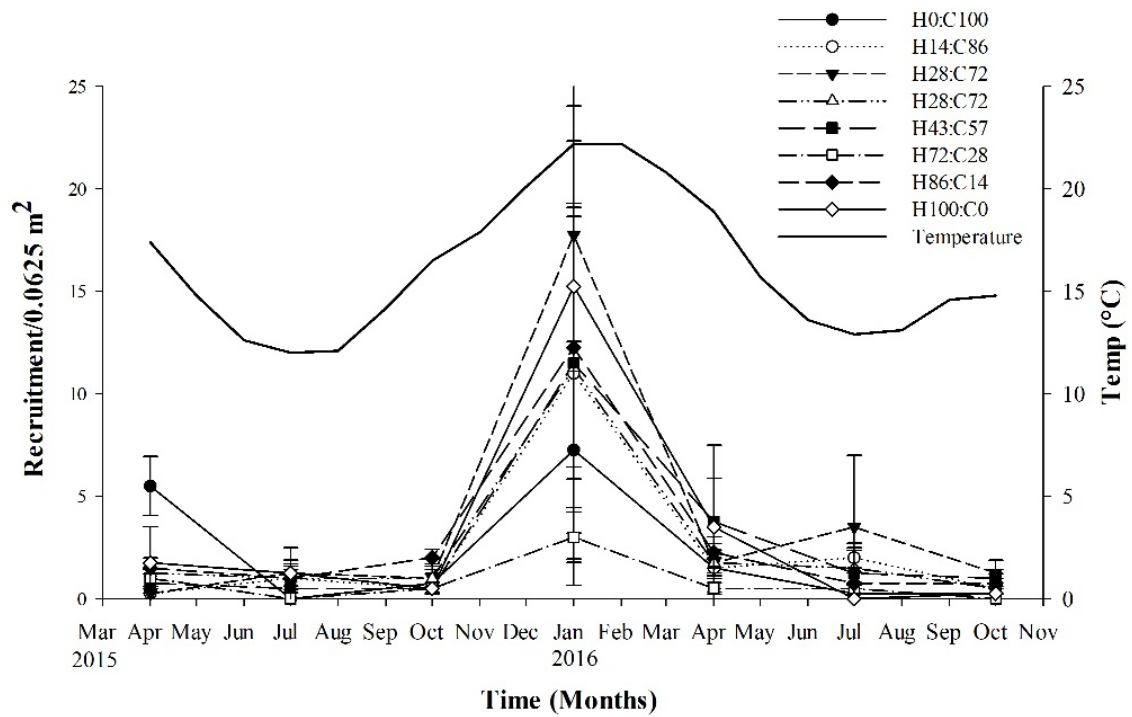


Figure 3.1. Mean (\pm SE) recruitment of *Hormosira banksii* into eight treatments of different combinations of initial cover of *H. banksii* and coralline turf over 18 months ($N = 4$ quadrats per treatment). The mean maximum air temperature at the site is also shown.

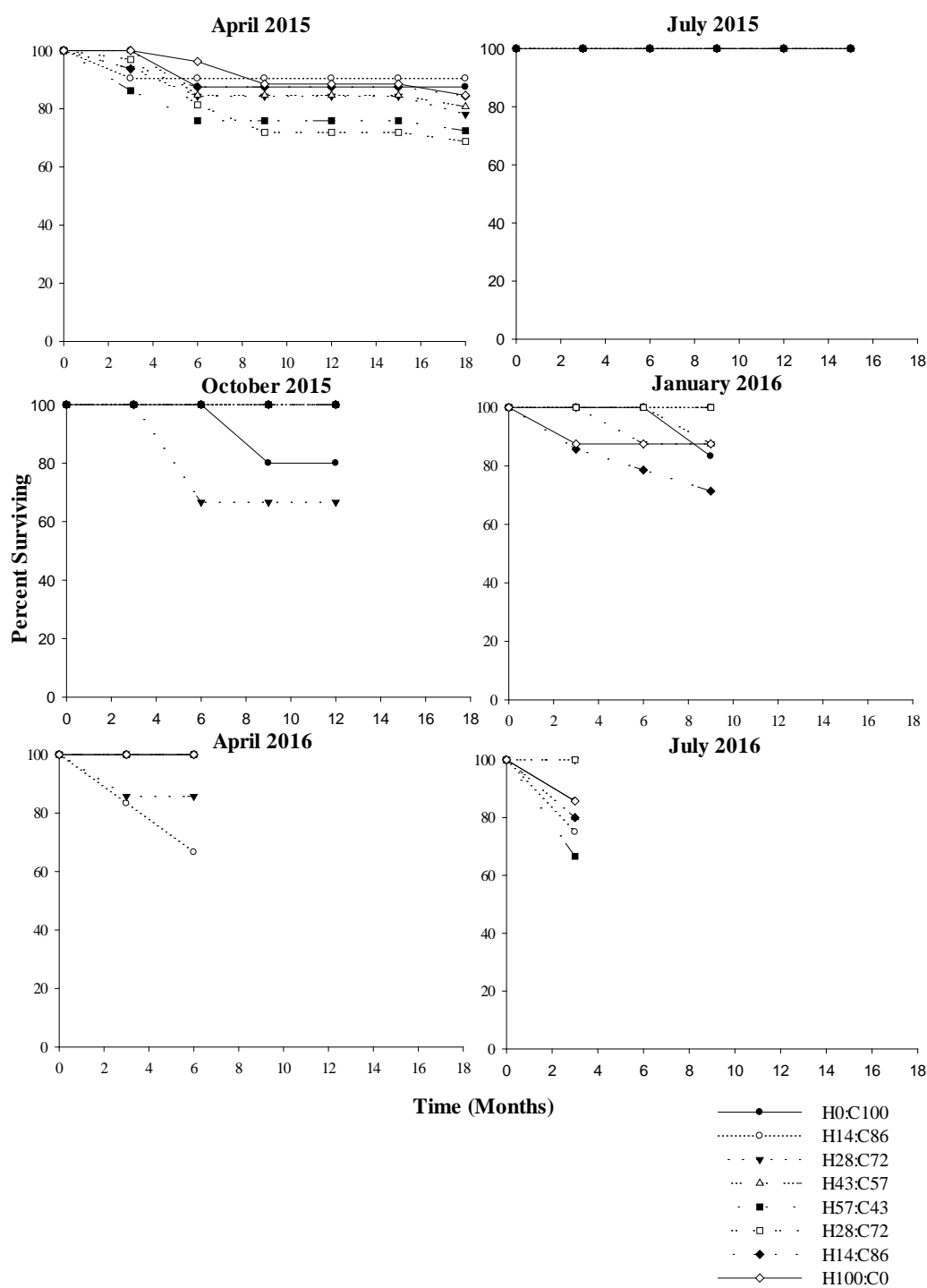


Figure 3.2. Survivorship curves for each cohort from April 2015 through to September 2016. No recruitment occurred in July 2015 for treatments H28:C72, H57:C43 and H100:C0, October 2015 treatments H28:C72 and H0:C100 and April 2016 treatment 6. Where symbols are overlaid the same percentage of recruits survived.

