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UNIVERSITY OF SAN DIEGO

San Diego

The temporal and spatial dynamics of larval supply, settlement, and adult populations of *Chthamalus fissus* within the La Jolla, California rocky intertidal

A thesis submitted in partial satisfaction of the requirements for the degree of

Master of Science in Marine Science

By

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2018

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ABSTRACT

The role of post-settlement processes in benthic invertebrate recruitment dynamics has been well established; however, more recently, studies have been resolving the pre-settlement processes and environmental variables that may shape initial settlement. We examined the major space occupying barnacle *Chthamalus fissus* to determine the spatial and temporal dynamics of settlement in relation to larval supply, adult populations, and habitat characteristics (including elevation as a proxy for immersion, proximity to water's edge, and the availability of free space) within the La Jolla, CA rocky intertidal. With respect to habitat characteristics, we investigated the influence of available free space on the dynamics of settlement through intensification, defined as a higher concentration of settlers with less available free space. Six larval traps were deployed daily to quantify larval supply, 12-14 PVC plates were deployed daily or weekly to quantify settlement, and 12-14 surveys were conducted during new moon periods every month to quantify adults and habitat cover. There was temporal variability, specifically with high rates of settlement, and high percentages of adult populations and habitat cover occurring mainly in the summer periods. Spatially, of the 14 locations studied within the site, two locations exhibited some of the highest settlement rates when compared to larval supply or adults and habitat cover. There was a non-significant relationship between larval supply and settlement, suggesting that the environment played a more important role in shaping spatial and temporal population dynamics. Settlement, when compared with habitat cover, was primarily driven by available free space, which was

determined by live barnacle and algae cover. We observed the highest settlement when free space was lowest, demonstrating evidence of intensification within our site. These results suggest that in some cases habitat dynamics may play a more important role in shaping settlement than larval supply. Understanding the extent of this role may help to more holistically establish the dynamics that shape initial benthic invertebrate settlement. Therefore, understanding the role of the environment in shaping settlement dynamics of benthic invertebrates can help further inform the importance of rocky intertidal locations in contributing to coastal marine productivity and diversity.

CHAPTER 1:

LITERATURE REVIEW AND INTRODUCTION

Rocky intertidal communities

Intertidal ecosystems are unique marine ecosystems given their diverse habitat structure and species richness (Scrosati and Heaven 2007, Zwerschke et al. 2013). They provide a transition from marine to terrestrial habitats with attachment and refuge for a multitude of organisms in the form of exposed cliffs, boulders, rubble, or wave-influenced rocky shelves (Brandon and Rokop 1985). Within these communities are various marine algal, gastropod, cephalopod, chordate, cnidarian, and arthropod species (Brandon and Rokop 1985, Newman 1989).

Predominant benthic invertebrates within rocky intertidal communities include barnacle species, which have long been used as model species in ecological studies (Connell 1961a, b, Connell 1970, Dayton 1971, Paine 1974, Lubchenco and Menge 1978). For this research, given their presence in southern California, our study focused on *Chthamalus* spp. (*Chthamalus fissus*).

Individuals are common on rocks, pier pilings, and hard-shelled organisms along the west coast of North America from Alaska to Baja California. This species occupies higher regions in the intertidal than most due to its overlapping, exterior plate configuration allowing this organism to withstand longer periods of desiccation through controlled opening of the opercular valve (Barnes and Barnes 1957, Foster 1971). The periods of highest reproduction for *Chthamalus* spp.

occur during the spring to fall months, with limited reproduction in the winter season (Hines 1979). All barnacle species undergo similar stages of development throughout their life history.

Barnacle life history

Barnacle species have a meroplanktonic life cycle, similar to other marine benthic invertebrates which include planktonic larvae and sessile, benthic adults (Alexander and Roughgarden 1996) (Figure 1). Through fertilization and the brood period, the population size is dependent on biological (e.g., size of the adults and food availability) and physical (e.g., temperature) factors (Hines 1978). First-stage larvae, the shield-shaped nauplii, are released into the water column, and are transported offshore through physical oceanographic processes. During naupliar development, the larvae undergo 6 stages of molting, and then develop into cyprid larvae (known as “the settling stage”) (Høeg and Møller 2006). Cyprids have the ability to manipulate their vertical position in the water column (Tapia et al. 2010). However, within the intertidal immediately prior to settlement, cyprids are limited to small-scale swimming or crawling on their first antennae across the substratum to test for suitable attachment locations (Høeg and Møller 2006).

