RETURN OF THE MAC: HOW DENSITY AFFECTS THE SURVIVAL OF JUVENILE GIANT KELP (*MACROCYSTIS PYRIFERA*) IN POINT LOMA KELP FOREST, SAN DIEGO, CA

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Breck Alyssa McCollum
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Thesis of Breck Alyssa McCollum:

Return of the Mac: How Density Affects the Survival of Juvenile Giant Kelp

(*Macrocystis pyrifera*) in Point Loma Kelp Forest, San Diego, CA

Matthew Edwards, Chair
Department of Biology

Todd G. Anderson

Todd Anderson
Department of Biology

Stephen Schellenberg
Department of Geological Sciences

1-20-17

Approval Date

ABSTRACT OF THE THESIS

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Adult giant kelp, *Macrocystis pyrifera*, release billions of zoospores into the surrounding kelp forest community during each reproductive season. The young sporophytes that ultimately develop from these zoospores undergo a process of self-thinning until their densities are reduced to levels that can be sustained by environmental conditions at that time. We examined the effects of recruitment density on the survival of juvenile *M. pyrifera* within naturally occurring patches in the Point Loma kelp forest, San Diego, CA and found that the total density of all macroalgae within the patch had no effect on *M. pyrifera* survival. Instead, we found that density-dependent mortality within each patch was driven almost entirely by the density of conspecifics. This pattern, and the direct effects of recruitment density on juvenile *M. pyrifera* survival was further tested experimentally by oputplanting two size classes of juvenile *M. pyrifera* (medium size class, 5-25cm in height; large size class, ~1m in height) at three densities (20, 60 and 120 individuals m-2, and 2, 4 and 8 individuals m-2 for medium and large size classes, respectively). While the large size class exhibited the overall greatest survival, declines in survival were consistent through time for all density treatments and for each size class, with the surviving sporophytes converging on similar densities (8 m-2 ±4 for the medium size class, and 1 m-2 ±1 for the large size class). Together, our observational and our experimental studies demonstrate that, regardless of the initial density at which *M. pyrifera* recruits, the resulting patches of juvenile sporophytes will thin to similar densities that are presumably appropriate for their survival under the existing environmental conditions. This self-thinning process is an example of density-dependent mortality that operates in addition to other stressors such as grazing, sand scour, entanglement and dislodgement due to wave energy, each of which effectively reduces the population size of new *M. pyrifera* recruits to a level that is sustainable by the kelp forest community.

TABLE OF CONTENTS

PAGE

LIST OF TABLES

LIST OF FIGURES

PAGE

CHAPTER 1

INTRODUCTION

Mathematical models such as those proposed by Pearl and Miner (1935) describe age-specific patterns of survival that can be used to describe general patterns in natural population fluctuations over the lifespans of individual organisms. For example, studies of terrestrial plants have found that many species experience high mortality as juveniles (i.e. Survivorship curve type 3 as purposed by Pearl and Miner [1935]), and that the survival of these early life stages has important implications for both the recruitment of adults and the propagation of future generations (Harper, 1967). However, the simplicity of these models often limits their applicability to organisms that exhibit complex life histories, especially if one or more of the life stages are difficult to observe in nature, as is the case with many species of kelp (Order Laminariales). Consequently, comprehensive ecological research on population dynamics will benefit by including questions that examine the differential survival of all life history stages (Carney and Edwards, 2006; Fejtek et al., 2011; this study), particularly if each stage may be differentially impacted by environmental conditions.

1.1 BACKGROUND

1.1.1 Kelp Forest Ecosystem

Kelp forests occur in rocky, wave-swept near shore habitats throughout temperate waters of the northern and southern hemispheres. The iconic foundational species of many of these forests along the west coast of North America is the giant kelp, *Macrocystis pyrifera*. Generally, *M. pyrifera* occurs from the shallow subtidal zone to ~20 meters depth and within the temperature range of 8-17°C (Edwards and Estes, 2006; Graham, 2004; Schiel and Foster, 2015). Nitrate is often the limiting factor for *M. pyrifera* growth within this temperature range, with levels below 1µmol L^{-1} generally resulting in stressful conditions for growth and gametogenesis (Dayton, 1985; Deysher and Dean, 1986; Schiel and Foster, 2015). Adult *M. pyrifera* are opportunistically reproductive once reaching sexual maturity, though spore release and juvenile recruitment can vary seasonally with changes in photoperiod, temperature and nutrient availability (Deysher and Dean, 1986). Successful recruitment of juvenile *M. pyrifera* depends on the occurrence of "recruitment windows", which characterize periods when temperature and light are adequate for gametogenesis (i.e., temperatures below 16.3 °C and irradiances above 4.6 μmols m^{-2} s^{-1}) (Deysher and Dean, 1986). These conditions occur most frequently between March and May in southern California, following winter storms that increase light availability to the benthos by removing patches of the kelp forest canopy. This increase in light availability often corresponds with a predictable oceanographic event referred to as the "spring transition" that increases the amount of cold nutrient rich water entering the kelp forest due to coastal upwelling. Theses recruitment windows often result in large-scale recruitment of juvenile kelp into dense patches that are then reduced over time by both density-dependent and density-independent factors (Schiel and Foster, 2015).

While *M. pyrifera* and other large kelp species create subtidal forest ecosystems, they also compete for resources with many other algae within the forests. Competition among macroalgae in a kelp forest is three-dimensional, as individuals need benthic space for attachment but also need access to sunlight. A number of opportunistic kelp species, such as the arborescent *Pterygophora californica* and *Eisenia arborea*, and the prostrate *Laminaria farlowii*, *Stephanocystis osmundacea*, and *Dictyoneurum californicum* may live below the *M. pyrifera* canopy but their recruitment success is limited by the availability of light and appropriate habitat substratum (e.g. Clark et al., 2004; Dayton, 1985; Dayton et al., 1984). Beneath these understory kelps exists a complex mosaic of algae such as the seasonal *Desmarestia ligulata*, the articulated coralline algae *Calliarthron tuberculosum* and *Bossiella californica*, many species of foliose red algae that grow both epiphytically on other kelp forest organisms and individually on the substrate, and a host of sessile invertebrates such as sponges and tunicates. As a result, these species may also impact *M. pyrifera* survival, especially when they co-occur at high densities.

1.1.2 *M. pyrifera* Life Cycle

M. pyrifera exhibits a biphasic life history, where macroscopic asexual, diploid sporophytes (“adults”) alternate with microscopic sexual haploid gametophytes. Haploid zoospores are released by the billions from sori on specialized blades called sporophylls that are located near the base of the adult sporophyte (Levyns, 1933) (Figure 1.1). Zoospore settlement appears to be most concentrated within a few meters of the adult sporophyte from which they were released, however dispersal may occasionally occur over kilometers (Alberto et al., 2010; Gaylord et al., 2006; Gaylord et al., 2004; Reed et al., 1988; Reed et al., 2004). Once settled, the microscopic zoospores germinate into male and female gametophytes that persist on the substratum until they undergo sexual reproduction (Deysher and Dean, 1986; Reed, 1990a). The female gametophyte releases the pheromone Lamoxirene, which induces the male gametophyte to release biflagellate sperm that can then swim distances of approximately one millimeter in order to find and fertilize the female gametophytes’ egg (Reed, 1990a). This need for the gametophytes to be in close proximity necessitates that high densities of zoospores be released into the water column, and that sufficient numbers of them survive to germinate into gametophytes. Following syngamy, the now diploid embryonic sporophyte undergoes cell division and begins the process of growing into a juvenile sporophyte (Neushul, 1963; Reed, 1990a). The embryonic sporophyte takes approximately 45 days to grow into a juvenile sporophyte that is large enough to see with the unaided eye when growth conditions are adequate (Dayton et al., 1984; Schiel and Foster, 2015).