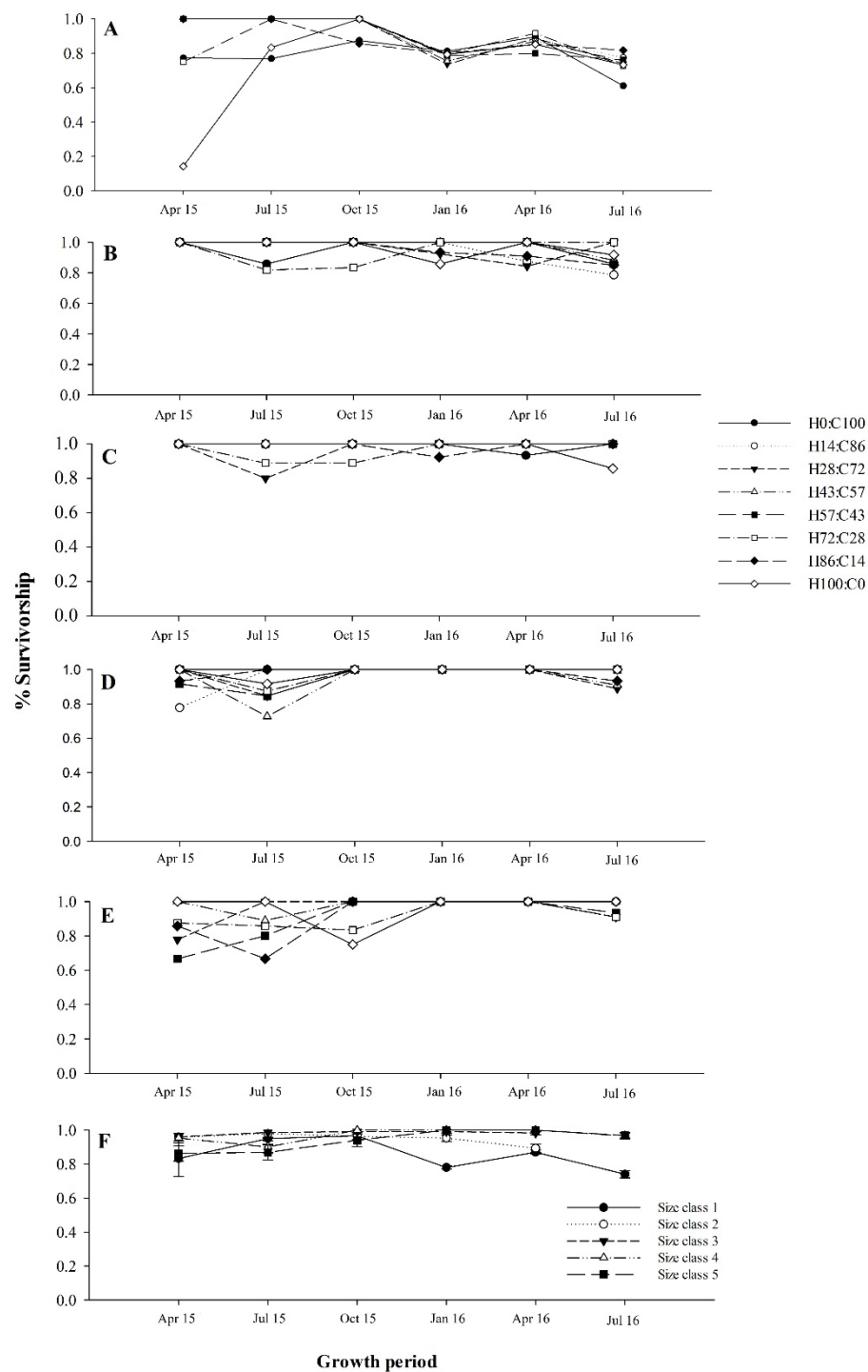


Figure 3.3. Survivorship of the five *Hormosira banksii* size classes for each treatment (pooled across N = 4 quadrats) every 3 months. A) Size class 1: < 10 mm, B) size class 2: 10-29 mm, C) size class 3: 30-49 mm, D) size class 4: 50-79 mm and E) size class 5: > 80 cm. F) Mean (± SE) survivorship of the eight treatments (pooled) for each size class every 3 months.

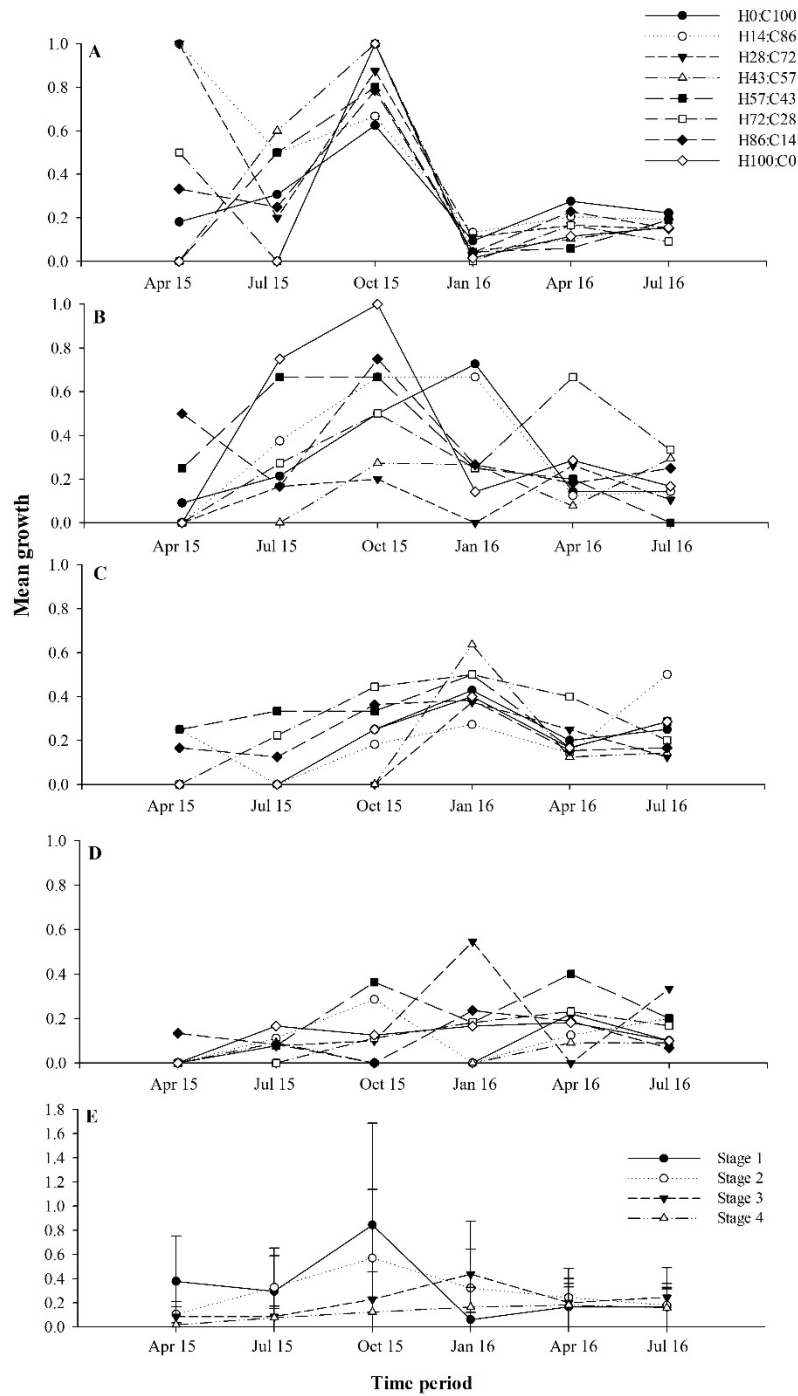


Figure 3.4. Growth based on the transition from one size class to the next for four *Hormosira banksii* size classes for each treatment (pooled across N = 4 quadrats) every 3 months. A) Size class 1: < 10 mm, B) size class 2: 10-29 mm, C) size class 3: 30-49 mm, and D) size class 4: 50-79 mm. E) Mean (± SE) growth of the eight treatments (pooled) for each size class every 3 months.

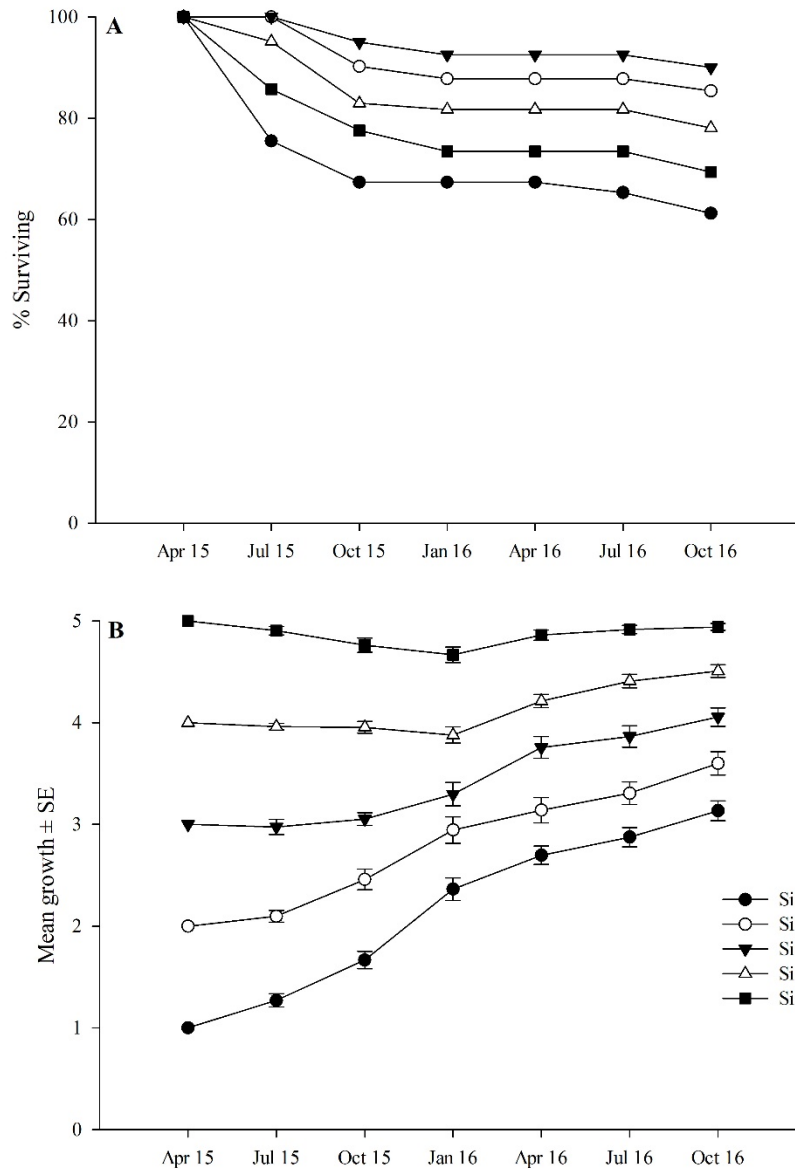


Figure 3.5. A) Percentage survivorship for each size class. B) Growth (transition to the next size class, mean \pm SE) for each of the five size classes over 18 months for thalli in April 2015. Data is pooled across treatments. Initial sample sizes for each size class: 1 (49), 2 (41), 3 (40), 4 (82) and 5 (49).

