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Demography of the intertidal fucoid *Hormosira banksii*: Importance of recruitment to local abundance[1]

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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.

Keywords: *Hormosira banksii*, coralline turf algae, demography, intertidal, fucoid, macroalgae, ecosystem engineer

Abbreviations: HSD - honestly significant difference, MLLW - mean lower low water, Q-Q - quantile-quantile

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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 and 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 and Fairweather 1989, Caley et al. 1996). For example, when post-recruitment mortality is density-independent, local abundance will largely reflect recruitment (Sutherland 1990, Doherty and Fowler 1994), but when post-recruitment mortality is density-dependent local abundance is typically regulated by post-recruitment processes (Menge 1991, Carr and Hixon 1997, Steele 1997, Menge 2000, Wright and Steinberg 2001).

For seaweed, there is still limited information of the relative importance of recruitment and post-recruitment processes in determining local abundance (Caley et al. 1996, Wright and Steinberg 2001, Schiel and Foster 2006, Capdevila et al. 2015). Many seaweeds form monospecific stands where recruitment is relatively high and intraspecific competition is predicted to be strong (Schiel and Choat 1980, Schiel 1985, Reed 1990, Creed 1995, Schmidt and Scheibling 2006, Mabin et al. 2013, Bennett and Wernberg 2014). A number of studies have shown density-dependent effects on recruitment (Reed 1990, Arenas et al. 2002, Schiel and Foster 2006, Bennett and Wernberg 2014, Capdevila et al. 2015) and post-recruitment mortality (Black 1974, Chapman 1984, Schiel 1985, Johnson and Mann 1988, Ang Jr and 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 and 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 1992a,b, Dayton et al. 1992, Wright and 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 and Walker 1991, Norton 1992), and recruitment varies greatly in space and time (Reed et al. 1988, Bennett and 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

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through time to determine patterns of post-recruitment mortality (density-dependent or density-independent; Caley et al. 1996).

Temperate intertidal rocky reefs are often dominated by canopies of fucoid algae including *Fucus* spp., *Ascophyllum nodosum* and *Pelvetia canaliculata* in the northern Hemisphere (Brawley and Johnson 1991, Aberg 1992a,b, Wright et al. 2004) and *Hormosira banksii* and *Durvillaea* spp. in the southern hemisphere (Cheshire and Hallam 1988, Keough and Quinn 1998, Schiel and Lilley 2007, Bellgrove et al. 2010). In temperate Australasia, *H. banksii* is often the dominant habitat-forming species in the mid-low intertidal zones (Schiel and 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 and Quinn 1998, Schiel and Lilley 2007, Bishop et al. 2009) 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. 2009) 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 and Connell 2004). It has been suggested that algal turfs can inhibit recruitment and growth of macroalgal species such as *H. banksii* (Sousa 1979, Benedetti-Cecchi and Cinelli 1992, Schiel and Taylor 1999, Bulleri et al. 2002) and also hypothesised that under certain conditions, macroalgae and articulated turf can form alternative stable states (Petraitis and Dudgeon 2004, Bellgrove et al. 2010, Chemello et al. 2018).

Many canopy forming macroalgal populations are in decline worldwide (Johnson et al. 2011, Wernberg et al. 2013, Krumhansl et al. 2016, Pocklington et al. 2017) due to impacts from climate change (increased air and water temperatures and wave intensity) and other local and/or anthropogenic stressors including; habitat destruction, overfishing, pollution and increased sedimentation (Underwood 1998, Jackson et al. 2001, Thompson 2002, Airoldi 2003, Schiel et al. 2006, Ling et al. 2008, Krumhansl et al. 2016, Wernberg et al. 2016). *Hormosira banksii* is sensitive to anthropogenic disturbances such as trampling (Povey and Keough 1991, Keough and Quinn 1998, Schiel and Taylor 1999), sedimentation (Schiel et al. 2006, Alestra and Schiel 2015), increased nutrients via sewage discharge (Fairweather 1990, Doblin and Clayton 1995,

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Kevekordes and Clayton 2000, Bellgrove et al. 2010) and combinations of local and global stressors (Alestra and Schiel 2015). 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, Kain 2015) and to our knowledge, none have followed those recruits over time to determine the extent to which recruitment explains subsequent abundance. Previous studies that have quantified changes in the cover of *H. banksii* found that canopies recovered fastest when only fronds were removed rather than complete plants, and from pulse disturbances compared to press disturbances (Keough and Quinn 1998, Underwood 1998, Schiel and 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 and Lilley 2007, 2011).