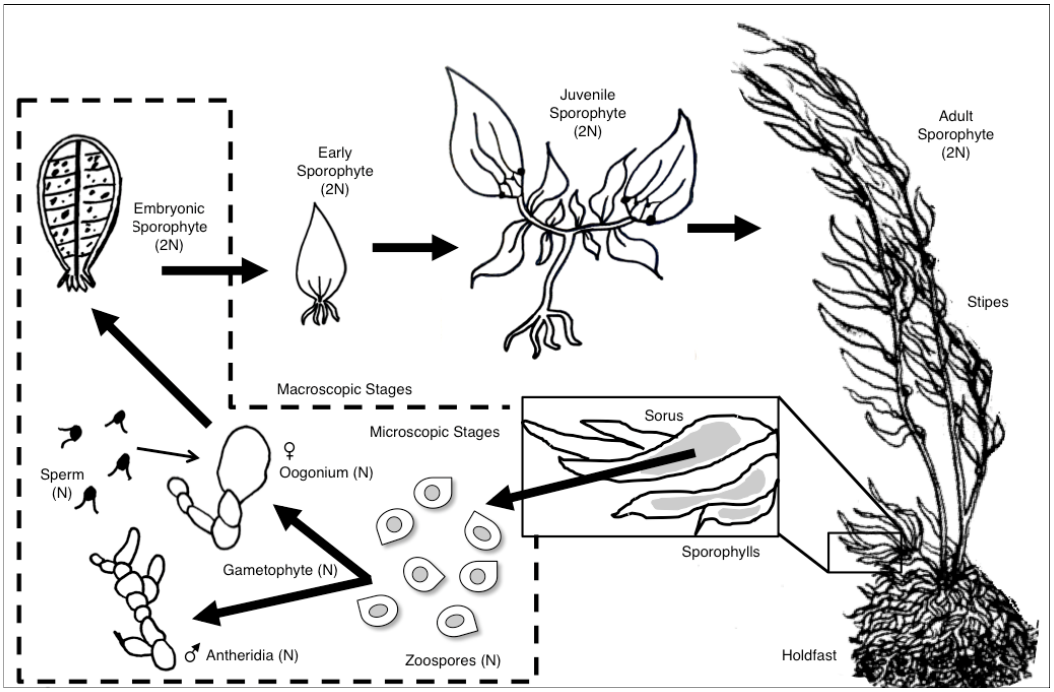

Figure 1.1. *Macrocystis pyrifera* life cycle. Microscopic life history stages are depicted in the dashed box. Modified from Gaitán-Espitia et al. (2014); with Adult Sporophyte drawing from Dayton et al. (1984), and juvenile drawings by B. McCollum.

Due to their small size, relatively few studies have experimentally examined the effects of physical or biological factors on these early life-history stages of *M. pyreifera* in the field; but see exceptions summarized in Table 1.1. For instance, Neushul and Haxo (1963), Reed and Foster (1984), Deysher and Dean (1986), Reed et al. (1988), Reed (1990a), Edwards (2000) and Carney et al. (2013) together conclude that the survival of juvenile *M. pyrifera* fluctuates with changes in the environmental conditions that exist at the time of their recruitment. However, while these studies were generally short-lived and therefore unable to track the survival of individuals to larger size classes (Table 1.1), it appears that similar processes occur among juvenile kelps as with those observed in terrestrial plant communities. Specifically, juvenile *M. pyrifera* often recruit into extremely dense patches (i.e. 100's per m^{-2}) and as these juveniles grow, they begin to compete with one another for resources such as light, space and nutrients. This increased competition can result in the expression of morphological plasticity such as eitiolation, which is the lengthening of stipes in a process similar to the density response of elongation by terrestrial plants, thereby providing these individuals with greater access to light by elevating them over their neighbors (Reed 1990b;

Schiel and Foster, 2006; White, 1977). This response, however, may be limited to particular periods of growth, and when individuals are no longer able to respond to density-dependent competition by eitiolation, many will perish (Schiel and Foster, 2006). Thus, how density affects the survival of juvenile *M. pyrifera* as they progress from one life history stage to another, and as they grow from juvenile to adult sporophytes, remains an unknown but important aspect of their life history.

Table 1.1. Summary of Previous Field Research on the Biology and Ecology of the Early Life History Stages of *Macrocystis pyrifera.*

Study	Findings	Reference
Transplanted laboratory-raised juveniles on floating rafts to examine the effects of light and depth on growth.	No difference in growth between individuals on rafts at 15m and those unmanipulated on the seafloor. Laboratory growth under constant illumination was nearly double that of individuals grown in the field.	Neushul and Haxo (1963)
Examined the effect of canopy cover and light on the recruitment and growth of juvenile kelp, including *Macrocystis*	Moderate recruitment following the removal of both *Macrocystis* canopy and understory algae canopy. No recruitment if one or both canopies were left intact.	Reed and Foster (1984)
Outplanted zoospores to the field and measured the effects of temperature, irradiance, seston flux, and nitrogen on sporophyte production	Sporophyte recruitment occurred only at temperatures below 16.3°C and at irradiation levels above 4.6 µmols m^{-2} s^{-1}, which they defined as a "recruitment window".	Deysher and Dean (1986)
Examined temporal and spatial variation in kelp recruitment at 0m, 3m, and 10m away from the adult source.	Recruitment fluctuated temporally with recruitment peaks and lulls. Dispersal of *Macrocystis* zoospores was highest at 0m, and negligible at further distances.	Reed et al., (1988)
Seeded boulders with known densities of zoospores and transplanted them in the field to determine how density affects sporophyte recruitment	Density of zoospores must be at least 1/mm2 for successful sporophyte recruitment however higher densities may produce more sporophytes. Density-dependent mortality is proportionally higher with increasing density.	Reed (1990a)
Examined the effect of delayed zoospore removal on the population genetics of juvenile kelp	While most recruits come from newly settled zoospores, the presence of delayed-development zoospores may contribute to the genetic maintenance of intact kelp forest populations.	Carney et al., (2013)

The growth and maturation of *M. pyrifera* into an iconic kelp forest is analogous in many ways to the growth and maturation of terrestrial forest-forming tree species where density-dependent mortality tends to remove the smallest individuals first (Adler, 1996; Antonovics and Levin, 1980; White, 1977; White and Harper, 1970), resulting in an increase in the average size of surviving individuals and a release from competition with the smaller individuals. This pattern of density-dependent, size-specific mortality then continues as individuals grow, further reducing their densities. This pattern has been empirically demonstrated with approximately 80 terrestrial plant species ranging from tiny mosses to forest-forming giant trees (Gorham, 1979; White, 1977). This process by which density-dependent mortality continuously reduces a population until the individuals are no longer negatively affected by their closest neighbors is referred to as “self-thinning” (Li et al., 2000; Schmitt et al., 1987; Schmitt et al., 1986). This was first proposed by Kira et al. (1953), and experimentally tested by Yoda et al. (1963) (reviewed in Dean et al., 1989; Flores-Moya et al., 1996; Gorham, 1979; Li et al., 2000; White, 1977; White and Harper, 1970). However, these experiments were conducted using monospecific stands of different species and on soils of various qualities. Yoda et al. (1963) found a correlation between the number of surviving plants in a stand and the mean weight of each individual. Using artificially constructed stands of herbaceous plants, Kira et al. (1953) found that a range of densities will converge in time to yield a similar biomass per stand. For decades, the existence of self-thinning as a general rule has been debated in the literature for both terrestrial plants and seaweeds (see Lonsdale [1990] for a review of the debate within the terrestrial plant literature; and Scrosati [2005] for a review within the seaweed literature). However the observations of negative relationships between density and survival across different size classes in *M. pyrifera* made by Dayton et al. (1984) suggests that self-thinning may be an important source of mortality among juvenile kelps and warrants further experimental investigation.

Natural survival of juvenile kelp in the field is highly variable during their early life-history stages (Dayton et al., 1984). For example, of 1543 *M. pyrifera* recruits that Dayton and colleagues identified at the time of their first appearance and monitored over nine months until they reached the sea surface, only 19.4% survived to reach 5 cm in height. Surprisingly, of those that reached 5 cm, 86.3% also survived to reach 1-2 m in height. These then experienced high density-dependent mortality and only 13.5% survived to reach the surface, with a significant source of mortality likely due to entanglement with neighboring individuals. Likewise, Dean et al. (1989) tagged >8000 juvenile *M. pyrifera* and found that only 2% grew large enough to reach the surface. Sources of mortality for these juvenile kelp included grazing, light limitation, nutrient limitation, unsuitable benthic substrate, recruitment density, burial in sediment, sand scour, and wave abrasion. In particular, the shearing force of wave energy can result in high mortality of adult and juvenile *M. pyrifera* alike. As successful large-scale recruitment events occur in southern California on average every 3-4 years (Dayton and Tegner, 1984:Rosenthal et al., 1974), the factors that affect juvenile survival can have lasting impacts on the entire kelp forest community (Dayton et al., 1984).

Understanding the life history of an organism, including differential survival among its different size or age classes is paramount to the study of population dynamics. This knowledge gives us a more complete overview of the ecology of a population and how that population is regulated throughout the various life stages of its individuals. Due to the importance of *M. pyrifera* as an ecosystem engineer in structuring and providing habitat for entire kelp forest communities, recognizing the factors that affect the survival of all of its life history stages will be crucial to future management objectives that pertain to rocky reef ecosystems. Despite the difficulty of manipulating the inconspicuous early life history stages of *M. pyrifera* in the field, the ecological importance of this species warrants additional study under realistic environmental conditions.