Cyprid selection of a settlement site is determined through the physical availability of substrate for settlement (Gaines et al. 1985, Pineda 1994) coupled with the chemical detection of the presence of conspecifics and predators (Raimondi 1988). Once cyprids are competent to settle, the first antennae, containing cement glands, attach to the substrate and the cyprid undergoes

metamorphosis becoming a juvenile barnacle. Juvenile barnacles steadily grow and mature over a period of weeks to months before reaching their adult size (Smith and Johnson 1996). Upon maturation, barnacles are an important biological component of the rocky intertidal serving as space occupiers and prey for predators including marine gastropods (e.g., periwinkle snails and whelks) (Brandon and Rokop 1985).

Benthic community ecology

Benthic ecology focuses on understanding how physical and biological characteristics shape the population dynamics of various benthic marine organisms. The rocky intertidal serves as a common location for the study of such dynamics given its diversity of benthic sessile invertebrates. Barnacles serve as a suitable model organism to understand how benthic invertebrate populations are established and structured within rocky intertidal communities. This suitability is due to their common presence throughout rocky intertidal regions worldwide.

Furthermore, their population dynamics can be tracked over time, through pre-settlement, settlement, and post-settlement processes. Factors influencing the establishment and subsequent structuring of benthic populations and communities within intertidal regions have often been separated into pre- and post-settlement processes (Paine 1966, Connell 1970, Pineda 1991, Alexander and Roughgarden 1996, Shanks 2005, Starczak et al. 2011). The aim of ecological research investigating the life histories of barnacles is to understand and resolve the factors that influence survival through reproduction and their impacts on population changes through time (Pineda et al. 2009).

Pre-settlement factors

In recent decades, pre-settlement processes have become more heavily addressed in the scientific literature, with the aim of understanding the physical and biological factors influencing the planktonic larval stage of marine organisms as it pertains to their population structuring (Todd 1998, Starczak et al. 2011, Pfaff et al. 2015). Pre-settlement processes affect the abundance of larvae, their delivery to adult habitats, and their settlement within adult habitats (Gaines et al. 1985, Farrell et al. 1991, Hughes et al. 2000, Starczak et al. 2011, Hoffmann et al. 2012, Pfaff et al. 2015). Understanding the influence of pre-settlement processes on early barnacle life history stages is a complex subject in that larval supply to adult habitats, or its operational equivalent, larval abundance near settlement sites, is influenced by factors affecting larval pool size, transport, and settling behaviors (Connell 1985, Pineda 2000) (Figure 2).

Overall, the population dynamics of marine species with a planktonic larval stage such as barnacles, are strongly influenced by interactions (e.g., larval transport) with their physical environment. Larvae develop offshore and are part of a “larval pool”. The larval pool may decrease in size due to either advection of larvae away from suitable habitats or through various physical transport processes transporting larvae to adult habitats (Farrell et al. 1991, Pineda 1991, Alexander and Roughgarden 1996, Connolly and Roughgarden 1998, Pineda et al. 2009, Tapía et al. 2010). A number of physical oceanographic features may function as larval transport mechanisms, including Stokes drift, wave events, and internal tidal bores (Pineda 2000, Gawarkiewicz et al. 2007). Upon arrival in the nearshore, larval

behavior influences the choice for a settlement location, based on the ability of cyprids to manipulate their vertical position within the water column to be retained in coastal areas (Pineda et al. 2010). Overall, the cyprids which are retained within the rocky intertidal will potentially contribute to the adult population.

The fraction of cyprids from the larval pool transported via pre-settlement processes, which are available for potential settlement within a given rocky intertidal location, is termed larval supply. There are several small-scale, intra-intertidal factors which influence larval settlement, the permanent adhesion on a hard substrate and metamorphosis of a cyprid to the juvenile stage. Settlement is the ecological interface linking pre- and post-settlement factors which culminates in the formation of adult populations (Pineda et al. 2009). During settlement, the microhydrodynamic conditions (the formation of microeddies along the shoreward faces of rocks creating small-scale currents within the rocky intertidal) coupled with the ability of cyprids to detect the chemical cues of their conspecifics given their gregarious nature, may influence the approximate location of a cyprid within the intertidal (Pawilk 1992, Pineda 1998, Pineda et al. 2009, Elbourne et al. 2011). Upon arrival within the intertidal, the amount of available substrate will influence the spatial area and temporal scale over which settlement will occur (Pineda 1994, Pineda and Caswell 1997, Pineda et al. 2010).