Despite its abundance and ecological importance, the demography of *Hormosira 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 understory 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?

METHODS

Natural history

Hormosira banksii is a perennial fucoid alga which dominates much of the rocky intertidal coastline of temperate Australian and New Zealand (Schiel and Taylor 1999, Bellgrove et al. 2010, Schiel and Lilley 2011, Bellgrove et al. 2017). It inhabits the mid to low intertidal zone and

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often forms a dense monotypic canopy with a standing biomass of up to 8 kg · m^{-2} and densities of several hundred plants per square metre (Schiel 2006). It is a slow growing perennial, dioecious species (Alestra and Schiel 2014) which is iteroparous and releases gametes at low tide (Levring 1949, Womersley 1967). *Hormosira banksii* shows large morphological variation depending on environmental conditions (Osborn 1948, Ralph et al. 1998, Macinnis-Ng et al. 2005, Bishop et al. 2009, Mueller et al. 2015). At the site of this study on the north coast of Tasmania, *H. banksii* 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).

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 km of coast. The reef selected for the study site was ~ 400 m long and ~ 80 m wide. It consisted of numerous small to medium basalt boulders up to 0.25 m^2 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 *Hormosira 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.

Experimental design and demographic sampling

Sampling of recruitment, post-recruitment growth and mortality of *Hormosira banksii* was done in 0.0625 m^2 (0.25 x 0.25 m) quadrats placed in the center of 1 m^2 plots. The plots were placed haphazardly across the reef where there was at least 80% canopy of *H. banksii* (R.D. Lewis, unpub. data) 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.

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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. Treatments were allocated at random to each quadrat. 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 and patchiness within this system. Natural disturbance on this reef was variable but generally low. Two y post-disturbance, the treatments appeared to be converging towards their pre-manipulation state.

In April 2015, seven months post-disturbance, we mapped the location of each visible *Hormosira banksii* individual within the 0.25 x 0.25 m quadrats (N = 811 plants in 32 quadrats). This followed a period of warmer weather and high *H. banksii* recruitment. We mapped individual *H. banksii* thalli in each quadrat using an x-y coordinate approach and estimated their size 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 its size class was recorded and new recruits identified and mapped. Recruits were defined as individuals which were in size class 1 (< 10 mm) that were not present in quadrats at the previous count (Wright and Steinberg 2001). Individuals in size classes 2-5 were considered to be reproductive adults, which is supported by Kain (2015); and we often observed conceptacles on size class 2 individuals. 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, 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.

Statistical Analysis

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Variation in recruitment (ln x + 1 transformed) was analysed using a two-factor Analysis of Variance (ANOVAs: Time x Treatment, both fixed). Post hoc analyses were conducted using a Tukey's HSD.

To explicitly test whether the total *Hormosira 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 all quadrats across treatments as there were no significant treatment effects on recruitment (see results).

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.

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 individuals from all quadrats across all treatments at each time to analyze survivorship and growth for each size class each time. Qualitatively, growth and survivorship appeared to vary among size classes and so to allow for meaningful analysis, we considered the pooled data for each treatment as the unit of replication for each size class at each sampling 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 proportion of individuals transitioning from one size class to the next, 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.

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 of *Hormosira banksii* explained post-recruitment mortality we ran a regression analysis between total *H. banksii* density (size classes 2-5) at time *t* (January 2016) and the percentage mortality of recruits in the

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first three months (time t + 3 months, April 2016). 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 were analysed using R Studio (Version 3.3.2, R Core Team 2016) with packages ggplot2 (Wickham 2016), lattice (Sarkar 2008) and MASS (Venables and Ripley 2002). Where ANOVA's were used, Q-Q Plots were visually inspected to ensure assumptions were met and transformed as needed.