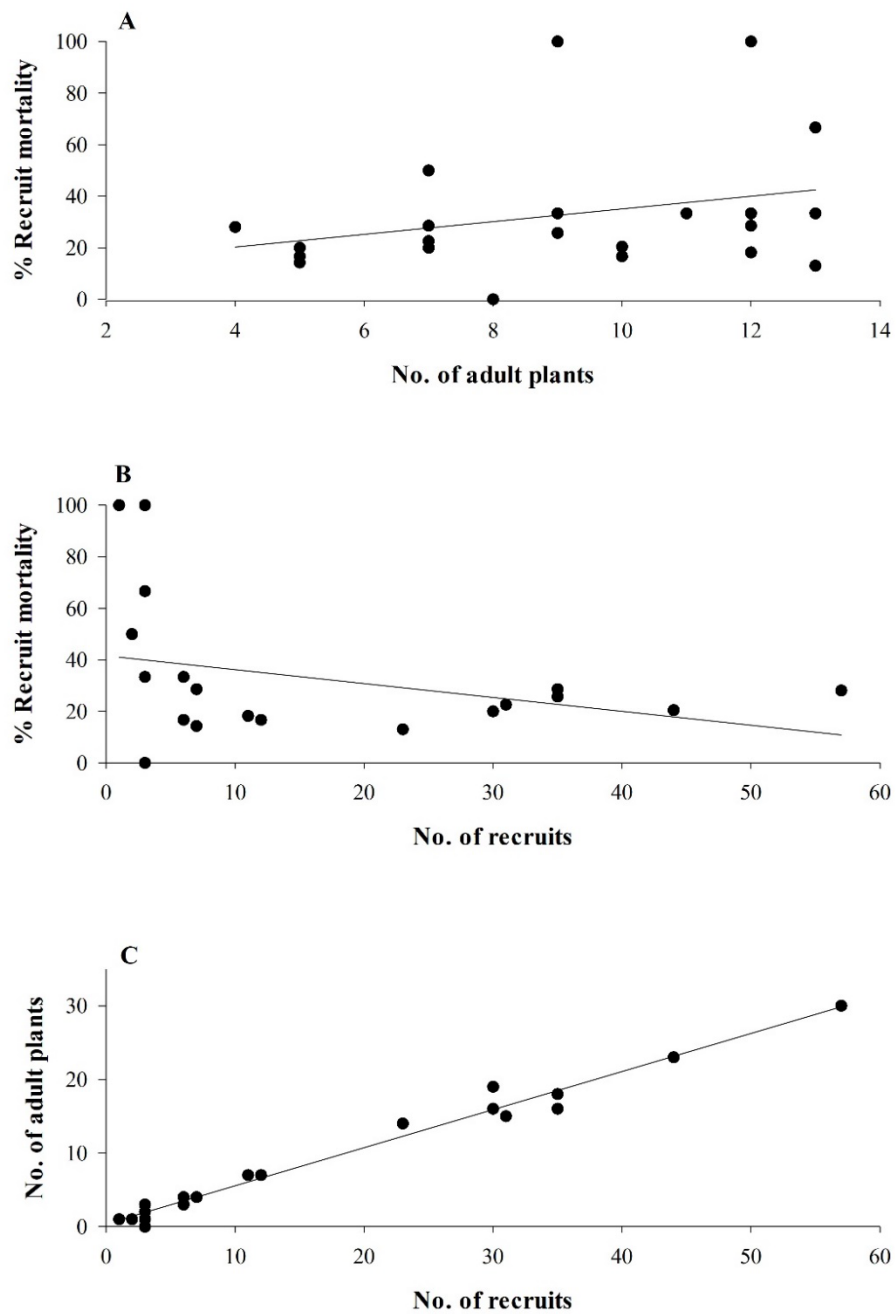


Figure 3.6. Relationships between (A) adult density vs. % recruit mortality, (B) recruit density vs. % recruit mortality and (C) recruitment in January 2016 vs. number that survived through to October 2016 for the January 2016 cohort. N = 32 quadrats.

4. Intraspecific facilitation in marine ecosystem engineers: a review

Ryan D. Lewis¹, James E. Byers², Craig R. Johnson¹, Cayne Layton¹, Victor Shelamoff^d, Masayuki Tatsumi¹, Jeffrey T. Wright¹

Institute for Marine and Antarctic Studies, Tasmania¹

Odum School of Ecology, University of Georgia²

4.1 Abstract

Ecosystem engineers form the basis of many marine systems and are known to strongly affect populations of co-resident species. Through their own physical structures, they alter abiotic conditions and provide habitat for other species. Literature suggests that these species also influence their own demography via their effects on environmental properties, however little is known about the extent of this intraspecific facilitation or the mechanisms that underpin it. Because of the pivotal role ecosystem engineers play in their environment, it is important to understand how widespread intraspecific facilitation might be. We reviewed the literature surrounding intraspecific facilitation in marine ecosystem engineers and conducted a meta-analysis on the studies that experimentally addressed this phenomenon. We examined the overall effects of these species on their own demographic traits (growth, recruitment and survivorship), whether the effects differed between intertidal and subtidal habitats, functional groups and between different types of manipulative studies (engineer present/absent and high/low density). We found that overall, published works on marine ecosystem engineers mostly revealed they facilitate their own growth, recruitment and survivorship. This effect was consistent across functional and habitat groups and demographic traits. Further research

is required into the extent of intraspecific facilitation of ecosystem engineers in marine environments and the mechanisms behind these positive feedbacks .

4.2 Introduction

Ecosystem engineers have major effects on associated species and in certain situations, entire communities depend on the presence of the engineer (Jones et al. 1994, Berkenbusch & Rowden 2003, Romero et al. 2015, Guy - Haim et al. 2018). In marine systems, ecosystem engineers include species such as; macroalgae, seagrasses, saltmarsh, shellfish and tubeworms. Their extensive effects occur because they provide physical structure to ecosystems and modify the local abiotic and biotic environment resulting in effects on a suite of other species (Jones et al. 1994, 1997, Alper 1998, Bendetti-Cecchi et al. 2001, Kochmann et al. 2008, Donadi et al. 2014, Wright et al. 2016, Alves et al. 2017a, Hanke et al. 2017, Haram et al. 2018). For example in the United States, the invasive seaweed *Gracilaria vermiculophylla* has been shown to provide a variety of benefits to the environment and other species, increasing the survivorship of native epifauna and density of shorebirds foraging in the mudflats (Byers et al. 2012, Wright et al. 2014, Ramus et al. 2017, Haram et al. 2018).

The effects of ecosystem engineers on associated species are often positive, facilitating enhanced population sizes and biodiversity (Stachowicz 2001, Bruno et al. 2003). Moreover, these facilitative effects are predicted to be especially important where abiotic stress is greater, because the engineer provides a greater reduction of harsh abiotic conditions (Bertness & Callaway 1994, Bruno et al. 2003, Craine & Bertness 2006, Brooker et al. 2008, Smith et al. 2018). Ecosystem engineers can also have detrimental effects on the environment and other species and this is often observed in invasive ecosystem engineers (Guy - Haim et al. 2018). Generally, where an engineering species increases habitat complexity through its structure, species diversity will also increase, whereas if the engineer reduces complexity (e.g. invasive oysters replacing native mussels or seaweeds), diversity can decrease (Crooks 2002, Padilla 2010).

Although the effects of ecosystem engineers on other species is well recognised, much less attention has been given to how engineering of the environment feeds back to facilitate the engineer itself. This self-facilitation, also termed an environment-engineer feedback (Jones et al. 2010), occurs when the demographic rates of the engineer themselves are positively affected by the engineered environment (Cuddington 2007, Jones et al. 2010). Intraspecific facilitation may occur when the engineer creates living spaces for conspecifics or creates an abiotic or biotic environment which benefits the engineer itself (Cuddington 2007, Jones et al. 2010). Although recognized conceptually, there appears to be relatively few studies of self-facilitation in ecosystem engineers compared to the plethora of studies of interspecific facilitation by both native and invasive ecosystem engineers (see reviews and meta-analyses of Romero et al. 2015, Coggan et al. 2018, Guy - Haim et al. 2018).