Events of intensification describe when less natural substrate is available for settlement, given the behavioral abilities of cyprids to search for suitable substrate, searching larvae will settle more intensively per unit area in the available substrate location (Pineda 1994, Pineda and Caswell 1997, Pineda et al. 2010).

Events such as these are termed the intensification effect (Pineda 1994, Pineda and Caswell 1997). As a result of this effect, seasonal and spatial variation in substrate variability may cause variability in barnacle larval settlement, further leading to patchiness of newly settled barnacles from season to season (Caffey 1985, Pineda and Caswell 1997, Pineda et al. 2010). Additional studies have investigated the intensification effect; when settlement reaches above a certain threshold it becomes more highly dependent on availability of space rather than larval availability (Pineda 1994, Jenkins 2005). For example, if two locations receive equal abundances of larval supply, but one location has more free space than the other, this may alter the patterns of settlement among these two locations (Bertness et al. 1992, Pineda and Caswell 1997, Jenkins 2005, Pineda et al. 2010). Specifically, when less space is available, there is a higher concentration of settlers within this available space (Pineda 1994, Pineda & Caswell 1997, von der Meden et al. 2012). By understanding the transition from larval supply to settlement and metamorphosis, we will better understand how larval input into an ecosystem modulates adult barnacle populations, and the overarching community processes within the intertidal (Alexander and Roughgarden 1996, Hughes et al. 2000, Jonsson et al. 2004).

Post-settlement factors

Research has also focused on identifying the post-settlement processes that impact juveniles and adults: predation, competition for space, disturbance by biotic and abiotic (e.g., desiccation via exposure to air) events, and positive interactions with the environment, including the space in which juvenile barnacles mature to

adults and reproduce (Stephenson and Stephenson 1949, Connell 1961 a, b, Paine 1966, Connell 1970, Dayton 1971, Connell 1985) (Figure 1). Classic investigations have revealed the specificity with which the above-listed factors determine the upper and lower limits of benthic invertebrates, specifically barnacle species. For example, through *in situ* observations and caging experiments, Connell (1961 a, b) found physical factors set the upper limits and a combination of biotic factors set the lower limits for species distributions when comparing *Chthamalus stellatus* and *Balanus balanoides*. These studies laid the framework for understanding rocky intertidal patterns of vertical zonation. To extend this theory, Paine (1966) established the role of predation in alleviating the intensity of competition in setting a species' lower limit, through predator removal events which led to localized extinctions of benthic invertebrate species including outcompeted *Balanus glandula*. Alternatively, Wethey (1983) furthered understanding of the geographic and zonation boundaries of *Balanus* spp. and *Chthamalus* spp. Specifically, the upper limit of *Balanus* spp. is set according to where this species can withstand the stresses of desiccation (Wethey 1983).

Within the rocky intertidal, a suite of physical and biological factors influences the distributions of organisms across environmental gradients (Beukema and Flach 1995), which may impact the long-term sustainability of these ecosystems (Alexander and Roughgarden 1996). The upper limits of species distributions are commonly set by physical factors (i.e. tolerance to desiccation or heat), whereas the lower limits are commonly set by biological interactions (i.e. interspecific competition for space, selective predation, and tidal disturbance)

(Connell 1961 a, b, Connell 1970). Post-settlement factors shape the dynamics of juvenile and adult barnacle populations and communities. However, these dynamics are influenced by the variability in recruitment of larvae across spatial and temporal time scales, tying these processes to pre-settlement processes (Connell 1985). Therefore, the impacts of pre- and post-settlement factors on shaping barnacle populations varies across time and space depending on the geographic location and physical parameters of a given ecosystem. Our study will focus on settlement and post-settlement factors with respect to their role in shaping rocky intertidal populations of barnacle species.

Main objectives

By studying the life history of barnacles from the larval stage through to development of adult populations, the interface between pre- and post-settlement processes can be further understood with respect to its role in structuring benthic invertebrate populations, specifically barnacles within the rocky intertidal (Pineda et al. 2009, Starczak et al. 2011). The spatial and temporal distribution of the life history stages of various barnacle species may help to extrapolate general life history patterns and distributions of other intertidal organisms with a two-phase meroplanktonic life cycle. In the past several decades studies investigating the role of larval input on the dynamics of rocky shore communities, known as “supply-side ecology” have increased in prevalence (Pineda et al. 2010). To understand the potentially non-linear relationship between larval supply, settlement, and adult populations, each factor must be studied separately and compared to the others to gain a comprehensive understanding of the life history of these marine

invertebrates. The questions I sought to answer, focusing on *Chthamalus* spp. within the Bird Rock rocky intertidal of La Jolla, CA, are:

1. How do larval supply (# of cyprids per trap per day), larval settlement (# of cyprids and metamorphs per plate per day), and adult populations (# of living versus dead barnacles) and habitat characteristics (% free space per cm² per month) vary temporally across a two year period?