1.1.3 Research Objectives

This study was motivated by frequent observation of large patches of extremely dense juvenile kelp occurring in the Point Loma kelp forest (Figure 1.2). Adult *M. pyrifera* are found regularly throughout their range occurring at densities near 0.1 m^{-2} (Edwards, 2004) However, little is known about how the different life stages of *M. pyrifera* are affected by density. Antonovics and Levin (1980) note that there has been a paucity of research involving the temporal variation in density-dependent mortality in plant biology, and likewise a paucity of research concerning the temporal aspect of density dependent mortality exists for the seaweeds as well (but see Dayton et al., 1984). By monitoring how changes in patch density relate to the survival of juvenile kelp, we aim to identify both an important survival bottleneck in the life history of this ecosystem engineer and to apply these findings to an experiment that allows us to determine what density produces the greatest survival among juvenile *M. pyrifera*. Thus, the overarching objective of this study was to determine how recruitment density impacts the survival of juvenile *M. pyrifera* as they grow to adulthood in the Point Loma kelp forest. In the first half of this study, the survival of juvenile *M. pyrifera* was monitored in naturally occurring patches of varying algal densities between July 2013 and January 2014. In order reduce environmental variability associated with our monitoring study, and to elucidate with certainty whether or not self-thinning is a leading cause of mortality within patches of juvenile *M. pyrifera*, we experimentally manipulated densities of different size classes of juvenile *M. pyrifera* according to the findings of our monitoring study. Additionally, we asked if density has a differential effect on different sizes classes of juvenile *M. pyrifera*.

Figure 1.2. A dense patch of juvenile kelp containing *Macrocystis pyrifera, Laminaria farlowii,* and *Pterygophora californica* in the Point Loma kelp forest. Mean size of individuals pictured is approximately 10cm. Photo by Joshua Greenwell.

CHAPTER 2

METHODS

2.1 STUDY SITE

This study was carried out in the Point Loma kelp forest, near San Diego, CA. As of July 2013, the Point Loma kelp forest was approximately 1 km wide and 11 km long, making it the longest continuous kelp forest in the United States. The size of the Point Loma kelp forest and its proximity to a number of research institutions has made it one of the most studied kelp forest communities in the world (e.g. Carney et al., 2013; Dayton et al., 1984; Dayton and Tegner, 1984; Dayton et al., 1999; Fejtek et al., 2011; Foster and Schiel, 2010; Graham, 2003; Parnell et al., 2010; Seymour et al., 1989; Tegner et al., 1997). The benthic substrate within the forest is characterized by an abundance of low-relief sandstone bedrock interspersed with patches of sand and cobble, with little vertical complexity.

A series of exploratory survey dives were conducted during 2012 to locate two study areas with patches of juvenile *M. pyrifera* suitable for experimental manipulation. Research sites were positioned with consideration to the research of Dayton and Tegner (1984) and Tegner and Dayton (1987), who found the greatest kelp survival in the central portion of the kelp forest and in deeper depths throughout the kelp forest. Logistical constraints led to the placement of our sites between 10-14m in depth. These sites were in the southern central portion of the forest and are approximately 370m apart from each other (N 32^0 41’ 20.7” x W 117^0 15’ 59.7” and N 32^0 41’ 10.68” x W 117^0 16’ 1.02”; Figure 2.1). The area around our sites is popular with commercial and recreational lobster fishers, and frequented by recreational divers. One of the two sites was used to monitor survival in naturally occurring patches of juvenile *M. pyrifera* while the other site was used to outplant experimentally modified patches of juvenile *M. pyrifera* of varying densities. These sites will henceforth be referred to as the “Monitoring site” and the “Experimental site”, respectively.

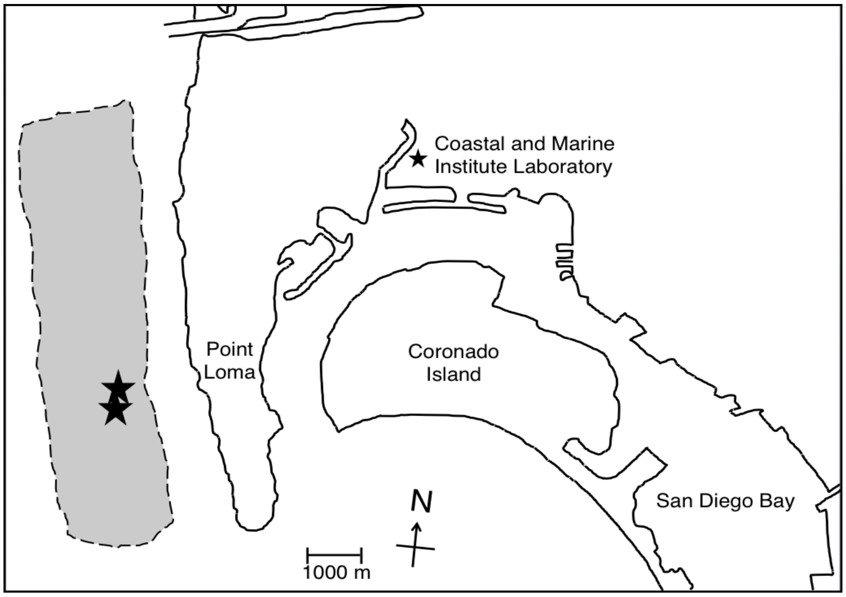

Figure 2.1. Map of Point Loma, San Diego, CA showing the location of the two research sites (large stars) within the Point Loma Kelp Forest (grey patch represents the approximate size and location of the kelp forest during 2013-2014). The northern site is the natural patch monitoring site and the southern site is the experimental site.

2.2 THE EFFECTS OF DENSITY ON THE SURVIVAL OF NATURALLY OCCURRING *M. PYRIFERA* JUVENILES

The monitoring site was characterized by relatively flat, low relief bedrock and contained areas with dense stands of adult *M. pyrifera*. Recruitment of juvenile kelp was widespread throughout this site at the time of the survey. Divers approached the site from the inside edge of the kelp forest and from a randomly determined starting point within the forest, began locating and marking patches of juvenile kelp. Patches were defined as $0.1m^{-2}$ to $2m^{-2}$ areas of the substrate containing two or more juvenile *M. pyrifera* individuals that were within close enough proximity that they could be reasonably expected to negatively impact each other. This negative impact proximity was defined as any linear distance between individuals that was shorter than the height of either individual. The first 30 patches meeting these criteria were marked at the corners with numbered tags hammered into the substrate with masonry nails. For analysis, patch area was standardized to $1m^{-2}$ so that the effect of density could be compared among patches.

In addition to *M. pyrifera*, patches also included other understory macroalgae, including juveniles of up to three other species of kelp; namely *Pterygophora californica, Eisenia arborea,* and *Laminaria farlowii*. The growth and survival of all individuals >5mm tall in the patches were recorded on four occasions between July 2013 and January of 2014. Individuals occurring within the marked patch boundaries were counted and measured by hand, but left attached to the substrate. The presence of new recruits to each patch were counted and measured during each survey as well. Stormy weather and occasional poor underwater visibility prevented our ability to locate and survey the patches between October-December 2013. During all surveys, care was taken to minimize disturbance to the patches to avoid impacting natural processes that influence the growth and survival of the juvenile kelps. While species other than *M. pyrifera* likely have an important role in structuring the community, they were not the focus of this study and are only considered peripherally for their role in expanding the density-dependent mortality concept to include other species.