Because marine ecosystem engineers often form extensive areas of habitat (Schiel & Choat 1980, Buschbaum et al. 2009, Bellgrove et al. 2010, Alves et al. 2017a), it seems likely the environmental modifications they make would facilitate their own demographic rates. Marine plants (such as sea grasses and mangroves) and seaweeds can ameliorate potentially stressful abiotic factors such as light, heat and sedimentation (Huxham et al. 2010, Bennett & Wernberg 2014, Adams et al. 2016, Layton et al. 2019), while mussels and oyster reefs are known to reduce temperatures and provide a refuge from predation (Gutierrez et al. 2003, Borthagaray & Carranza 2007).

Although density dependence is usually considered to be negative because competition for resources increases as density increases (Svanfeldt et al. 2017), positive density-dependence has been described for some marine ecosystem engineers. For example, kelp show positive-density dependent growth and reproduction (Schiel & Choat 1980) and have higher recruitment under kelp canopies compared to no canopy (Layton et al. 2019). Similarly, terrestrial plant ecosystem engineers can also show positive density-dependent recruitment

and survivorship (Dickie et al. 2005, Svanfeldt et al. 2017). Moreover, environmental stress may alter the balance between intraspecific competition and facilitation, the interactions between the engineer and environment may still occur along a stress gradient, however a shift from positive to negative may occur under different conditions due to environmental modifications. For example, Biswas and Wagner (2014) found that seasonal variations in environmental stressors in the terrestrial plant *Alliaria petiolata* lead to negative density-dependent survival in summer, but during harsh winter conditions, survival was positively density dependent. Similarly, intertidal barnacle populations can experience either positive or negative intraspecific density-dependence depending on abiotic stressors such as increased temperatures, heat and desiccation (Leslie 2005, Schiel & Lilley 2007).

Here, we undertake a review and meta-analysis of the current state of knowledge of intraspecific facilitation in marine ecosystem engineers. Specifically, we examined whether different demographic processes (recruitment, growth and survivorship) were positively affected by the presence of the conspecific engineer and whether the type of engineer (invertebrate or macrophyte) or habitat (intertidal vs. subtidal) influenced this intraspecific facilitation. Demographic processes might be predicted to differ in their response. For example, small marine propagules such as larvae and spores are likely to be susceptible to abiotic stressors (Davis et al. 2013, Przeslawski et al. 2015) and thus recruitment may be predicted to be more strongly facilitated by the engineered environment than growth or survivorship. The level of abiotic stress may also influence the strength of facilitation on the demography of an engineering species. For example, kelp in a relatively benign subtidal system may rely less on facilitation compared to furoid algae living on an exposed intertidal reef. The marine intertidal zone is typically considered more stressful than the subtidal because organisms are exposed to high temperature, desiccation and light during low tide and increased wave activity at some sites (Davison & Pearson 1996, Tomanek & Helmuth 2002).

Thus, we predict that self-facilitation in engineers may be stronger for intertidal areas compared to subtidal. The morphology of the engineer may also influence the strength of facilitation due to varying structural attributes or life history strategies which may differentially influence abiotic or biotic changes. For example, large seaweeds may reduce water motion (Williams et al. 2013) or temperature and desiccation at low tide (Oates 1985), while smaller invertebrates such as mussels form high-density mats which provide lots of protective spaces for recruitment (Commito et al. 2014).

4.3 Method

4.3.1 Data Collection and Eligibility Criteria

A literature search was conducted using the Web of Science database on the 22nd February 2019. We used search criteria which included terms relating to 1) density, 2) ecosystem engineering or feedbacks or facilitation, and 3) marine environments [Search Terms: TS= (Density) AND TS= ((positive AND feedback) OR (self AND facilitat*) OR "ecosystem engineer*" OR (environment* AND engineer*) OR (intraspecific AND facilitat*)) AND TS= (marine OR intertidal OR subtidal OR benthic OR littoral)]. Web of Science categories which were not relevant to our topic, such as 'electrochemistry' or 'construction' were excluded prior to the search being conducted. The references identified in the search were added to an Endnote Online database and shared with all authors.

We chose twenty papers at random from our search results which were reviewed and assessed by all authors against agreed criteria for initial inclusion in this study. The studies were required to relate specifically to intraspecific facilitation by marine ecosystem engineers and authors determined whether each paper was relevant and recorded relevant data in a spreadsheet. The responses to whether studies were to be included or excluded were

compared to highlight any differences in interpretation among reviewers. The responses from all authors were consistent.

Once we had this consensus, we divided all the papers identified in our search between reviewers. Each paper was initially checked for broad relevance and if it was deemed not relevant (e.g. freshwater or terrestrial, examined interspecific facilitation) it was subsequently excluded. The remaining studies were deemed as 'possibly relevant' and the abstract, keywords or full-text of these papers were then examined in further detail. For papers that were determined to be relevant based on the agreed criteria, we then extracted the following data: the term used to describe the phenomenon (intraspecific facilitation, environment-engineer feedback), habitat (intertidal vs. subtidal), location of the study, genus and species of the engineer, type of ecosystem engineer (autogenic or allogenic), demographic trait/s examined (recruitment, growth or survivorship), whether the feedback was positive or negative.

4.3.2 Data Collection and Effect Size Calculation

This meta-analysis aimed to determine the effects of an ecosystem engineer on their own demography. We focussed on field studies where the engineers were experimentally manipulated to provide unambiguous evidence for intraspecific facilitation. Thus, studies required data on the response of the engineer's own demographic traits compared between manipulated treatments when the ecosystem engineer was present vs. absent or, when the ecosystem engineer was at different densities (low vs. high). Several studies included multiple densities and for these we only compared between the highest and lowest (non-zero) density treatments. Where studies included both presence/absence and different densities we focussed only on presence/absence.

For the relevant studies, data was mostly extracted by manually calculating the mean, standard error, standard deviation and sample size from figures included in publications or by extracting data from tables, text and statistical analyses. Studies which appeared relevant but did not provide the necessary data to calculate effect size were not included in the analysis. Where the results of a publication contained data for more than one demographic trait (recruitment, survivorship or growth), relevant data was included for each trait as a separate entry (Table 1). Where studies had other treatments that were crossed with presence/absence or different densities of the engineer (e.g. cages to exclude consumers compared to uncaged treatments: Bertness et al. 1999b, Beermann et al. 2013) we used data from the most natural treatment (e. g. uncaged).

Hedges' g (Hedges 1981), the unbiased mean difference, was then used to determine effect size by calculating the difference in recruitment, growth or survivorship between ecosystem engineer present vs. absent or high vs low density treatments for each study.

4.3.3 Meta-analysis

The effect size estimates between ecosystem engineer treatments were analysed using Meta-Essentials: workbooks for meta-analysis (Suurmond et al. 2017). These workbooks calculated effect size (Hedges' $g \pm 95\%$ CI) and produced figures and analysis. Initially, a random effects meta-analysis was conducted to calculate the overall effects of the presence or high density of ecosystem engineers. We then examined the data in more detail to determine whether facilitation differed: 1) among demographic traits (recruitment, growth and survivorship), 2) between intertidal vs subtidal engineers, 3) between invertebrates and plants/seaweeds, and 4) between studies where engineers were present vs. absent compared to at high vs. low density.

Because we only included studies with specific data sets that met our requirements we did not need to include any form of moderator analysis. We did however use subgroup analysis to separate our different demographic metrics (growth, recruitment, survivorship), systems (intertidal, subtidal), general functional groups (invertebrate, macrophyte) and types of study (engineer present/absent, high/low density). A funnel plot was also produced to account for publication bias. This provided an adjusted overall effect size and confidence intervals by projecting alternative points to represent the opposite outcome to those included in the study (i.e. if a Hedges' g of +1.0 was included in the results, a simulated point was added to the funnel plot at $g=-1.0$).

4.4 Results

The literature search resulted in 817 papers which matched the search terms. Of these, 731 were initially excluded based on information derived from the abstract or where required, from further examination of the study.

The remaining 86 studies were then examined in detail to determine the final list of studies to include in the meta-analysis. This identified 17 studies where the ecosystem engineer was experimentally manipulated in the field and a relevant demographic trait was measured (Table 1). Two of these studies (Silliman et al. 2015, Dell et al. 2016) included data on growth and survivorship while one (Layton et al. 2019) included data on recruitment, growth and survivorship resulting in a total of 21 comparisons for our analyses.

The focal taxa included in our meta-analysis were barnacles (Bertness et al. 1999a, Leslie 2005, Beermann et al. 2013), bivalves (Petrovic & Guichard 2008, Donadi et al. 2014) and corals (Vermeij 2005, Miller et al. 2007, Dell et al. 2016, Davis 2018) for invertebrates and; mangroves (Huxham et al. 2010, Kumara et al. 2010), saltmarsh (Silliman et al. 2015),

seagrasses (Tsai et al. 2010) and macroalgae (Bertness et al. 1999b, McConnico & Foster 2005, Barner et al. 2016, Layton et al. 2019) for plants/seaweeds. These are all well known habitat-forming ecosystem engineers.