- H₀: There will be no change in larval supply, larval settlement, and adult populations within seasons (spring-summer and fall-winter) across a two-year period.

2. How do larval supply (# of cyprids per trap per day), larval settlement (# of cyprids and metamorphs per plate per day), adult populations (# of living versus dead barnacles), and habitat characteristics (% free space per cm² per month) vary spatially within the study site?

- H₀: There will be no change in larval supply, larval settlement, and adult populations within the study site.

a) Are there spatial differences with respect to larval supply (# of cyprids per trap per day) and larval settlement (# of cyprids and metamorphs per plate per day)?

- H_0 : Larval supply and larval settlement are not correlated with one another.

b) If there are intra-site differences in larval supply (# of cyprids per trap per day) and larval settlement (# of cyprids and metamorphs per plate per day), how do they relate to habitat suitability with respect to % free space?

- H_0 : There is no association between larval supply, larval settlement, and % available free space within the study site.

CHAPTER 1 FIGURES

Figure 1. General life history of barnacle species from development in the coastal ocean through recruitment in the rocky intertidal (Hines 1978, Pechenik et al. 1998).

ROCKY INTERTIDAL

Figure 2. Processes influencing recruitment in bottom-dwelling species, as previously described in Pineda (2000).

CHAPTER 2:

Decoupling of larval supply and settlement and the potential habitat factors which influence settlement of *Chthamalus fissus* across space and time in the rocky intertidal of La Jolla, California, USA

ABSTRACT

The rocky intertidal contains a diversity of benthic, sessile invertebrates including the barnacle *Chthamalus fissus*, a primary space occupier. Barnacles serve as ideal model organisms for understanding the influence of pre- and post-settlement processes on the structure of intertidal populations. We examined the spatial and temporal dynamics of larval supply and settlement, their relationship, and how habitat characteristics (i.e. elevation as a proxy for immersion, proximity to the water's edge, and availability of free space) shaped settlement within the La Jolla, CA rocky intertidal. First, we deployed 6 larval traps to quantify the rate of daily larval supply, and 6 PVC settlement plates to quantify the rate of daily settlement in the Spring-Summer of 2014 and 2015. Secondly, we deployed 12 settlement plates from November 2014 to December 2015 and 14 plates from December 2015 to December 2016 to measure daily or weekly settlement, with monthly adult surveys conducted throughout this period. Settlement rate was higher in 2014 compared to 2015, with variability among settlement plate locations. Highs and lows in both larval supply and settlement corresponded across locations measured for a sample period. However, there was a limited relationship between larval supply and settlement. The decoupling between larval supply and settlement may result from the primary role the environment of the

nearshore plays in shaping each life history stage independent of one another in the La Jolla rocky intertidal. Settlement was minimally related to elevation as a proxy for immersion and not related to proximity to water, indicating these habitat characteristics play a less substantial role in shaping *C. fissus* settlement.

However, a negative relationship between settlement rate and available free space provided support for the intensification effect, and free-space was driven by live barnacle and algae cover. This research suggests that, in addition to larval supply, local environmental processes or characteristics determine settlement of benthic invertebrate populations.

INTRODUCTION

The study of intertidal systems has contributed disproportionately to understanding community ecological processes including competition (Connell 1961 a, b), predation (Lubchenco & Menge 1978, Menge 1983), disturbance (Dayton 1971), and the role of larval supply (Lewin 1986, Minchinton & Scheibling 1991). Within these systems, benthic invertebrates such as barnacles serve as primary space occupiers, compete with other sessile organisms for space, are important prey, and contribute to community structure (Dayton 1971, Lubchenco & Menge 1978, Chan et al. 2008, Zwerschke et al. 2013). Settlement and recruitment serve as fundamental processes in building the population dynamics and distributions of such species, acting as a pelagic-benthic transition between the larval and juvenile stages (Hatton 1938, Connell 1985, Gaines & Roughgarden 1985, Carlon & Olson 1993, Pineda et al. 2009). Settlement is the

transition from a planktonic larva and includes the processes of habitat selection, permanent adhesion to a substrate, and metamorphosis to the benthic, juvenile stage (Pawlik 1992). Settlement rate (S) is usually defined in units of # of larvae per unit area per time (e.g., # larvae / cm² day) (Pineda and Caswell 1997, Pineda et al. 2010).