2.2.1 Statistical Analyses for the Monitoring Study

Statistical tests were performed using R (R Core Team 2015). Residuals were evaluated for normality using graphical interpretation, and were found to be approximately normal. Our study design required repeated sampling the same patches of juvenile kelp, therefore our analyses required the use of repeated measures. Different factors specific to the microhabitat of that patch likely contributed to the overall survival of the individuals within that patch. Therefore, each density count during each sampling event of each patch could not be treated independently. Likewise, the amount of time that passed between sampling dates moderated the effect of density that was observable during the next sampling date; greater changes in density were expected to occur over the longer gaps between sampling than during the shorter gaps between sampling. Also, if the density in a patch declined sharply during one time period (e.g. between July and August), then the expected rate of density-dependent mortality experienced between subsequent time periods (e.g. between August and September) should be reduced simply because the starting density for that time period was lower. For this reason, a linear mixed effects model with patch considered as a random effect and *M. pyrifera* starting density at each time period as a covariate was used for analyses (Pinheiro et al., 2017). A chi-square log ratio test was then used to examine how factors affected the final density of juvenile *M. pyrifera.* In order to test the hypothesis that the density of juvenile *M. pyrifera* is affected by the density of all individuals in their patch, we fit the model:

$$Y = \beta_o + \beta_1 x_1 + \beta_2 x_2 + \beta_3 x_1 x_2 + \varepsilon \tag{2.1}$$

Where x_1 is the number of days since the last sampling event, as it will be in the first three models, and x_2 is the total density of the patch during the previous sampling event. Next, we separated out the variance associated with density of *M. pyrifera* and the variance associated with the density other species present in the patch (i.e. intraspecific and interspecific competition, respectively) by testing the hypothesis that the presence of conspecifics and the presence of other species will differentially affect the density of *M. pyrifera* juveniles in the patch. This was done so by fitting the model:

$$Y = \beta_o + \beta_1 x_1 + \beta_2 x_2 + \beta_3 x_3 + \beta_4 x_1 x_2 + \beta_5 x_1 x_3 + \varepsilon \tag{2.2}$$

Here x_2 is the density of *M. pyrifera* juveniles in the patch during the previous sampling event, and x_3 is the density of other species in the patch during the previous sampling event. We tested the hypothesis that previous *M. pyrifera* juvenile density affects the absolute number of *M. pyrifera* juveniles that can persist in a patch using the model:

$$Y = \beta_o + \beta_1 x_1 + \beta_2 x_2 + \beta_3 x_1 x_2 + \varepsilon \tag{2.3}$$

Here, as in the previous model, x_2 is the density of *M. pyrifera* juveniles in the patch during the previous sampling event. We also tested the hypothesis that initial *M. pyrifera* density will affect the final density of *M. pyrifera* juveniles that we observe in our patches using the model:

$$Y = \beta_o + \beta_1 x_1 + \beta_2 x_2 + \beta_3 x_3 + \beta_4 x_1 x_2 + \beta_5 x_1 x_3 + \varepsilon \tag{2.4}$$

x_1 in this model is the number of days that have passed since the initial survey, x_2 is the initial density of juvenile *M. pyrifera* in the patch, and x_3 is the initial density of the other species present in the patch.

2.3 THE EFFECTS OF DENSITY AND SIZE ON THE SURVIVAL OF EXPERIMENTALLY OUTPLANTED *M. PYRIFERA* JUVENILES

The Experimental Site was characterized by relatively flat bedrock with areas containing dense stands of adult *M. pyrifera*, though there was some additional vertical complexity present in the form of large boulders and rocky outcrops. As with the monitoring site, recruitment of juvenile kelp was widespread throughout this site at the time of the initial outplanting. The experimental portion of this study set out to examine the effects of recruitment density on the survival juvenile *M. pyrifera*. Therefore, the experiments detailed here were designed to test the effects of density on two different size classes of juvenile *M. pyrifera*, medium individuals (5-25cm in height), and large individuals (1m in height). A small size class (embryonic sporophytes ~2mm in height), was initially used as well, however high mortality in this treatment precluded the collection of any useable data. For each size class, low, medium and high densities were determined from previous density-dependent mortality research on juvenile kelp (Devinny and Volse, 1978; Deysher and Dean, 1986; Reed et al., 1997), from field observations, or when neither existed as in the case of the large-size class juveniles, logistical constraints (minimum of 2 individuals m^{-2}).

2.3.1 Medium Size Class

In May 2013, the Experimental Site was surveyed for patches of juvenile kelp of approximately 5-25cm in height; this is the smallest size at which positive identification in the field can be accomplished by most divers with a trained eye (Dayton et al., 1984). From this survey, “low”, “medium”, “high” density values were determined, and these values were used as target densities for the following experiment. Approximately 300 juvenile (5-25cm) *M. pyrifera* were collected from an area near the experimental site, transported to San Diego State’s Coastal Marine Institute Laboratory (CMIL) and placed in tanks filled with 12^{0} C filtered seawater where they were maintained under 20μmol PAR on a 14:10 light dark cycle for approximately one week. After this acclimation period, the kelps were attached to 25cm^{-2} experimental mats and prepared for outplanting. To construct the low-density treatment, five juvenile *M. pyrifera* were inserted into the braided rope fibers of each of five replicate 25cm^{-2} mats in a way that uniformly distributed them across the mat (20 m^{-2}). The holdfast of each individual was approximately 5cm away from its closest neighbor. The same process was repeated for the medium-density mats, using 15 individuals, with each holdfast being approximately 2cm from their nearest neighbor (60 m^{-2}), and for the high-density treatment, using 30 individuals distributed approximately 1cm from their nearest neighbor (120 m^{-2}) (Figures 2.2 and 2.3). Mats were stacked gently in three insulated coolers filled with 12°C chilled filtered seawater for transportation to the experimental site. On site, mats were transferred to black plastic bags in the shade to limit exposure to sunlight and transported to their permanent location in the kelp forest by divers. The mats were attatched to the bedrock seafloor at random locations throughout the Experimental Site usng masonry nails.

Figure 2.2. Photograph of paper models of juvenile kelp inserted into the actual 25cm^{-2} experimental mats prior to use in the experiment. The paper juvenile kelps are representatively-sized to accurately depict the low (20 m^{-2}), medium (60 m^{-2}), and high (120 m^{-2}) density treatments used for the medium size class experiments (with 5, 15, and 30 individual *Macrocystis pyrifera* per 25cm^{2} mat, respectively).

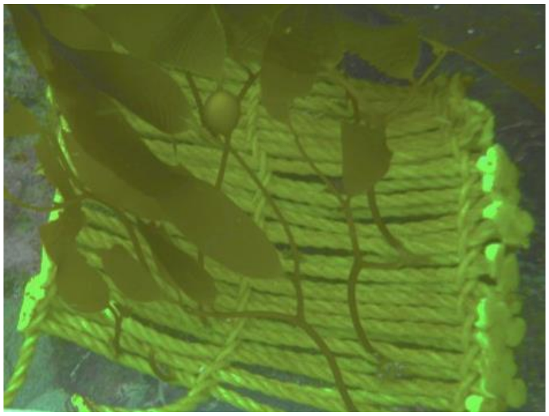

Figure 2.3. Photo of a medium size class experimental mat (25cm^{2}) from the medium-density treatment (60 juveniles m^{-2}) after approximately one month in the field.

2.3.2 Large Size Class

Unlike juvenile *M. pyrifera* in the 5-25 cm range, we were unable to locate enough patches of 1m tall juvenile *M. pyrifera* to determine accurate ranges of natural densities for this size class. Therefore, densities of 2, 4 and 8 individuals m^{-2} were selected as low, medium, and high-density treatments for this experiment. These numbers were based around the low-density treatment, as a minimum of two individuals were required to elicit a density dependent response. In July 2013, 70 juvenile *M. pyrifera* approximately 1m in height were collected from an area near the experimental site. As with the medium sized (5-25 cm) individuals, these juveniles also were stored in recirculating filtered seawater at 12^{0}C. At this size, the juveniles have developed a number of small pneumatocysts that cause them to be positively buoyant. To prevent disintegration of the portion of the juveniles floating above the water line, paper towels moistened with seawater were placed over each juvenile. This reduced the amount of light reaching each kelp but did not appear to negatively affect their survival during the short period they were held in the laboratory (i.e. no mortality was observed). Due to the holdfast size of these juveniles, individuals were woven into single 10cm segment of polypropylene rope with a stainless steel washer and concrete nail at each end. As with the experimental mats, ropes were placed into black plastic bags inside coolers filled with filtered 12^{0}C water for transportation to the field. Individual kelp ropes were then nailed to the seafloor in randomly placed 1m^2 plots according to density treatment of 2, 4 8 individuals m^{-2} (Figure 2.4). As with the medium density treatments, there were five replicates of each treatment.

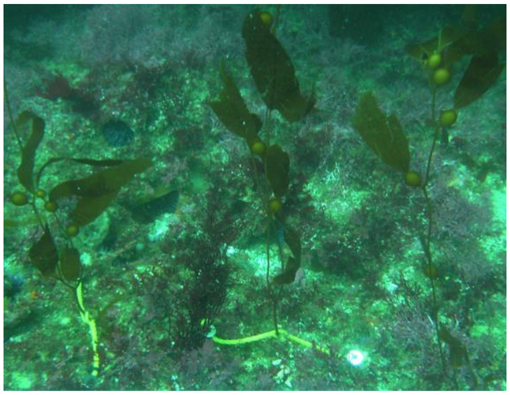

Figure 2.4. Photo of a medium density treatment plot from the large-size class treatment after approximately 1 month in the field. Each yellow rope is 10cm for scale.