None of the final 17 studies were published before 1999 and the number of publications examining intraspecific facilitation in ecosystem engineering species did not appear to increase over time (Fig. 1). This stands in contrast to previous meta-analyses of both ecosystem engineers in general (Romero et al. 2015) and invasive marine ecosystem engineers (Guy - Haim et al. 2018) which indicated exponential increases in studies of interspecific effects of ecosystem engineers since 1990.

More studies (58.8 %) examined ecosystem engineers present vs. absent compared to 41.2 % which compared high vs. low density. Studies more frequently examined recruitment and survivorship (42.9 % and 38.1 % respectively) compared to growth (19.1 %). A similar number of intertidal (52.9 %) vs. subtidal (47.1 %) and invertebrate (52.9 %) vs. macrophyte (47.1 %) studies were identified.

The funnel plot test for publication bias resulted in a significantly positive adjusted overall effect ($g = 0.6 \pm 0.2$, effect size \pm SE, $p = 0.002$). Although this was smaller than the non-adjusted effect size ($g = 0.8 \pm 0.17$, effect size \pm SE, $p = <0.0001$), it indicated the overall effect of marine ecosystem engineers on their own demography remained significantly positive after taking into account possible publication bias.

4.4.1 Effects of intraspecific facilitation on the demography of ecosystem engineers

Overall, the combined effect of engineers on their own demographic traits was significantly positive ($g = 0.8 \pm 0.17$, effect size \pm SE, $p = <0.0001$, Fig. 2). In nine out of the 21 studies the presence of the ecosystem engineer had a strong positive effect on their demography.

Although three studies had negative g values, no studies showed a significantly negative impact on the species' demography.

For the individual demographic traits, ecosystem engineers had a positive effect on recruitment ($g = 0.51 \pm 0.41$, $p = 0.001$), survivorship ($g = 1.11 \pm 0.82$, $p = 0.001$) and growth ($g = 0.79 \pm 0.79$, $p = 0.002$; Fig. 3A). The subgroup analysis showed no significant difference in the effects of ecosystem engineers among recruitment, survivorship or growth ($p = 0.320$).

4.4.2 Is intraspecific facilitation in ecosystem engineers stronger in intertidal compared subtidal systems?

There was no significant difference between the effect size of intertidal compared to subtidal ecosystem engineers ($p = 0.42$). In both the intertidal ($g = 0.92 \pm 0.6$, $p = 0.001$, Fig. 3B) and subtidal ($g = 0.66 \pm 0.4$, $p = <0.0001$, Fig. 3B) ecosystem engineers had a significantly positive effect on the demography of conspecifics.

4.4.3 Does intraspecific facilitation differ between invertebrate and macrophyte ecosystem engineers?

There was no significant difference between the effect sizes of invertebrates and plants/seaweeds ($p = 0.69$). Both invertebrates ($g = 0.67 \pm 0.36$, $p = <0.0001$) and plants ($g = 0.97 \pm 0.65$, $p = 0.001$, Fig 3C) had a significantly positive effect on their own demographic traits.

4.4.4 Does intraspecific facilitation differ between studies which focused on the presence vs. absence or high vs. low density of ecosystem engineers?

There was a significant difference between the overall effect sizes of studies which focused on ecosystem engineer presence/absence and high/low density ($p = 0.035$). Although both comparisons had positive effects, overall, there was a greater positive effect between high/

low-density treatments ($g = 1.14 \pm 0.55$, $p = <0.0001$, Fig. 3D) compared to present/absent treatments ($g = 0.53 \pm 0.46$, $p = <0.001$, Fig. 3D).

4.5 Discussion

This meta-analysis indicated that the presence of marine ecosystem engineers has positive effects on the demographic traits of conspecifics. Overall, when these species were removed or reduced in density their recruitment, survivorship and growth were negatively affected.

This study highlights that ecosystem engineering is not only important in affecting entire communities via interspecific facilitative interactions (Hastings et al. 2007, Jones et al. 2010), but also benefits the demography of the engineer itself via intraspecific facilitation which is likely to strongly influence the stability and resilience of these habitats.

Despite only a small number of studies examining intraspecific facilitation by marine ecosystem engineers, the significantly positive overall effect, even when taking into account the potential for publication bias suggests this result is robust. Other meta-analyses examining the state of knowledge surrounding ecosystem engineers found several hundred relevant studies short-listed from thousands of studies in some cases (Romero et al. 2015, Coggan et al. 2018, Guy - Haim et al. 2018). Our search of the literature going back more than 20 years identified 814 papers that met our search terms but only 17 that met the criteria for inclusion. This low number of studies highlights the limited focus on intraspecific facilitation by ecosystem engineers on conspecifics compared to interspecific facilitation by native ecosystem engineers on species diversity (Romero et al. 2015) and by invasive ecosystem engineers on biodiversity and ecosystem functions (Guy - Haim et al. 2018). Our focus on marine ecosystem engineers could have also narrowed the number of studies, however Guy - Haim et al. (2018) also focused solely on invasive marine ecosystem engineers.

Interestingly, there was no significant difference between the effects of marine ecosystem engineers on growth, recruitment or survivorship with all demographic traits being

significantly positive in the engineered environment. The presence of adult conspecifics is known to have a positive facilitative effect of reducing abiotic stress and predation, and increasing recruitment in seaweed and invertebrate communities (Menge & Sutherland 1987, Brawley & Johnson 1991, Burnaford 2004). Increased survivorship with increased population density occurred through sediment accretion and changes in water dynamics in mangrove communities (Kumara et al. 2010) and in barnacle communities, through improved settlement, feeding efficiency and reproductive output (Leslie 2005). Layton et al. (2019) found that kelp canopy modifies the physical environment and reduces sub-canopy flow, sedimentation and irradiance although these modifications were dependent on adult density and patch size. A change in abiotic variables in the presence of an adult conspecifics appears to be responsible for the majority of positive influences on demography although, further research is required to identify the mechanisms behind this relationship.

Abiotic stress can be higher in the intertidal zone compared with subtidal habitats (Davison & Pearson 1996, Tomanek & Helmuth 2002). In such harsh environments, habitat provided by ecosystem engineers plays a strong role in facilitating the survival of other species (Altieri et al. 2010, Wright et al. 2014). Similarly, ecosystem engineers that can ameliorate harsh abiotic conditions and facilitate their own demography may be able to tolerate and persist in harsh habitats due to self-facilitation (Bertness & Callaway 1994, Bertness & Leonard 1997, Hastings et al. 2007, Schiel & Lilley 2007, Mueller et al. 2015). Although the importance of interspecific facilitation may increase with environmental stress because the ecosystem engineer provides a greater relative reduction in harsh conditions this may not be the case for intraspecific facilitation. We found that both intertidal and subtidal ecosystem engineers had a significantly positive overall effect with no difference in effect size between the two systems. Similarly, Romero et al. (2015) found that facilitation was not necessarily stronger in harsher environments, although only marine environments supported this theory. It is

possible that there was no significant difference between intertidal and subtidal systems here, because the physical structures perform the same facilitative function. For example, subtidal and intertidal seaweeds may provide the same or similar benefits to conspecifics (e.g. modification of water movement by kelps and seaweeds in Layton et al. (2019) and Brawley and Johnson (1992)) .

The positive effect on the demography of the ecosystem engineer occurred regardless of species functional group or physical structure. Due to the small number of studies which met our requirements, we placed all species into one of two functional groups, invertebrates and macrophytes (plants/seaweeds). Marine plants (seagrass, mangrove, salt marsh plants) and seaweeds may have different effects due to different biology and habitat-structure they create. Similarly, oysters, barnacles and coral are also likely to have different effects from one another. Nonetheless, our grouping indicated similar and consistent positive effects between the two functional groups. It is possible that the facilitative effects rely on the physical structure of the ecosystem engineer rather than biological or behavioral factors such as for example, chemical cues affecting settlement in bivalves (Davis & Moreno 1995, Barnes et al. 2010). Moreover, the facilitative effect of the physical structures of many marine invertebrates likely continues post-mortality (Wright & Gribben 2017).

It was surprising that there was a significant difference between the overall effect of ecosystem engineers at different densities (high/low) compared to when engineers were present vs. absent. Although in both types of experiment ecosystem engineers had an overall positive effect, it was greater in studies which examined high versus low densities. We hypothesized that the effect size would be greater in presence/absence of engineers, considering the total removal of conspecifics results in an absence of abiotic and biotic engineering effects. Further investigation is required to determine the mechanisms behind

why the type of manipulation (i.e. total removal vs density manipulation) to an ecosystem engineer can alter the outcome of experiments.