The investigation of settlement dynamics is helpful to understand mechanisms of larval transport which supply populations with new individuals or recruits (Pineda 1994, Wing et al. 1995). Previous studies have suggested that processes influencing settlement dynamics include: a) adjusting settlement for immersion time to account for tidal fluctuations (Jarrett 1997, Shanks 2009), b) proximity to water (Gaines et al. 1985), c) free space for settlement (Gaines and Roughgarden 1985, Pineda 1994), d) larval behavior (Crisp and Meadows 1962, Pawlik 1992, Satumanatpan & Keough 2001, Jenkins 2005), e) small-scale hydrodynamics (Crimaldi et al. 2002), and f) cannibalism (MacIsaac et al. 1991). Specifically, this research focuses on the dependence of settlement rate on the number of larvae near a settlement site, termed larval supply (Marshall et al. 2009, Pineda et al. 2010), and free space and the characteristics of the benthic habitat where larvae settle (Chabot & Bourget 1988, Pineda & Caswell 1997).

Understanding pre-settlement processes that influence early barnacle life history is a complex subject in that larval abundance or supply near settlement sites is influenced by a multitude of factors affecting larval pool size, transport, and settling behavior (Connell 1985, Pineda 2000). Specifically, the relationship between larval supply and settlement is complex, as some studies have indicated a

clear correlation, where larval supply predicts settlement (Minchinton and Schiebling 1991, Ross 2001, and Ma 2005), while other studies found no correlation between these two life history stages (Miron et al. 1995, Olivier et al. 2000, Rilov et al. 2008). The study of this transition is important to better understand how larval input modulates barnacle populations and community processes within the intertidal (Alexander and Roughgarden 1996, Hughes et al. 2000, Jonsson et al. 2004).

Most settlement studies addressing population dynamics and distribution emphasize the importance of larval supply (which determines the # of larvae in calculating settlement rate). Few studies have addressed the importance of the benthic characteristics of the habitat area and the time interval when settlement is measured (which determines the area and time when calculating settlement rate), and substrate characteristics are often ignored (but see von der Meden et al. 2012). A series of recent studies have considered surf-zone width and characterized dissipative versus reflective beaches to examine the relationship between surf-zone hydrodynamics and settlement (e.g., Shanks et al. 2017, Morgan et al. 2018). While these studies have demonstrated higher settlement on dissipative compared to reflective beaches (Shanks et al. 2017, Morgan et al. 2018), they do not consider confounding effects; on dissipative beaches, where rock patches are usually surrounded by uninhabitable areas of sand, there should be less available substrate for settlement, which could act to intensify settlement (Morgan et al. 2018: Figure 8a, 8b from this article). When habitat availability is limiting, particularly for intertidal invertebrates, the settlement of individuals

increases (e.g., Bertness & Gaines 1993, Pineda 1994, Osman & Whitlatch 1995a, Pineda & Caswell 1997, von der Meden et al. 2012) and is termed the intensification effect (Pineda 1994, Pineda and Caswell 1997). Thus, it is important to consider the benthic characteristics of the substrate, and how they vary across a site when characterizing settlement patterns.

Research studies exploring spatial variability in settlement within intertidal shores (at few to 100 m scales) have considered three fundamental processes relating to the substrate. First, the result of spatial variation or patchiness in settlement is influenced by less free space (Gaines & Roughgarden 1985, Minchinton & Scheibling 1993, Pineda 1994, von der Meden et al. 2012, Scrosati & Ellrich 2017). Secondly, the settlement dynamics of proximity to water indicate that sites closer to the water's edge receive more settlement (Gaines et al. 1985). The theory of proximity to water was supported by research that demonstrated the first suitable settlement sites encountered depleted larval supply to downstream sites, known as settlement shadow (Gaines et al. 1985). Finally, researchers assume the longer a settlement substrate is immersed in water, the more larval supply may be available for settlement (Minchinton and Scheibling 1991). Operationally, this is accomplished by standardizing settlement by immersion time (Minchinton & Scheibling 1991, Jarrett 1997, Brown & Swearingen 1998, Satumanatpan & Keough 2001, Shanks 2009; but see Hatton 1938).