2.3.3 Mat and Plot Surveys

Surviving kelps that were observed in the monitoring site patches and those outplanted to the experimental site were counted after two weeks. After this initial survey period the mats and plots were both checked for *M. pyrifera* growth and survival approximately monthly, conditions permitting, and as soon as possible following storms. Mats and plots were surveyed until all individuals were either deceased, the mat or plot was lost due to a storm event, or all remaining individuals survived to reach the surface.

2.3.4 Statistical Analysis for the Experimental Study

Statistical tests were performed using JMP® (SAS Institute 1989) and R (R Core Team 2015). Residuals were evaluated for normality using graphical interpretation, and those not meeting the assumptions of parametric tests were transformed and retested to ensure problems were corrected. Temporal patterns of survival of the outplanted *M. pyrifera* were compared among the different outplant density treatments within each size class separately using independent non-linear ANCOVAs, with density as a categorical factor and time since outplanting as a covariate. Following determination that temporal patterns of survival were not significantly different among three outplant densities within either size class (ANCOVA: time x density interactions, $p = 0.66$ and 0.99 for medium and large size classes, respectively), temporal patterns of survival were further assessed for each size class separately using separate non-linear regressions (negative exponential and negative logistic/sigmoidal, for medium and large size classes, respectively).

CHAPTER 3

RESULTS

3.1 NATURAL PATCH MONITORING SURVEYS

Patch density, referring to of all macroalgae contained within a patch, ranged from 3 – 240 individuals m^{-2}. The initial patch surveys identified an average of 60 ±12 individuals m^{-2}(mean ± se), with over half of the patches containing fewer than 25 individuals m^{-2} (Figure 3.1). By the second survey date in August 2013, average patch density had increased to 78 ±16 individuals m^{-2} (mean ± se) as new recruits of *M. pyrifera* and other species appeared in the patches. Densities continued to increase by the 3rd survey in September 2013, to 90 ±22 individuals m^{-2}(mean ± se) though the proportion of *M. pyrifera* juveniles relative to other species declined (Figure 3.1). This decline was likely related to both natural mortality of *M. pyrifera* juveniles and additional recruitment of other species, mainly *P. californica* and *L. farlowii*. Winter storms and water conditions prevented the monitoring of patches again until January 2014. By this time, average kelp density in the patches had increased to 149 ±68 individuals m^{-2}(mean ± se) (Figure 3.1). In September 2013, while the other species in the patches continued to increase in density, the number of *M. pyrifera* decreased (Figure 3.1). As of January 2014, many of the few surviving *M. pyrifera* individuals reached the surface and were nearing reproductive maturity while the slower growing *P. californica* and *L. farlowii* remained in their juvenile states.

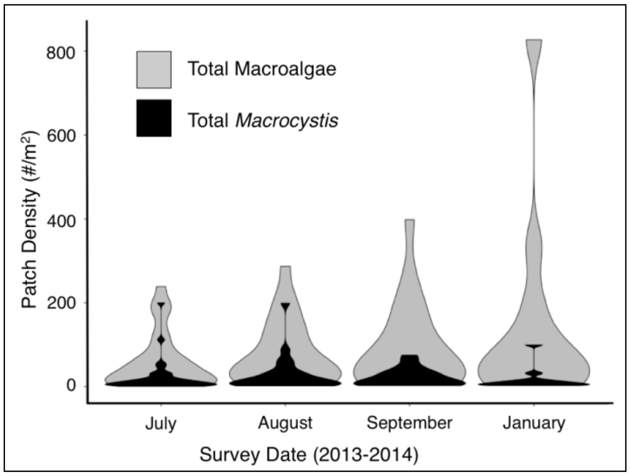

Figure 3.1. Violin plots representing variation in the densities of both all macroalgae and *Macrocystis pyrifera* alone in the natural monitoring patches between July 2013 and January 2014. Densities were standardized to an area of 1m^2. Grey shaded areas represent density of all macroalgae including *Macrocystis pyrifera* within the patch, while black shaded areas represent *Macrocystis pyrifera* density alone. Width of each figure indicates the relative frequency of patches occurring with that density during each sampling month.

Total macroalgal density in each monitoring patch did not significantly impact the number of of juvenile *M. pyrifera* occurring in each patch during the study (p=0.286) (Table 3.1, Test 1), though there was a slight trend in which *M. pyrifera* densities appeared to decline the fastest in patches with higher overall macroalgal densities (Figure 3.2). Instead, time (Days since last sample) was the only factor that significantly affected juvenile *M. pyrifera* density (p=0.005). In contrast, the number of juvenile *M. pyrifera* present in a patch was negatively affected by their previous density in that patch (i.e. density-dependent mortality) (p<0.001), as well as the number of days that have passed since the previous sample (p<0.001) (Table 3.1, Test 3). Specifically, *M. pyrifera* survival in patches that previously had low *M. pyrifera* densites remained high throughout the study, while patches that previously had medium *M. pyrifera* densities experienced a slight decrease in survival, and those patches that previously had high *M. pyrifera* densities exhibited a substantial decline in survival during the study (Figure 3.3). Likewise, the negative effect of *M. pyrifera* density on their survival appeared to become stronger with increasing days since last sample (p<0.001), while there was no effect of the previous density of other species (p=0.122) nor an interaction between other species density and days since last sample (p=0.744) (Table 3.1, Test 2). Together, our data indicate that the density of other species in the patch does not affect *M. pyrifera* survival whereas the presence of conspecifics has a negative effect. Additionally, when examining the effects of initial density on the final density of each patch, we found that days since initial survey, initial *M. pyrifera* density, and initial density of other species in the patch all negatively affected the final density of *M. pyrifera* juveniles (p=0.001 for each respectively, Figure 3.4), indicating a general trend of density-dependent mortality. However, we are restricted in our interpretation of this result due to low power that can be attributed to the few patches encountered with initially high densities of juvenile *M. pyrifera* and because only nine of the initial 30 patches were relocated on all of the sampling dates throughout the course of the monitoring study (Figure 3.4).

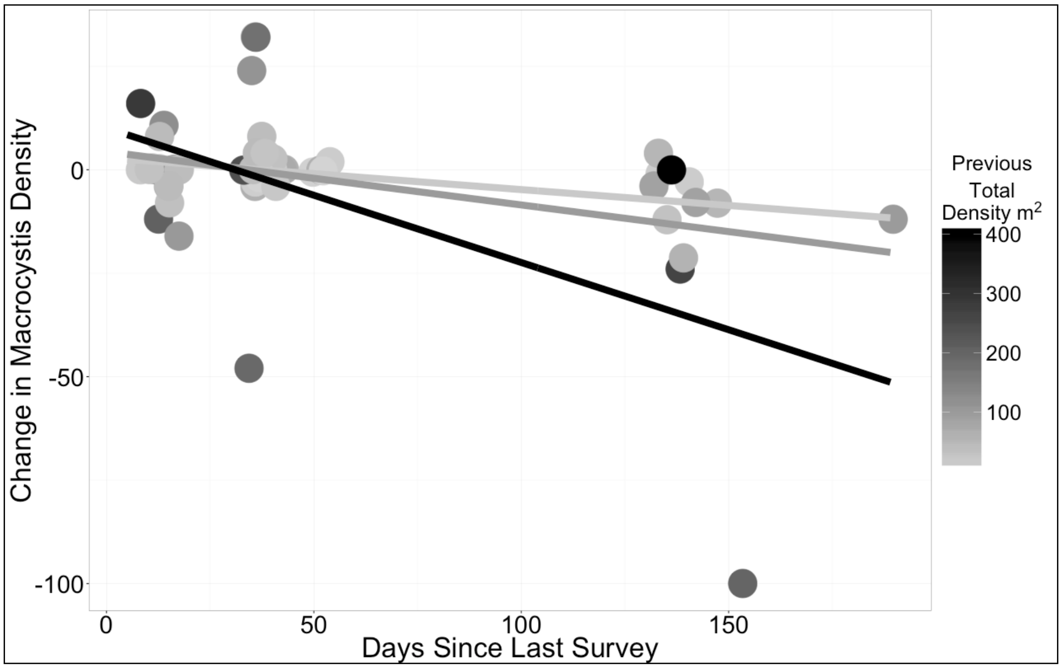

Figure 3.2. The effects of previous total macroalgal density (all species combined) in each patch on the change in *Macrocystis pyrifera* density over the course of the study. Dots represent the change in *Macrocystis pyrifera* density (# m^{-2}) that took place in each individual patch, and are shaded according to the previous total macroalgal density observed in that patch. Patches that contained a low density of individuals are in light grey, patches that contained a medium density of individuals are in dark grey, and patches that contained a high density of individuals are in black.