RESULTS

Recruitment of *Hormosira 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 $\cdot$ 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.

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

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All cohorts had relatively high post-recruitment survivorship and there was no evidence of any differences among treatments, although we were unable to quantify this difference due to low recruitment at most sampling occasions. 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).

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-October 2016 (74%) compared to between August-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-October 2015 (87%; Fig. 3). Size class 1 had lower survivorship than all other size classes in February-April 2016 and August-October 2016 and lower survivorship compared to size classes 2 and 3 in May-July 2015 (Table 3, Fig 3).

Growth (i.e., transition from one size class to the next over a 3-month period) 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 1 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-July 2016, August-October 2016 and May-July 2015 (Table 3, Fig 4). In contrast, size class 3 had higher growth between February-April 2016 (43% grew) compared to August-October 2016 and May-July 2015. Size class 1 had higher growth than size class 4 between May-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-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

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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.

Post-recruitment mortality of *Hormosira 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) and vs. the number of recruits (r^2=0.120 P=0.114) were both non-significant. However, there was a significant positive relationship between the number or recruits per plot and abundance 9 months later (r^2=0.982 P=<0.001).

DISCUSSION

This study highlighted spatial and temporal variation in *Hormosira banksii* demography and showed that this is not affected by 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 y 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.

Hormosira banksii is fertile all year round, similar to other fucoids (Ladah et al. 2003, Wright et al. 2004, Dunmore 2006), and this was reflected by iteroparous 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 and Taylor 1999), but differs to findings for recruitment in rockpools 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

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described previously in other temperate intertidal brown and red algae (Sousa 1979, Schiel and Taylor 1999).

Seasonal differences in *Hormosira banksii* recruitment at our site will reflect variable gamete production and settlement or post-settlement survivorship of embryos. Reproduction in other fucoids has been observed to be more closely related to tidal or environmental variables rather than seasonal variation (Pearson et al. 1998, Serrao et al. 1999, Lamote and Johnson 2008). Gamete release in fucoids is often dependent on water motion (Serrao et al. 1999) and restricted to calm days (Pearson et al. 1998, Serrao et al. 1999). For *H. banksii*, the peak in recruitment during summer could reflect lower wave activity from October 2015 through January 2016 allowing for increased gamete release. Post settlement survivorship of fucoid embryos is typically low (Schiel and Foster 2006) and a range of factors strongly influence post-settlement survivorship of *H. banksii* and other fucoid embryos. Dislodgement by waves reduces the attachment and survival of *H. banksii,* zygotes (Taylor and Schiel 2003, Taylor et al. 2010). Taylor and Schiel (2003) observed that only 24% of *H. banksii* zygotes which had been 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. Intertidal rocky shores where *H. banksii* occurs are subjected to high temperatures with summer temperatures in northern Tasmania often exceeding 25-30°C during low tide (Wright and Gribben 2017) which, can be exacerbated by canopy loss due to factors such as sun burn of fronds (Keough and Quinn 1998, Lilley and Schiel 2006). Kain (2015) found that the maximum water temperature in rock pools could be 10°C higher than seawater with a mean of 35°C. At our site, as well as being exposed to high air and substrate temperatures at low tide during summer, they are also likely to be subject to high desiccation. Moreover, *H. banksii* embryos have increased mortality to elevated temperatures (Miller et al. 2020). Fucoid embryos are thought to survive better in cooler, moist environments such as beneath a canopy formed by adult thalli (Brawley and Johnson 1991, Brawley and Johnson 1993) although we found no relationship between recruitment and the *H. banksii* canopy cover here.