The extent to which these settlement processes and habitat characteristics influence a benthic population can help further inform the interaction of life

history stages with one-another and the environment during the settlement of new individuals. Previous research suggests a discrepancy in the relationship between larval supply and settlement (Satumanatpan and Keough 2001, Jenkins 2005, Pineda et al. 2010). Investigating the dynamics of this disconnect may further help inform the role which the rocky intertidal habitat or environment (e.g., intensification, elevation as a proxy for immersion, and proximity to water) plays by influencing the early development of *C. fissus* and other benthic invertebrate populations (Minchinton and Scheibling 1991). This study addresses the following questions:

- (a) What are the temporal (across sample periods) and spatial (few to 10's m) patterns in the variability of larval supply and settlement?
- (b) Do locations that receive higher larval supply result in higher settlement?
- (c) What are the temporal (weeks to years) and spatial (few to 10's m) patterns of settlement, as shaped by the benthic habitat? Are there consistent trends where some sites get more settlement than others, and are these trends persistent in time and space?
- (d) Are these trends related to the intensification effect (do settlement sites surrounded by less suitable substrate for settlement receive more

settlement), proximity to water or immersion time (do settlement sites closer to the edge of the water and/or immersed for a longer time-period receive more settlement)?

MATERIALS AND METHODS

Study Site

We examined the temporal-spatial dynamics of *Chthamalus fissus* larval supply, settlement, adult populations and habitat characteristics during a 2-year period in the rocky intertidal of Bird Rock, La Jolla, California, USA (Figure 1A). Bird Rock was selected for study because of the abundance of *C. fissus* adult barnacles and ample rocky intertidal habitat. This site is characterized by a gently-sloping intertidal shore, mainly consisting of cobbles and boulders with sizes ranging from 50-200 cm and a semidiurnal tide with a vertical range of -0.87 to 0.76 m. The rocky intertidal extends along the coast for ~ 575 m to the south before transitioning to a sandy beach. To the north of our site are ~ 100 m of loose cobble beaches interspersed with sandy pocket beaches, where there is no habitat for barnacle settlement.

C. fissus was the most abundant barnacle species at our site (Hagerty et al. 2018). *C. fissus* larvae develop in the coastal ocean over a period of weeks, passing through six naupliar stages before developing into a cyprid stage (Brown & Roughgarden 1985). Cyprids must return to the nearshore, find suitable habitat, settle, and undergo metamorphosis to the early juvenile stage to complete the initial phases of the barnacle life cycle (Pechenik et al. 1998).

Larval Supply and Settlement

To compare larval supply and settlement, we established 8 locations within our study site where larval supply and settlement were concurrently measured (Figure 1B). Larval supply and settlement were measured daily at locations 3, 7, 8, 9, 12, and 14 during June 16 to July 16, 2014 (referred to as ‘2014’) and during April 24 to June 5, 2015 (referred to as ‘2015a’). However, study locations were altered during June 6 to August 2, 2015 (referred to as ‘2015b’), after larval traps (described below) at locations 3 and 8 were lost and had to be re-established at new locations: 1, 2, 7, 9, 12, and 14 (Figure 1B).

We deployed 6 cylindrical PVC larval traps modeled after those described in Chen et al. (2013) during the lowest low tide at locations approximately 0.66 to 12.6 m west from each settlement location to measure larval supply. Traps measured 18.2 cm high by 8.7 cm in diameter and the interior consisted of a segmented funnel that emptied into a 100 μ m mesh collection net (Appendix A). Rate of larval supply was estimated as the number of *C. fissus* and *Balanus glandula* cyprids collected per trap each day. The 2014 raw samples were sorted using a Meiji Techno RZ stereo microscope (3.75x-300x magnification). Barnacle cyprids by species and nauplii by stage (early vs late stage) were quantified. In spring-summer 2015, the traps collected substantial volumes of sand. Therefore, to facilitate further sorting, each sample was first stained with a rose Bengal and 100% ethanol solution. The sediment was then removed from the samples through a multi-step dilution. This process started by pouring a sample into a 1 L beaker, then water was added until the beaker was nearly full, and the sand particles were

left to settle to the bottom. The water from the sample was decanted through a 100 μm mesh sieve and the above process was repeated until the water in the beaker was clear with no visible plankton retained on the mesh. The resulting sample was then reviewed in its entirety using the same method as the 2014 samples.