Table 3.1. Results of Chi-square Log Ratio Tests on Factors Affecting Change in *Macrocystis pyrifera* Density.

Test	Chi-Square	DF	p
1) Total patch macroalgal density on change in *M. pyrifera* density over days since last sample			
Days since last sample	7.9687	1	**0.005**
Previous total macroalgal density	1.1367	1	0.286
Days since last sample X previous total macroalgal density	1.823	1	0.177
2) Other macroalgal density on change in *M. pyrifera* density over days since last sample			
Days since last sample	19.6124	1	**< 0.001**
Previous *M. pyrifera* density	48.7965	1	**< 0.001**
Previous other macroalgal density	2.3961	1	0.122
Days since last sample X previous *M. pyrifera* density	27.7441	1	**< 0.001**
Days since last sample X previous other macroalgal density	0.1067	1	0.744
3) *M. pyrifera* density on change in *M. pyrifera* density over days since last sample			
Days since last sample	16.489	1	**< 0.001**
Previous *M. pyrifera* density	45.849	1	**< 0.001**
Days since last sample X previous *M. pyrifera* density	28.971	1	**< 0.001**

Note: Significant p values (< 0.05) are in bold.

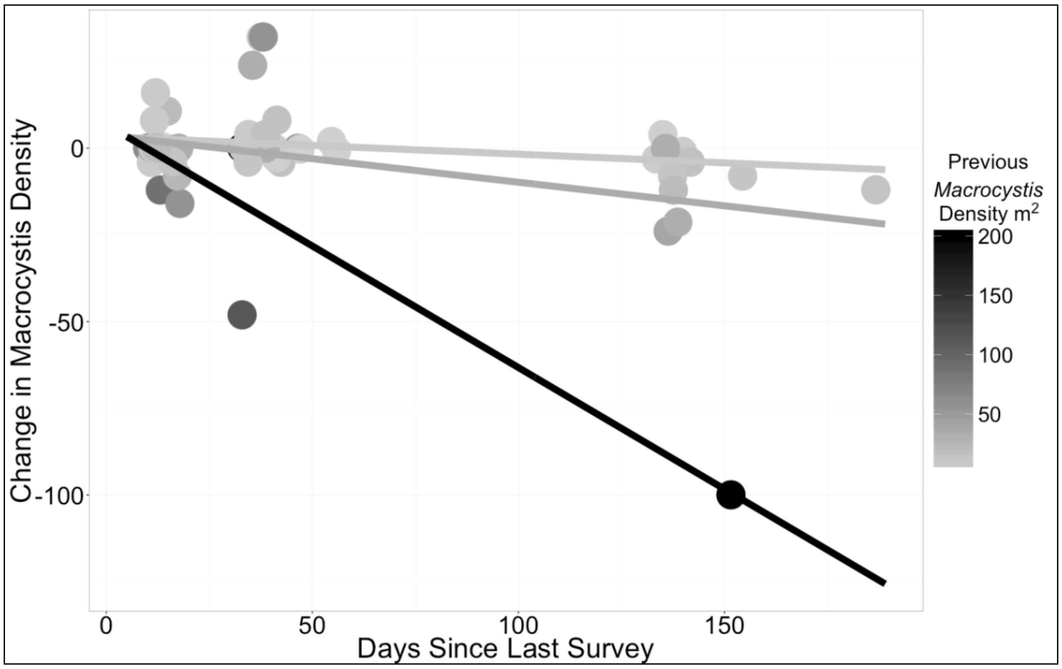

Figure 3.3. The effect of previous *Macrocystis pyrifera* density in each patch on the change in *Macrocystis pyrifera* density over the course of the study. Dots represent the change in *Macrocystis pyrifera* density that took place in each individual patch, and are colored according to initial patch densities. Patches that contained a low density of individuals are in light grey, patches that contained a medium density of individuals are in dark grey, and patches that contained a high density of individuals are in black.

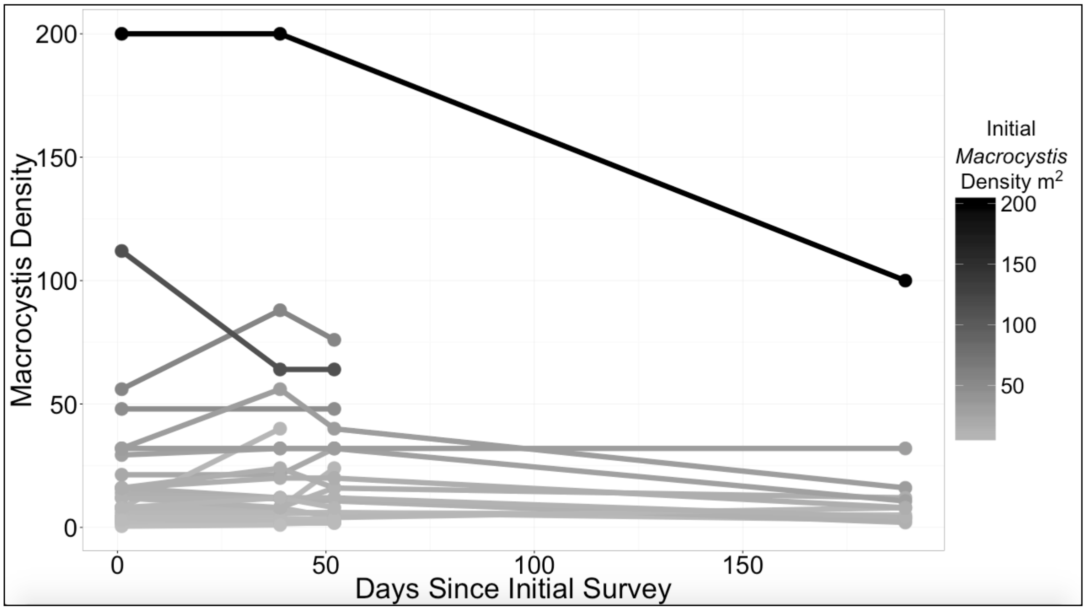

Figure 3.4. The effect of initial *Macrocystis pyrifera* density on final *Macrocystis pyrifera* density on all of the original 30 patches initially sampled. Several patches were lost over the course of the study period, or were unable to be relocated on the final survey date.

3.2 MEDIUM SIZE CLASS

Macrocystis pyrifera survival in all three medium size class densities, low (20 m^{-2}), medium (60 m^{-2}) and high (120 m^{-2}), exhibited negative exponential relationships with time that accounted for approximately 90% of the total variation in their survival ($R^2 = 0.897$). Early in the sampling, these juvenile *M. pyrifera* experienced low survival, especially in the low and high-density treatments (Figure 3.5). However, there were no differences in absolute number of survivors between treatments on the last day of the study (p-value = 0.562) i.e. treatments converged on the same density, likewise, the temporal patterns of survival were consistent among the three density treatments (ANCOVA: time x density interaction, p = 0.66). On the final day of the experiment, the surviving *M. pyrifera* density across all treatments was 8 m^{-2} (±4) regardless of their starting density, with temporal patterns of survival being consistent among the three density treatments (ANCOVA: time x density interaction, p = 0.66) (Figure 3.6).

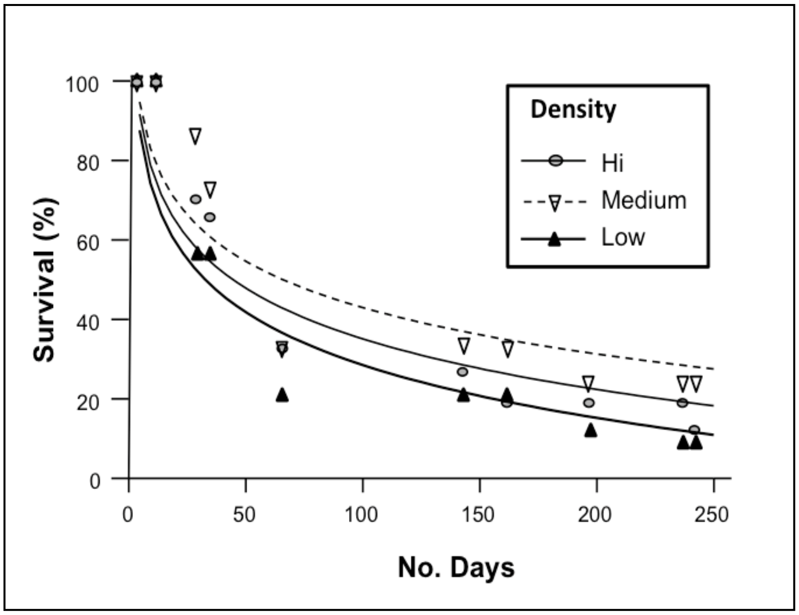

Figure 3.5. Percent survival of medium size class (5-25cm) juvenile *Macrocystis pyrifera* through time when outplanted to the Pt. Loma kelp forest at low (20 individuals m^{-2}), medium (60 individuals m^{-2}), and high (120 individuals m^{-2}) densities. Survival did not differ among the density treatments (ANCOVA: time x density interaction, P = 0.66) See Table 3.2 for regression equations for the percent survival of each density treatment.