In New Zealand, *Hormosira 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 and Schiel 2014). Finally, micrograzers such as

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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 and 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 *Hormosira 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 (Lilley and Schiel 2006, R.D. Lewis unpub. data) and the negative effects of turf in increasing sedimentation (Schiel et al. 2006, Alestra et al. 2014). The coralline turf in this system was variable in height, ranging from around 5-30 mm across the study site and it is possible that the height or density of the turf could determine its impact on *H. banksii* recruitment (Schiel and Lilley 2011, Alestra et al. 2014). A greater *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. Fucoid algae such as *H. banksii* generally have short range dispersal, with propagules often settling close to parents (Dunmore 2006, Coleman et al. 2011). 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 fucoids < 5% of embryos settling survive to the macroscopic juvenile stage in the field (Schiel and 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 $500 \cdot cm^{-2} \cdot week^{-1}$, much higher than the densities observed here; however 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 *Hormosira banksii* canopy cover (Doblin and Clayton 1995, Keough and Quinn 1998, Schiel and Taylor 1999, Lilley and Schiel 2006, Schiel et al. 2006, Schiel and Lilley

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2007, 2011 Bellgrove et al. 2010, 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 recruitment. However, to the naked eye, no growth from remnant holdfasts was observed where we were aiming for total removal of an individual. The percent cover of *H. banksii* and coralline turf within the plots appeared to be gradually reverting to the pre-manipulation state over time. 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 y 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 *Hormosira banksii* and coralline turf. Three-monthly survivorship varied between size classes and over time but was also typically high. 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 over summer (Keough and Quinn 1998, Schoenwaelder 2002, Lilley and Schiel 2006, McKenzie and Bellgrove 2008), 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 based on transition to the next size class. On average over 18 months, the smallest size class grew approximately 50 mm into size class 3. Fucoids are characterised by slow growth and *Hormosira banksii* is relatively slow growing

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compared to other fucoid alga (Dunmore 2006, Kain 2015). We found that growth occurred all year round but increased during late spring and summer (November 2015-January 2016 and January-April 2016), likely due to warmer conditions, increased light (Dunmore 2006) or potentially nutrient availability (Kain 2015), although the latter might be more likely at this site during winter or early spring where rainfall leads to increased run-off.

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 *Hormosira banksii* largely being determined by recruitment of size class 1 individuals. Similarly, the post-recruitment mortality of other fucoids has been observed to be independent of density (Lamote and Johnson 2008). Moreover, Schiel (1985) found that recruitment of *Sargassum sinclairii* was positively correlated with density although survivorship declined at lower adult densities. Recruitment in the red alga *Delisea pulchra* was density-independent although this did not always translate into high population abundance due to high mortality from grazing sea urchins (Wright and 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. 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.

Given *Hormosira banksii* is often the dominant habitat-forming species in the mid-low intertidal zones of temperate Australia and New Zealand, understanding its demography and the factors determining its local abundance is important. It provides important insights into the demography of *H. banksii* showing that it is 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 in *H. banksii* and reinforces the importance of

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recruitment for macroalgal populations. As many habitat-forming macroalgae face increasing threats from climate change and other stressors, increasing our understanding of their demography when exposed to anthropogenic disturbance will enhance the management and conservation of these vital and productive ecosystems.

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Table 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		

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Table 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

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Table 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 × 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×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×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.

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Figure 1. Mean (± 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 per month at the site is also shown.

Figure 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. 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 4. Growth based on the proportion transitioning 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 (note different y-axis for E).

Figure 5. A) Percentage survivorship for each size class. B) Growth (transition to the next size class, mean ± 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) (note different y-axes).