Daily settlement was measured by deploying settlement plates on rocks adjacent to larval traps during the lowest low tide (with the distances between described above). The tops of the larval traps and center line of the settlement plates were deployed at approximately the same elevation (average elevation of all traps and plates was 0.4 m relative to mean lower low water (MLLW), with a range of 0.3 m to 0.5 m relative to MLLW) (Appendix B). Settlement rate, the number of individuals per cm^2 per day was measured using PVC settlement plates (as in Pineda 1994) with three grooves that provided 1.9 cm^2 (each ~95 mm long, 6 mm wide, 1 mm high) (Appendix C). Plates were processed using a Meiji Techno RZ stereo microscope (3.75x-300x magnification) to identify barnacle metamorphs (newly metamorphosed juveniles) to species.

Larval supply and settlement records did not meet the assumptions of parametric statistical tests, thus a Wilcoxon rank sum test with a continuity correction was used to determine if larval supply and settlement were different between 2014 and 2015. To investigate intra-site differences in larval supply and settlement, a Friedman's test with a multiple pairwise comparison using Nemenyi's procedure/two-tailed test was conducted to identify differences in each variable across locations within the site, by sample period. The relationship

between $\log(x+1)$ transformed larval supply and raw settlement was examined using a linear regression analysis in R-studio.

Settlement and Habitat Characteristics

To further compare settlement dynamics with respect to habitat characteristics, we measured the following variables at the 14 locations established within the site (Figure 1C). *C. fissus* settlement (# of individuals per $\text{cm}^2 \text{ d}$) was measured from April 2014 to December 2016 using the same PVC settlement plates described above. These plates were oriented along the contours of the rocks within the site and were collected and replaced at the lowest low tide of each day, then plates were processed as described above. Plates were collected at both daily and weekly timescales depending on the time of year and accessibility of the site due to the tides (Table 1); all settlement however, was reported as a daily rate. From April 24, 2014 to June 5, 2015, 12 plates were deployed along boulders within ~50 m area along our study site (plates 3-14; Figure 1C). Then, to further test for the intensification effect, two additional plates (plates 1-2; Figure 1C) were also deployed for a total of 14 plates from June 6, 2015 to December 15, 2015 along the northernmost edge of the study site where suitable adult habitat was more limiting.

From daily and weekly settlement rates, monthly *C. fissus* settlement rate (# of individuals per $\text{cm}^2 \text{ d}$) was calculated by taking the average settlement rate for all plates deployed during each 30-day period leading up to the dates of the adult/habitat surveys (Table 1). To meet the criteria of calculating settlement for the 30 days prior to each survey, a minimum of 15 days of daily-collected

settlement, three weeks of weekly-collected settlement, or a combination of both daily and weekly minimums were necessary. As such, May 2015, September 2015, and March 2016 were excluded from our analyses as settlement collections during these months did not meet the minimum requirements (Table 1). Because settlement from weekly sampling was lower than daily settlement, we used the regression describing the relationship between daily and weekly settlement previously established for our site (Pineda et al. in press). This regression was used to convert settlement data collected daily and averaged for the week, to weekly settlement values (weekly settlement, $y = 0.657x$, when daily settlement $(x) \leq 25.7$ individuals and $y = 11.17 + 0.22x$ when daily settlement > 25.7 individuals) (Pineda et al. in press). The raw weekly values and/or daily-collected converted to-weekly values were then used to calculate monthly-averaged settlement (average # settlers per cm^2 d) for the remaining 21 months of complete data for each location (Table 1).

To understand how the distribution and cover of adult *C. fissus* populations and habitat characteristics varied across the site, monthly surveys were conducted from December 2014 through December 2016 during new moon periods at the lowest low tide when the entire intertidal was accessible (Table 1). A 4 x 4 cm quadrat was haphazardly placed on top of the same rocks where settlement plates were deployed. Within the 16 cm^2 area of the quadrat, percent cover of free space, live barnacles, dead barnacles, and algae were quantified by sampling 30 randomly selected (x, y) points within the quadrat (Appendix D).

The elevation of plates 1 - 14 were measured in April 2017 using a Trimble R10 GNSS system which used a minimum of 5 satellites to obtain an average elevation (in meters) of the bolt at which each settlement plate was fastened to the boulder. These elevations were calculated by using the averages of the satellites to calculate the altitude of a specified position measuring how far away the position is from the satellites. Additionally, the position of each settlement plate relative to the water was determined in Google Earth Pro. From a satellite images of the research site, the longitude of plate 8 was used as a reference line, given this plate's closest proximity to the water (Google Earth 2016) (Figure 1). The distance between each location's longitude and the reference line was then calculated.