Table 3.2. Medium Size Class Regression Equations

Treatment	Regression Equation	R^2
Low Density (20 m^{-2})	Survival = $11.48+99.51e^{(-0.024 \text{ x Julian Date})}$	0.95
Medium Density (60 m^{-2})	Survival = $15.64+96.65e^{(-0.018 \text{ x Julian Date})}$	0.87
High Density (120 m^{-2})	Survival = $13.79+95.46e^{(-0.018 \text{ x Julian Date})}$	0.95

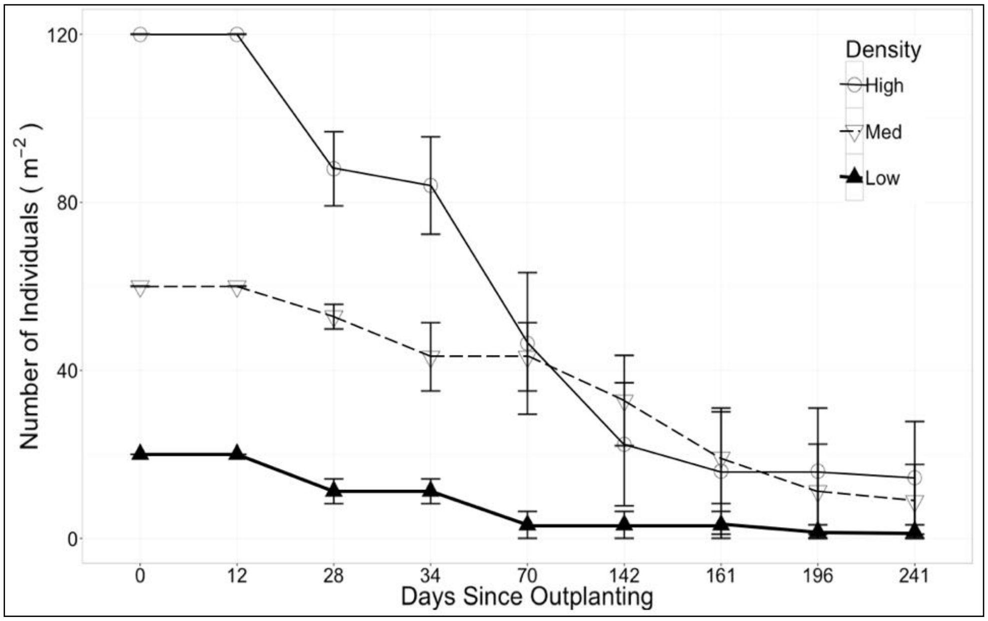

Figure 3.6. The number of surviving medium size class juvenile *Macrocystis pyrifera* m^{-2} (experimental mat 0.25 m^{-2}), according to density treatment over the course of the experiment. Bars indicate standard error.

3.3 LARGE SIZE CLASS

Juvenile kelp in the large size class (>1m in height) exhibited higher overall survival than those in the medium size class (5-25cm in height), especially during the first few weeks of the experiment (Figure 3.7). However, survival in all three density treatments within the large size class exhibited negative logistic/sigmoidal relationships with time that accounted for approximately 91% of the total variation in survival (R^2=0.905). As with the medium size class, overall patterns of temporal survival were consistent among the densities (ANCOVA time x density interaction, p-value = 0.99), and there was no difference in *M. pyrifera* density among the three density treatments on the final day of the study (p-value = 0.62) (Figure 3.8). Further, as with the medium-size class individuals, the large size class individuals also converged to similar final densities of 1 m^{-2} (±1), which is consistent with reports of *M. pyrfera* adult sporophyte density reported by Edwards (2004). Lastly, individuals from three plots in the medium-density treatment and three plots from the high-density treatment had reached the surface by the end of the study, and these had well-developed sporophylls.

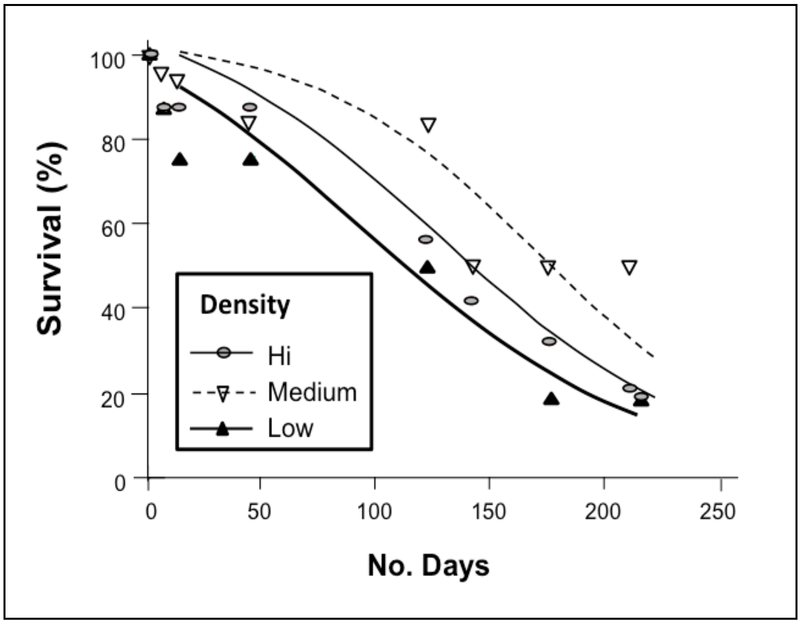

Figure 3.7. Percent survival of large size class (1m) juvenile *Macrocystis pyrifera* through time when outplanted to the Pt. Loma kelp forest at low (2 individuals m^{-2}), medium (4 individuals m^{-2}), and high (8 individuals m^{-2}) densities. Differential survival among treatments produced a P-value = 0.99. See Table 3.3 for regression equations for the percent survival of each density treatment.

Table 3.3. Large Size Class Regression Equations

Treatment	Regression	R^2
Low Density (2 m^{-2})	Survival = 107.94/(1+e$^{((0.016 \text{ x Julian Date})-96.29))}$	0.99
Medium Density (4 m^{-2})	Survival = 95.88/(1+e$^{((0.02 \text{ x Julian Date})-171.07))}$	0.78
High Density (8 m^{-2})	Survival = 104.21/(1+e$^{((0.017 \text{ x Julian Date})-126.329))}$	0.98

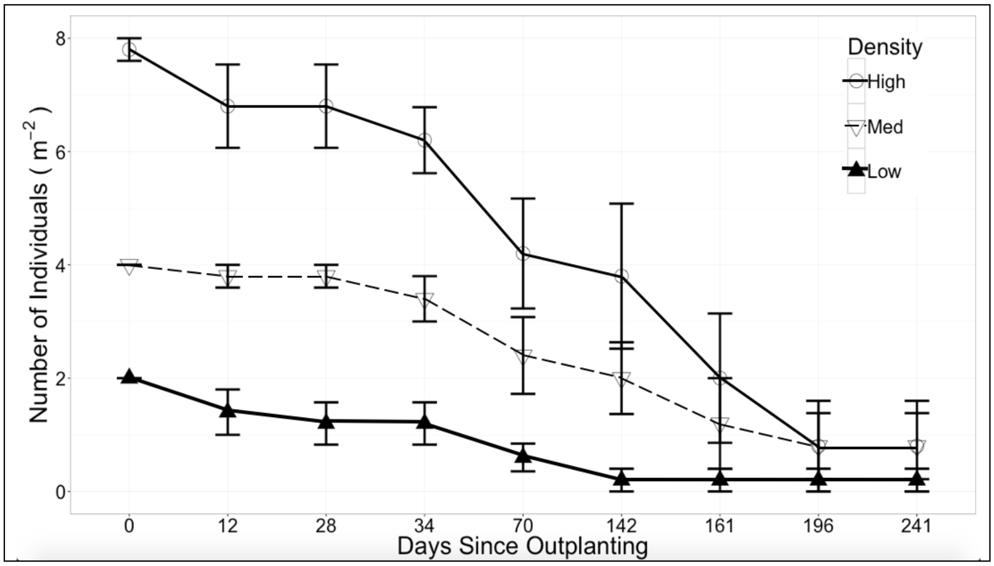

Figure 3.8. Number of surviving *Macrocystis pyrifera* per experimental plot ($1m^2$) according to density treatment over the course of the experiment. Bars indicate standard error.