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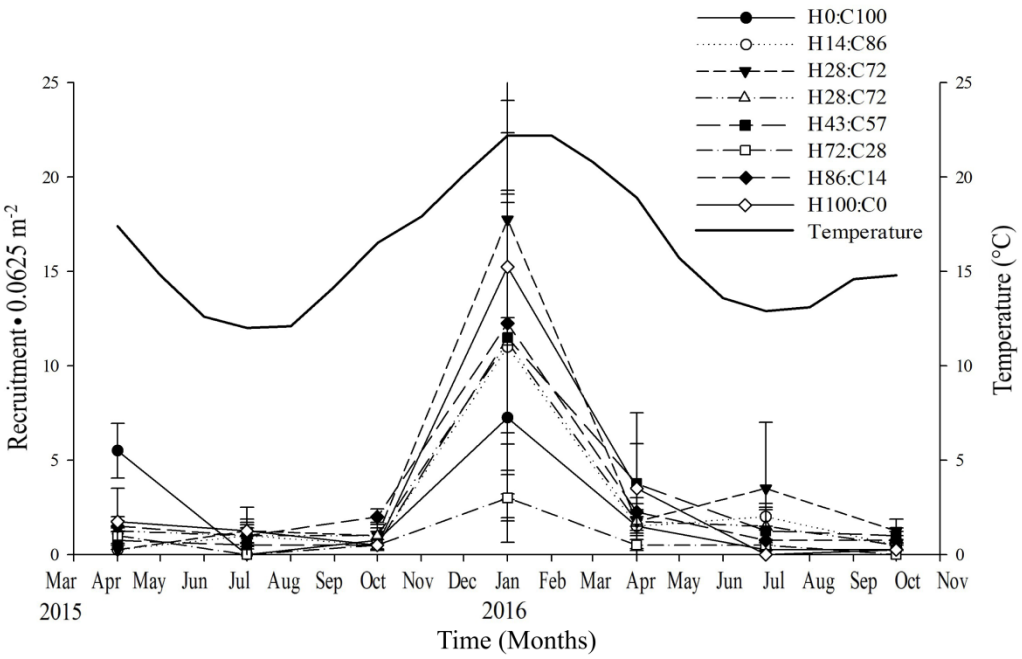

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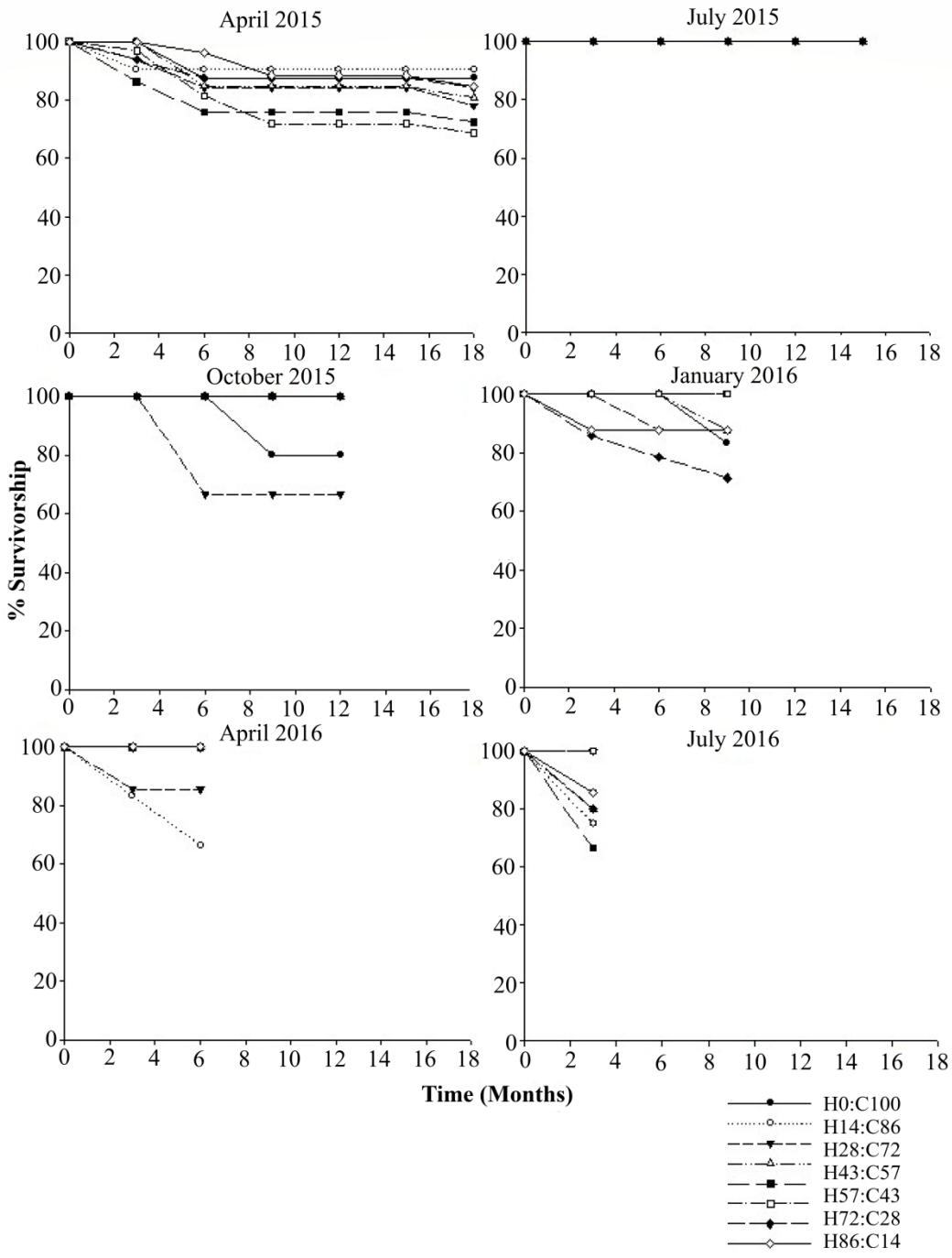