This review and meta-analysis found that there is a relatively small amount of experimental study of intraspecific facilitation in marine ecosystem engineers. However, the studies which have examined this phenomenon typically show strong positive effects of the engineering species on their own demography. Considering the benefits these species provide to ecosystems and the extent to which they facilitate their own demography, the mechanisms behind this require further investigation. Ecosystem engineers are often foundation species and can form the basis of facilitation cascades (Altieri et al. 2007, Bishop et al. 2012, Burlakova et al. 2012, Bennett & Wernberg 2014, Dell et al. 2016, Thomsen et al. 2016). Given the positive effects of these species on marine ecosystems, managing them more effectively will be important in counteracting the negative effects of human activity and climate change (Romero et al. 2015).

Further research would increase our knowledge of how these species influence their resilience and thus the persistence of the ecosystems they often anchor. It would be beneficial to determine if the specific mechanisms behind facilitative functions differ with increasing stress, such as in relatively benign subtidal systems in comparison to intertidal systems, and whether these mechanisms differ between species or functional groups.

Table 4.1. Summary of the studies included in the meta-analysis.

Study No.	Reference	System	Type of ecosystem engineer	Location	Demographic trait examined
1	Barner et al. (2016)	Rocky shore	Alga	USA	Recruitment
2	Beerman et al. (2013)	Rocky shore	Invertebrate	Scotland	Recruitment
3	Bertness et al. (1999)a	Subtidal reef	Invertebrate	USA	Survivorship
4	Bertness et al. (1999)b	Rocky shore	Alga	USA	Recruitment
5	Davis (2018)	Coral reef	Invertebrate	USA	Survivorship
6	Dell et al. (2016)	Coral reef	Invertebrate	Fiji	Growth and Survivorship
7	Donadi et al. (2014)	Soft sediment	Invertebrate	The Netherlands	Recruitment
8	Huxham et al. (2010)	Mangroves	Plant	Kenya	Survivorship
9	Kumara et al. (2010)	Mangrove	Plant	Sri Lanka	Survivorship
10	Layton et al. (2019)	Subtidal Reef	Alga	Australia	Growth, Recruitment and Survivorship
11	Leslie (2005)	Rocky shore	Invertebrate	USA	Survivorship
12	McConnico & Foster (2005)	Rocky shore	Plant	USA	Recruitment
13	Miller et al. (2007)	Coral reef	Invertebrate	USA	Survivorship
14	Petrovic & Guichard (2008)	Rocky shore	Invertebrate	Canada	Recruitment
15	Silliman et al. (2015)	Saltmarsh	Plant	USA	Growth and Survivorship
16	Tsai et al. (2010)	Seagrass meadow	Plant	USA	Growth
17	Vermeij (2005)	Coral reef	Invertebrate	USA	Recruitment

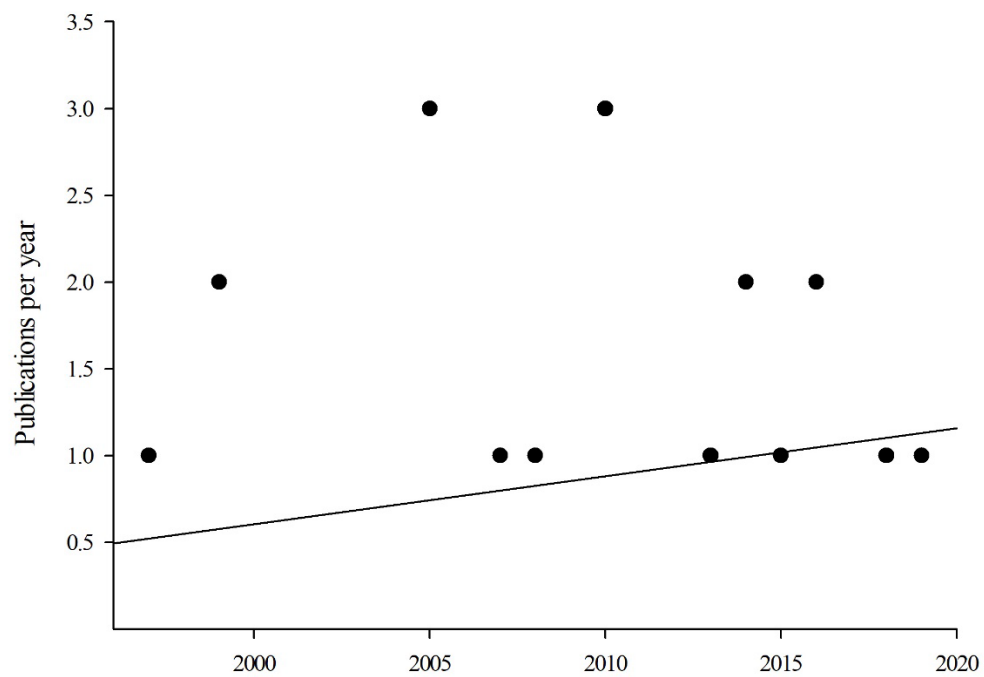


Figure 4.1. Number of publications which focused on intraspecific facilitation per year from 1999 to 2019. Studies involved ecosystem engineers being manipulated in the field and recruitment, growth or survivorship of the engineer measured.

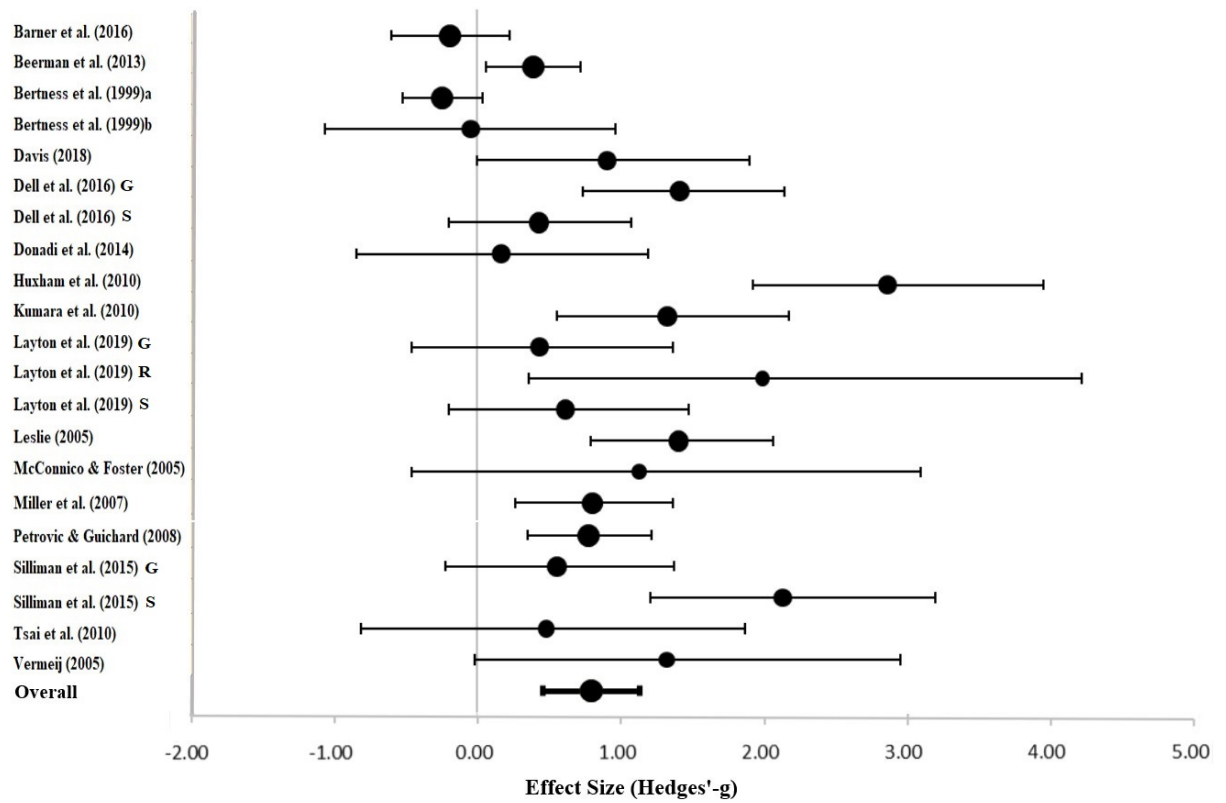


Figure 4.2. Forest plot of overall effect size of the studies included in the analysis (Hedges'-g \pm 95% CI). Three studies (Dell 2016, Layton 2019, Silliman 2015) assessed multiple demographic traits. R (recruitment), G (growth), S (survivorship).