CHAPTER 4

DISCUSSION

This study set out to determine how recruitment density impacts the survival of juvenile *Macrocystis pyrifera* as they grow to adulthood in the Point Loma kelp forest. In the first half of this study, the survival of juvenile *M. pyrifera* was monitored in naturally occurring patches of varying densities between July 2013-January 2014. We found that the initial density of co-occurring macroalgae in our monitoring patches had no measureable effect on *M. pyrifera* survival. However, when separated out from other macroalgae, the density of other juvenile *M. pyrifera* had a strong negative effect on *M. pyrifera* survival. This indicates density-dependent mortality (self-thinning) within patches of juvenile *M. pyrifera,* rather than interspecific competition is a crucial factor determining the final *M. pyrifera* within a patch. As a consequence, the initial *M. pyrifera* density within a patch did not appear to impact the final density within the patch, as all patches converged on a similar ending density regardless of their starting density (8 m^{-2} ±4 for the medium size class, and 1 m^{-2} ±1 for the large size class). This may help explain, at least in part, why *M. pyrfera* tends to occur at similar densities throughout its range (Edwards, 2004) .

The experimental study was used to further examine the relationship between initial patch density and final patch density using experimentally constructed patches of *M. pyrifera* at different stages of development. As with the monitoring study, initial density had no discernable impact on final density, regardless of the size of the juveniles examined. This suggests that juvenile *M. pyrifera* occurring in patches of higher density will thin at a faster rate than individuals occurring in patches of lower density, further supporting our hypothesis that *M. pyrifera* juveniles undergo density-dependent mortality until they reach a patch density sustainable by resources available at that time, and this density will be independent of their starting density. What density is appropriate for an individual or patch at any given time is likely dependent on several factors including individual size, ability to acquire resources, resource availability, grazer presence, and wave disturbance, among others and can be expected to change frequently with the fluctuation of these factors (Schiel and Foster 2015). This finding is analogous to the self-thinning documented for monospecific stands of terrestrial plants (Gorham, 1979; White, 1977). Interestingly adult *M. pyrifera* tend to be found regularly at densities of 0.1 m^{-2} throughout their geographic range along California and Mexico. Whether this ultimate density is a result of the large size that *M. pyrfera* obtains as adults (i.e. >30 m in height) remains unknown. However, Schiel and Choat (1980) found no evidence for self-thinning in the brown algae *Sargassum sinclairii* or *Ecklonia radiate,* while both *Pterygophora californica* and *Laminaria farlowii* are found in dense patches even as adults (M.S. Edwards, Personal communication; Reed, 1990b).

Our original hypothesis that juvenile *M. pyrifera* occurring at low densities would experience the greatest per capita survival due to a reduction in intra-cohort interactions (i.e. self-thinning) was supported by our data. Settlement density must be high enough to ensure that sexual reproduction by the resulting gametophytes can occur with high enough frequency to eliminate evolutionary costs of self-fertilization (Gaylord et al., 2006; Graham, 2003; Johansson et al., 2013; Raimondi et al., 2004; Reed et al., 1988). At the level of density required for reproduction and subsequent development of gametophytes and sporophytes, self-thinning is likely to happen due to a lack of available space for growing individuals and because irradiance and nutrient levels found in the kelp forest are unable to support these numbers. In patches with higher density, proportionally fewer *M. pyrifera* individuals survived to reach the surface. This finding is supported by prior research by Dean et al. (1989) who found that density-dependent mortality reduces the differences in intra-cohort survival among *M. pyrifera* juveniles. Additionally, patches with differing initial density eventually produced more similar numbers of adults than would be expected from a random survey of the population. Dean et al. (1989) estimate that a ten-fold increase in kelp recruitment would only produce a two-fold increase in survival. Similarly, Reed (1990a) found strong density-dependent mortality of zoospore with settlement densities above 10 mm^{-2}, despite the fact that maximum absolute recruitment was observed at 750 zoospores mm^{-2}. In the monitoring study, patches of varying initial densities appeared to converge on similar final densities over time regardless of their starting densities. This pattern was supported by our experimental results that showed no differences in final densities in the medium and large size-classes despite their varying initial densities when outplanted.

The theory of self-thinning, as derived from a terrestrial forestry perspective, suggests that the removal process is not random, but that it in fact removes the smallest or weakest members of the population first (White, 1977; White and Harper, 1970). Smaller or weaker individuals are unable to compete effectively with their more fit intra-cohort neighbors, and in the case of juvenile kelp, are more susceptible to dislodgement by wave surge (Dean et al., 1989). Antonovics and Levin (1980) predict that when stands of sessile organisms are not uniformly distributed, as in the recruitment of juvenile *M. pyrifera*, competition resulting in mortality will lead to fewer individuals than expected by chance in the immediate proximity of other individuals. Further, the high recruitment density of *M. pyrifera* cannot be sustained under naturally occurring conditions (Reed, 1990a; Reed et al., 1991). Density-dependent competition for resources, in addition to grazing, the whiplash effect of storm surge, warm-water stress, sediment burial, and entanglement, continuously reduces the randomly distributed juvenile patches to the regularly distributed stands found among mature populations of *M. pyrifera* throughout its range (Edwards, 2004). While we did not test for the traits that may lead to differential survival among individuals, this study did find that, in conjunction with other factors that affect the survival of juvenile *M. pyrifera*, self-thinning continuously alters the number of individuals within a patch, presumably to meet a density that can be sustained by the resources available at that time. As these individuals continue to grow larger into adult sporophytes, they will likely experience further thinning. This may explain why previous studies on M. pyrifera along the west coast of North America have observed the species to converge on a generalized density of 0.17 individuals m-2 regardless of recruitment densities or proximity to other species (Edwards, 2004).

As the pending threat of climate change includes predictions of more frequent, more intense storms (Reed et al. 2011), understanding the ecology of the entire life-history of *M. pyrifera* will be critical to both mitigating the consequences of these storms and applying effective restoration efforts. Kelp forests are generally able to recover from intense storms due to rapid recruitment processes and the span of time between large-scale events. However, if the frequency and severity of storms increase as predicted in conjunction with a warming ocean, kelp forest recovery may not be able to keep up (Byrnes et al., 2011). Transplanting juvenile kelp may be a useful tool in kelp forest restoration efforts, and the addition of nutrients as suggested by Hernández-Carmona et al. (2001) may help to quickly establish lost kelp forest communities. Our study found higher survival overall in the large size class outplants, likely because these individuals had already undergone the process of self-thinning that presumably reduced the number of smaller or weaker individuals. Therefore, future restoration efforts will benefit from transplanting larger individuals to areas that require rapid reforestation.

After 60 years of kelp forest research, we have made incredible strides in understanding the ecology of this ecosystem engineer. This study follows up on a legacy of kelp forest ecology in the southern California region that has documented the challenges to growth and survival faced by *M. pyrifera* and the communities that depend on its presence. Previous work has described the ecology of large, experimentally amendable *M. pyrifera* sporophytes in a natural setting (e.g. Aleem, 1956; Dayton, 1985; Dayton et al., 1984; Dayton and Tegner, 1984; Dayton et al., 1998, 1999; Dayton et al., 1992; Parnell et al., 2010; Seymour et al., 1989; Tegner and Dayton, 1987, 1991; Tegner et al., 1997) but our understanding of the ecology of the early life history stages is still lacking. Essential background information has been provided by numerous laboratory studies (Amsler and Neushul, 1989, 1990, 1991; Arzee et al., 1985; Carney, 2011; Carney and Edwards, 2006, 2010; Devinny and Volse, 1978; Deysher and Dean, 1986; Johansson et al., 2013; Kinlan et al., 2003; Lüning and Neushul, 1978; Reed et al., 1992; Reed et al., 1991, Sala and Dayton, 2011) but only a few studies have tested hypotheses in the field (see Table 1.1). Besides the current study, few field experiments have extended beyond one life history stage (e.g. Dayton et al., 1984). In this study, we found that density-dependent mortality differentially affects the different life history stages of *M. pyrifera*. While the effect of density-dependent mortality is similar across stages, the extent of its effect and the mechanism by which it exerts itself varies by size of the individuals. This highlights the importance of conducting studies with longer time scales in environments structured by perennial ecosystem engineers.

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