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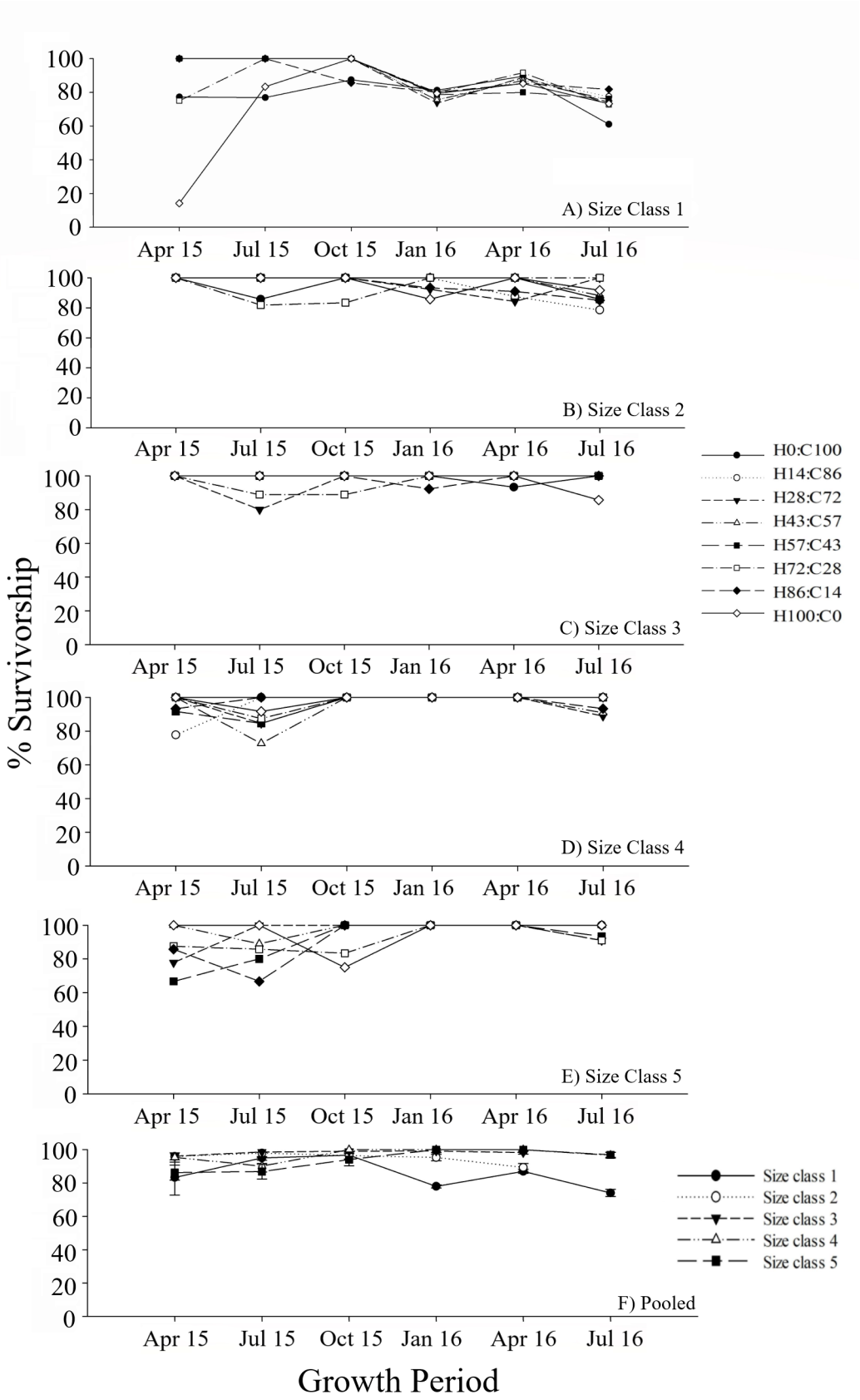