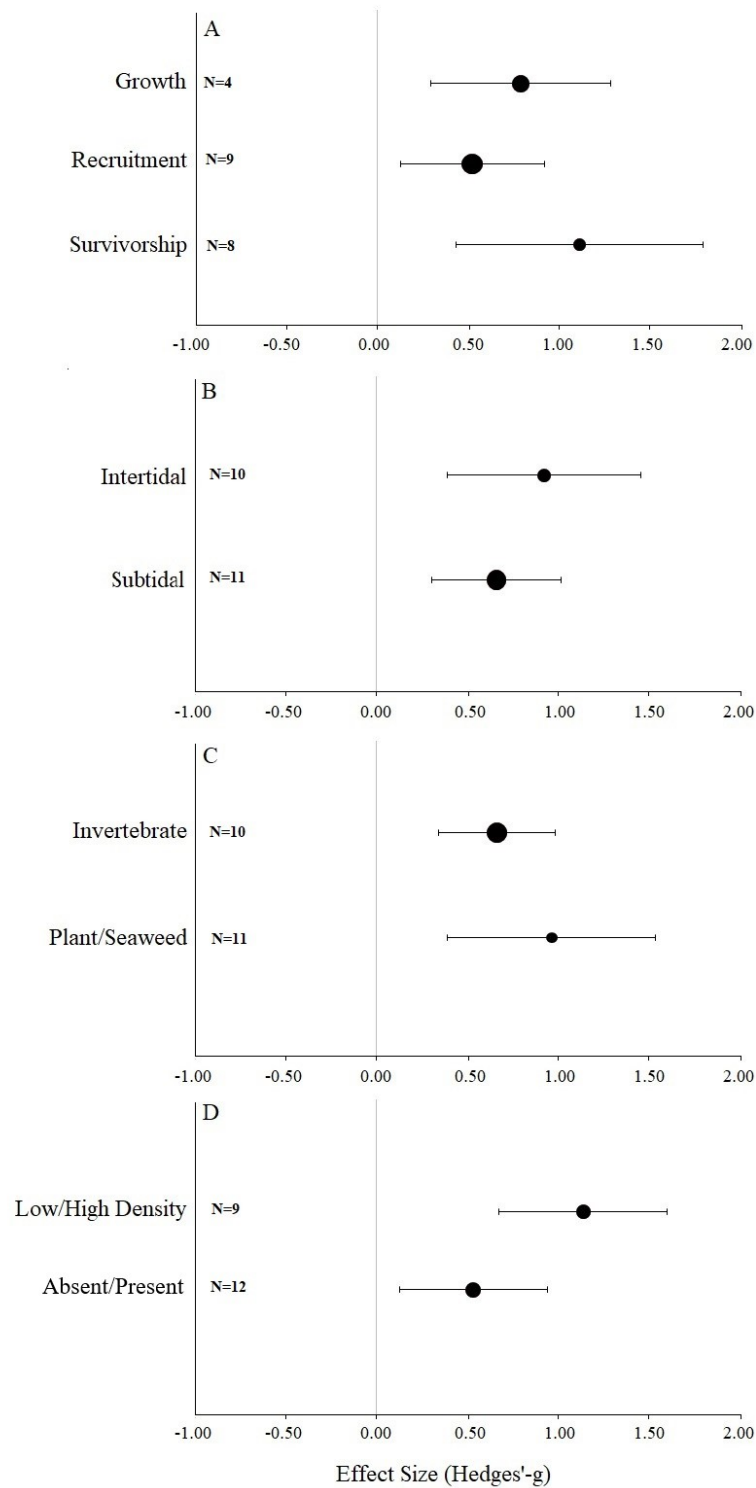


Figure 4.3. Forest plots of the overall effect size (Hedges' g ± 95% CI) comparing intraspecific facilitation between A) different demographic traits (growth, survival, recruitment), B) intertidal vs. subtidal ecosystem engineers, C) invertebrate vs. plant ecosystem engineers, and D) overall effect of ecosystem engineers in studies where presence vs. absence and low vs. high density were tested. Numbers shown inside the y-axes indicate the number of studies for each category.

5. Synthesis

Many temperate marine macroalgae are declining in distribution and abundance due to a number of natural and anthropogenic causes and, the decline or loss of these species often leads to a decrease in biodiversity and major ecosystem-wide consequences (Schiel et al. 2004, Serisawa et al. 2004, Thompson et al. 2010, Johnson et al. 2011, Wernberg et al. 2011b, Scherner et al. 2013). The reasons behind these declines are varied, but include increased sea temperatures and storm intensity due to climate change, increased nutrient run-off from land due to agricultural land use and urbanisation, and human trampling and harvesting (Povey & Keough 1991, Doblin & Clayton 1995, Keough & Quinn 1998a, Underwood 1998, Schiel & Taylor 1999, Serisawa et al. 2004, Coleman et al. 2008, Bellgrove et al. 2010, Wernberg et al. 2011a, Bellgrove 2013, Wernberg et al. 2013, Wernberg et al. 2016, Douglas et al. 2017).

There has been considerable effort put into researching the effects of global change on some systems such as coral reefs and terrestrial forests (Dale et al. 2000, Kleypas et al. 2001, Bonan 2008, Knowlton & Jackson 2008, Abatzoglou & Williams 2016, Hoegh-Guldberg et al. 2017, Hughes et al. 2017), while until recently macroalgal communities have received less attention (Harley et al. 2012). Recent work has described the effects of climate change on macroalgae, particularly kelp (Johnson et al. 2011, Harley et al. 2012, Mabin et al. 2013, Wernberg et al. 2016) but the capacity of canopy-forming macroalgal communities to resist natural and anthropogenic stressors requires further investigation (Bertocci et al. 2010).

Intertidal macroalgal communities are among the most productive temperate ecosystems and provide food resources and form complex habitats that provide protection from predation and abiotic stressors for themselves and their community (Porzio et al. 2011, Harley et al. 2012, Wright et al. 2014). Intertidal habitats are also considered among the most stressful

environments due to constant changes in abiotic stressors such as temperature and desiccation at low tide as well as strong wave energy (Wright et al. 2004, Harley et al. 2012). Intertidal canopy-forming macroalgae are often vulnerable to disturbances, which can result in changes to community structure (Underwood 1999, Bendetti-Cecchi et al. 2001) and long recovery times for ecosystems (Schiel & Foster 2006).

Many marine ecosystems including seaweed forests, seagrass beds, salt marshes, mangrove forests and coral reefs are shaped by a single habitat-forming species, which directly or indirectly alters the available resources for the associated community (Jones et al. 1994, Schiel et al. 2004, Bishop et al. 2009b). Jones et al. (1994) coined these habitat-forming species as ecosystem engineers for their ability to modify and change environmental variables through their structure and/or function. Ecosystem engineering organisms, such as seaweeds provide structure and complexity to habitats, they provide protection and resilience to disturbance for themselves and associated communities (Rabaut et al. 2007, Thomsen et al. 2011, Johnston & Lipcius 2012, Alestra & Schiel 2014, Bennett & Wernberg 2014, Barner et al. 2016). Understanding which ecosystem engineers perform the most critical ecosystem functions is important for conservation and natural resource management (Jones et al. 1997, Wright & Jones 2006).

The important role of macroalgae in marine ecosystems makes understanding demographic factors underpinning their response to disturbance important. *H. banksii* is an abundant intertidal ecosystem engineer in southern temperate waters of Australasia and it ameliorates harsh abiotic conditions and provides habitat for a diverse range of other species (Schiel & Lilley 2007, Bellgrove et al. 2010).

This thesis aimed to explore the demography of *Hormosira banksii* using field experiments to investigate how *H. banksii* responds to different levels of disturbance. Initially, I examined

whether alternative stable states exist between *H. banksii* and coralline turf on the rocky shores of Tasmania. I then investigated whether the *H. banksii* canopy cover influenced their own recruitment by following the growth and survivorship of individual recruits and how this might influence their resilience against disturbance. Finally, I conducted a global literature review and meta-analysis of intraspecific facilitation in marine ecosystems, aiming to explore the current state of knowledge on this concept and how it has been tested experimentally.

5.1 Alternative Stable States

Ecological communities dependent on ecosystem engineers can be susceptible to disturbance and, where the disturbance is intense or persistent, can result in a switch to an alternative stable state (Petraitis & Dudgeon 2004, Petraitis 2013). The concept that ecosystems can occur in one or more alternative stable states was first suggested by Lewontin (1969) and since then ecologists have been gathering empirical evidence to expand on and support this theory (Beisner et al. 2003).

Marine ecosystems were among the first examples of alternative stable states and macroalgae dominated rocky intertidal zones provide an ideal system to test these concepts (Knowlton 2004). Difficulties in conducting experiments which successfully tests for alternative stable states led to robust discussion, which resulted in criteria in order to demonstrate that multiple states exist within a system (Connell & Sousa 1983, Peterson 1984, Sousa & Connell 1985). At a minimum, Peterson (1984) suggested that an experiment must show that the same site can be occupied by different self-replacing communities, known as Peterson's criterion (Petraitis & Latham 1999). The other criteria were that; the alternative states must occur in the same environment; manipulation to test for the existence of alternative stable states must be in the form of a pulse perturbation which is large enough to initiate a change from one state to another, and that the experiment must be conducted over a sufficient time-scale to

ensure the alternative state is self sustaining (Connell & Sousa 1983, Petraitis & Latham 1999, Petraitis & Dudgeon 2004). The experiment in Chapter II was designed to fulfil these criteria, *H. banksii* and coralline turf both occurred at the experimental site, the pulse perturbation was as large as reasonably possible and on a relevant spatial scale and the time-scale was long enough to observe recovery of both species. However, I was unable to demonstrate that the persistence of different states was possible in this system.