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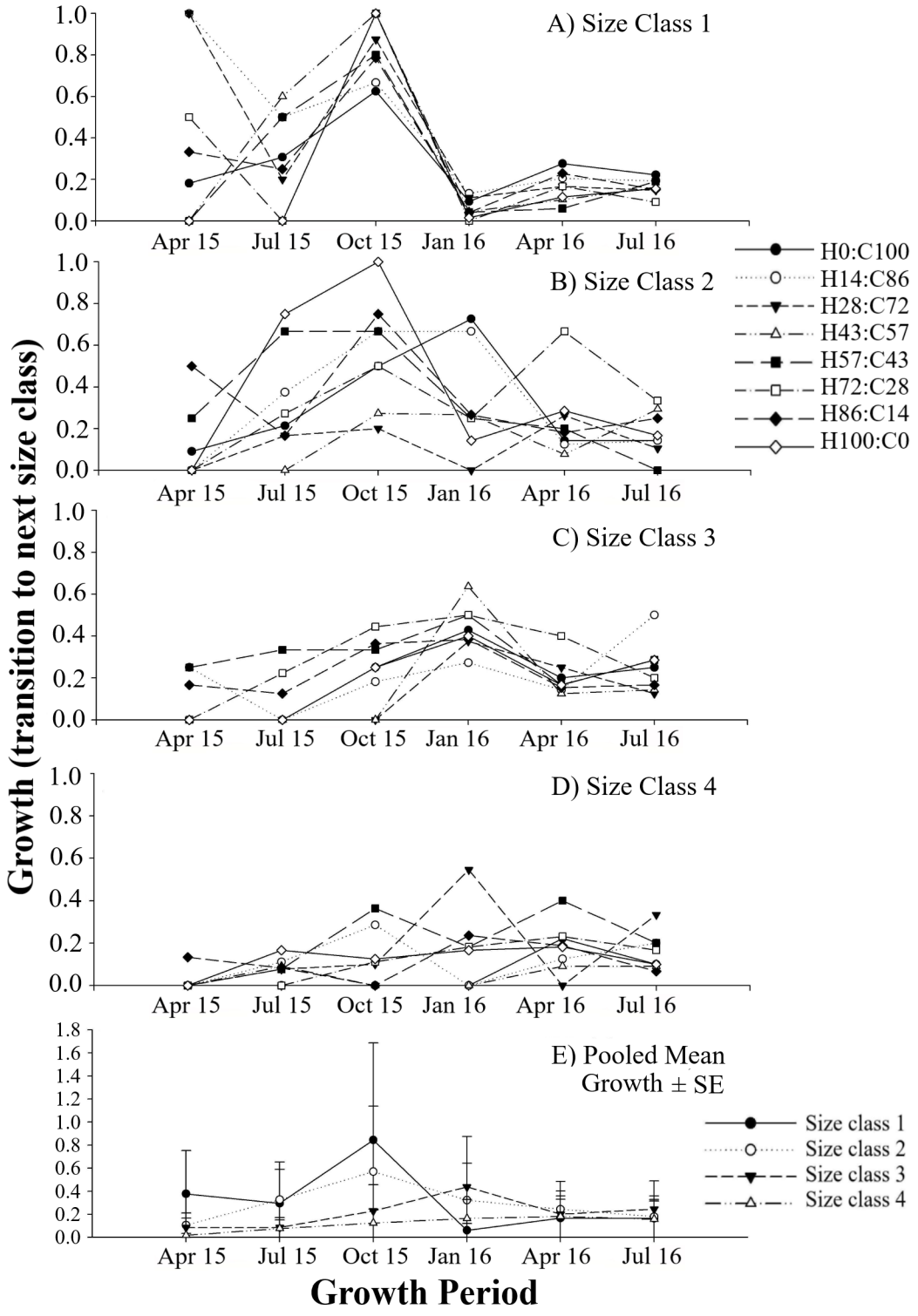

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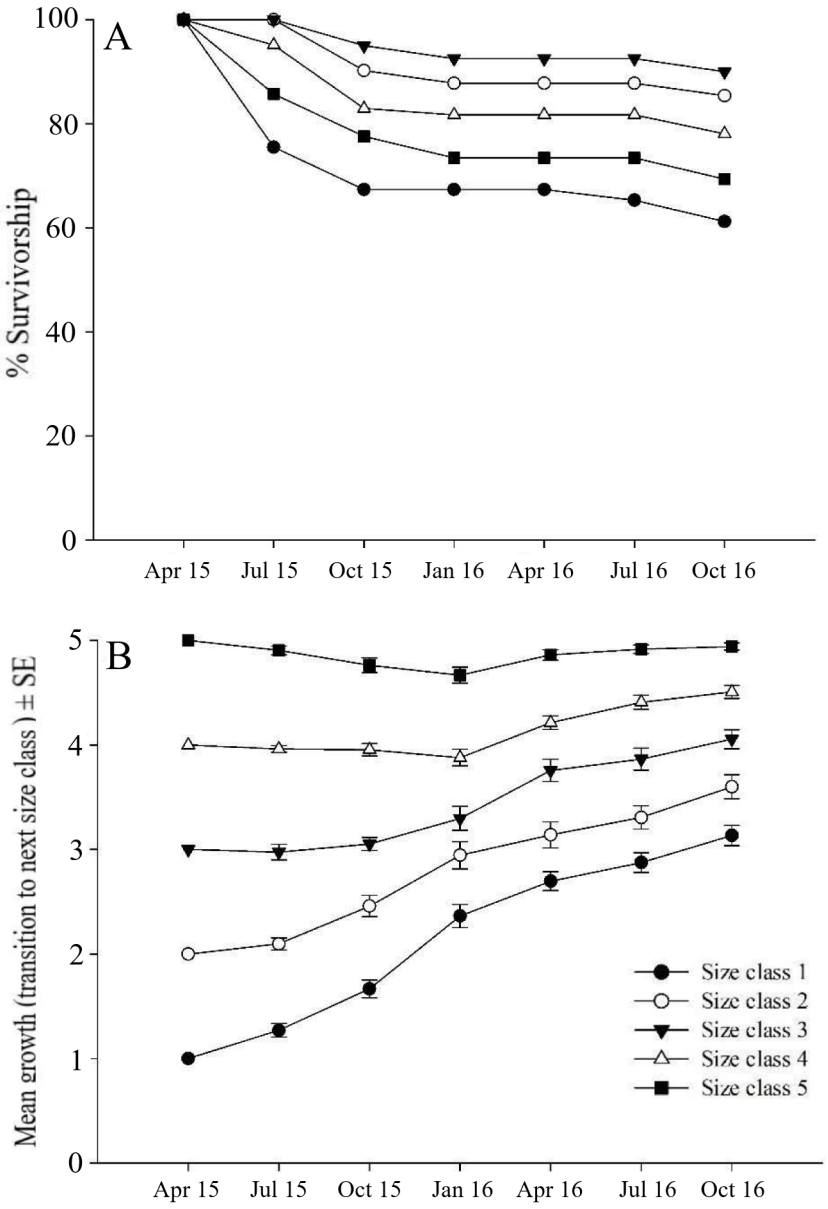

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