Previously, it has been suggested that the removal of *Hormosira banksii* canopy can lead to the persistence of a coralline turf algae dominated state because coralline turf algae inhibited *H. banksii* recruitment (Bellgrove et al. 2010). However, Schiel and Lilley (2011) found the interactions between the two species to be more complex, with different locations and types of perturbation (i.e. press or pulse) visibly different seven years after the experiment. They found that *H. banksii* recruitment was high at 40-50 percent coralline turf cover and, all treatments had almost returned to their original state eight years later, although this occurred slower at one site, where the coralline turf appeared to contain a different composition of species (Schiel & Lilley 2011).

After two years in my experiment, irrespective of the level of disturbance, *H. banksii* and coralline turf algae both appeared to be returning to equilibrium covers with no evidence to support the presence of alternate stable states. Even the most disturbed plots which were initially manipulated to zero cover of *H. banksii* or coralline turf recovered and followed the same trajectory as the less disturbed plots. This is in contrast to findings of Bellgrove et al. (2010), where surveys indicated there appeared to be a threshold cover of coralline turf algae (> 40%) where *H. banksii* was never greater than 20% cover. Bellgrove et al. (2010) suggested that the loss of *H. banksii* canopy and possible existence of an alternative stable state, was due to anthropogenic disturbance (i.e. excess nutrients from sewage outfall) but that more detailed experimental analysis of these interactions was needed. Similarly,

Bendetti-Cecchi et al. (2001) found that decreased recruitment of *Cystoseira* spp. with increased cover of turf could be linked to the indirect effects of anthropogenic disturbance in the form of urbanisation. The reef I conducted my experiments on appeared relatively free of anthropogenic impacts such as high nutrient input and trampling and our results more closely match that found in Schiel and Lilley (2011) which was also conducted at a site with relatively low levels of anthropogenic impacts.

A range of processes including ecosystem engineering of abiotic factors, possible demographic feedbacks in both *H. banksii* and coralline turf algae, competition or facilitation, as well as the type and intensity of disturbance and environmental factors are all likely to contribute to the occurrence of an alternative stable state. To understand the interactions between *H. banksii* and coralline turf algae following disturbance, all factors must be taken into account (Schiel & Lilley 2007). Facilitative interactions may be present between *H. banksii* and coralline turf algae. For example, I observed that initially after canopy removal the coralline turf bleached and initially declined in percent cover, Schiel and Lilley (2011) also found that without *H. banksii* canopy cover, coralline turf algae quickly bleached and underwent a reduction in cover.

This research suggests that in the absence of large-scale persistent anthropogenic disturbances, alternative stable states between *H. banksii* and coralline turf are unlikely to persist and they will co-exist. However, alternative stable states may be maintained by long-term excess nutrients from sewage (Bellgrove et al. 2010) or other anthropogenic impacts such as urbanisation (Bendetti-Cecchi et al. 2001). It would be interesting to conduct a manipulative experiment where these disturbances are maintained over a long time (~ 8 years, Schiel & Lilley 2011) to determine whether they initiate and maintain alternative states.

5.2 Recruitment, survivorship and growth of *Hormosira banksii*

I found that *H. banksii* is a relatively long-lived perennial species whose demography is density-independent, which seems to promote resilience and recovery from disturbance. Surprisingly, the level of disturbance did not appear to affect recruitment, growth or survivorship at this site, possibly because the experimental site was absent of variables which could strongly affect the demography of this species. Schiel and Taylor (1999) found that different intensities of trampling across *H. banksii* canopy resulted in progressively greater levels of canopy removal, with greater than 96 percent of canopy removed in the highest intensity of trampling (200 passages across the transect). After five months, all treatments had recovered to at least 50 percent cover, and after 21 months the spring treatments had recovered to control condition (>97 % cover). The trend we observed appeared to be similar to what was observed by Schiel and Taylor (1999).

There is still limited information on the relative importance of recruitment and post-recruitment processes in determining local population abundance of seaweed (Capdevila et al. 2015). Chapter 3 provided an insight into the importance of these processes for *Hormosira banksii*. I found that recruitment was an important predictor of future abundance, suggesting recruitment limitation, and that if *H. banksii* continues to supply gametes, populations should persist. Large scale disturbance or removal of adult plants could reduce propagule supply and thus recruitment with negative consequences for population abundance (Caley et al. 1996). However, I did not observe this at the scale of this experiment suggesting the high density of adults surrounding our manipulations may have allowed propagules to disperse, successful recruitment to occur and population recovery following disturbance. Although we did not find evidence that recruitment increases as adult density increases adults may create conditions which facilitate juvenile conspecifics (Layton et al. 2019).

Several studies have found differences in *H. banksii* recruitment among seasons. For example, in Victoria, Bellgrove et al. (2004) found recruitment was highest in April and lowest in February and October. In contrast, Schiel and Taylor (1999) found that recruitment in New Zealand occurred all year round but there was a large peak in summer, which is also what we found. A peak recruitment in summer may be due to calmer wave conditions being conducive to successful zygote settlement. In New Zealand, survival of *H. banksii* zygotes was relatively low with only 5-8 percent surviving after 12 hours in the field (Taylor & Schiel 2003). However, increased temperature and desiccation that occur in summer may alternatively have negative effects on fucoid embryos. Where the adult canopy is present, moisture is retained and zygotes and embryos are somewhat protected from abiotic stressors (Brawley & Johnson 1991, 1993). In other systems such as tide pools studied by Kain (2015), abiotic conditions may have been less variable allowing for more consistent recruitment of *H. banksia* over time.

We were unable to determine survivorship in the early microscopic life stages but as demonstrated previously for *H. banksii* and other fucoids (Schiel & Foster 2006), it is likely that high mortality occurs before the juveniles are visible. We observed high survivorship of all size classes once they were visible and this high survivorship at the macroscopic level coupled with high recruitment, long life span and the resilience to disturbance would suggest that this population is relatively stable.

It is possible that the limiting factor of *H. banksii* recruitment may not be increasing adult density, but facilitation through the presence of adult conspecifics regardless of their density, however further research is required to quantify the mechanisms behind this.

5.3 Intraspecific facilitation by ecosystem engineers in marine environments

Our meta-analysis was the first to review the literature surrounding intraspecific facilitation by ecosystem engineers in marine environments. We found that although this is likely to be

an important factor in their persistence and positively affect their demography, thereby maintaining habitats which are utilised by other species, this phenomenon is not well studied.

Despite the small number of studies that have examined intraspecific facilitation, the evidence was overwhelmingly positive. In the experimental studies we examined, the presence of conspecifics had positive effects on their own growth, recruitment and survivorship. This occurred regardless of the type of ecosystem engineer (macrophytes or invertebrates) or whether they were intertidal or subtidal ecosystem engineers.

Interestingly, there was a greater difference in the overall effect of conspecifics on their demography in studies which compared high and low densities of an ecosystem engineer versus studies that compared the presence and absence of the ecosystem engineer. This was unexpected because we hypothesised that the higher level of disturbance and total removal of a species would have a greater effect on that species' demography than where the species was still present, albeit in a lower density. Further investigation is required to explain this finding and whether an increased number of studies would still support this outcome.

More broadly, a greater understanding of the processes and mechanisms behind intraspecific facilitation in marine environments is essential to managing ecosystems which are based on ecosystem engineering species. Studies inferred the importance of the engineers reducing abiotic stressors (e.g. Bertness et al. 1999a) and/or grazer pressure (e.g. Davis 2018) but none of the 17 studies experimentally tested the mechanism responsible for the facilitation.

5.4 Conclusion

This research has contributed to knowledge of the life history of *Hormosira banksii*, an important ecosystem engineer in southern temperate intertidal ecosystems. This two-year long manipulative experiment was the first study to follow individual *H. banksii* recruits and measure recruitment, growth and survivorship.

Despite evidence that possible alternative stable states can exist between *H. banksii* and coralline turf, in this system, we did not find any evidence to support this. Although we acknowledge that the interactions between *H. banksii* and coralline turf could differ with the influences of a variety of biotic and abiotic variables, in different systems (e.g. other macroalgal species), or under different circumstances (e.g. proximity to urban areas, more intense or more frequent anthropogenic disturbance).

This study shows that ecosystem engineers can not only benefit their surrounding assemblages, but also facilitate their own demography. Despite the positive services these species provide for conspecifics and their community, they can also vary in their response to disturbance. A negative response to disturbance can lead to ecosystem wide changes in species composition and diversity, hence it is crucial that we understand how these species function and respond to disturbance.

This study has gone some way to understanding how *H. banksii* will respond to increasing levels of disturbance in the future. *H. banksii* appears to be reliant not only on its own life history but also localised combinations of biotic and abiotic factors, suggesting the demographic response and recovery from disturbance is likely to vary among sites. This should be taken into account to enable effective management of these ecosystems.

6. References

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