Given collinearity (variance inflation factor, $VIF > 5$) among habitat characteristics (percent free space, live barnacles, dead barnacles, and algae), we used separate linear regressions to examine the relationship between monthly-averaged *C. fissus* settlement and each individual monthly-averaged habitat characteristic. To meet the assumptions of normality, we applied a log-transformation to the settlement record, and a hyperbolic arcsin-transformation to the percent cover of dead barnacles and algae. The percent free space and percent cover of live barnacles met assumptions of normality without need of transformation.

To identify which habitat characteristic best explained the variability in settlement, we assessed AIC and R^2 values following Burnham & Anderson (2002). A second-order corrected AIC (AIC_c ; used when $n < 40$) and Akaike

weights were calculated to select the most parsimonious regression model describing the relationship between barnacle settlement and habitat characteristics (Burnham & Anderson 2002). We also used this approach to assess the relationship between percent free space (the best-fit regression model explaining settlement variability), and the remaining habitat characteristics (percent cover of live barnacles, dead barnacles, and algae) to better understand the dynamics influencing percent free space within the rocky intertidal.

To examine consistency or intra-site variability in settlement, we calculated the average settlement per plate and average proportion of settlement per plate separately for the time periods corresponding to when 12 and 14 plates were deployed. Our data violated the assumptions of parametric tests despite transformation, thus a Friedman's test was used to determine if settlement differed among plates. Post-hoc pairwise comparisons using Nemenyi's multiple comparison tests were used to determine which plates were significantly different from one another. Pearson's product-moment correlations were also used to examine the relationship between the average proportion of settlement by plate in 2014 versus 2015, and the average proportion of settlement by plate with respect to plate elevation and proximity to water.

RESULTS

Larval Supply and Settlement

Temporal patterns of larval supply and settlement

Larval supply and settlement were higher in 2014 than 2015, with little to no larval supply observed in 2015 (Table 2). Additionally, the majority of cyprids and metamorphs collected were *Chthamalus fissus* (Table 2). There were significant differences between 2014 and 2015 for early-stage nauplii (Wilcoxon rank sum test, $W = 63851$, $p < 0.0001$), *C. fissus* cyprids (Wilcoxon rank sum test, $W = 31949$, $p < 0.0001$), *Balanus glandula* cyprids (Wilcoxon rank sum test, $W = 22140$, $p = 0.01$), other cyprid species (Wilcoxon rank sum test, $W = 22415$, $p < 0.001$), and *C. fissus* metamorphs (Wilcoxon rank sum test, $W = 319528$, $p < 0.0001$).

Spatial patterns of larval supply and settlement

Larval supply was temporally variable; however, peaks in larval supply were synchronous across traps, particularly during summer 2014 and 2015a (Figure 2A, 2B), but not in 2015b (Figure 2C). Larval supply was not significantly different by trap during all sample periods (Friedman's test, with all p -values > 0.05) (Figure 2A, 2B, 2C). Settlement was also temporally variable (Figures 2D, 2E, 2F). There were significant differences in settlement across plates for 2014 (Friedman's test, $Q = 58.69$, $df = 5$, $p < 0.0001$), 2015a (Friedman's test, $Q = 80.05$, $df = 5$, $p < 0.0001$), and 2015b (Friedman's test, $Q = 75.74$, $df = 5$, $p < 0.0001$; Figure 2D, 2E, 2F). Thus, settlement was ranked by location, and fell into three groups based on similarity of ranks in 2014 (Table 3),

four groups in 2015a (Table 4), and two groups in 2015b (Table 5). In all three periods, settlement was highest at locations 7 and 9 and lowest at locations 12 and 14 (Tables 3, 4, and 5).

Relationship between larval supply and settlement

The relationship between larval supply and settlement was highly variable across each sample period (2014, 2015a, and 2015b) and 8 locations (Figure 3A, 3B, 3C). In 2014, there was a positive relationship between average larval supply and settlement by location, however, this relationship was non-significant (Linear regression, $R^2 = 0.46$, $p = 0.14$; Figure 3A). When examined by location, larval supply was significantly related with settlement only in 2014, when larval supply was high, at location 4 ($R^2 = 0.31$, $p = 0.001$), location 7 ($R^2 = 0.24$, $p = 0.005$), and location 8 ($R^2 = 0.14$, $p = 0.03$). In 2015a, there was a non-significant relationship (Linear regression, $R^2 = 0.18$, $p = 0.40$; Figure 3B), while in 2015b there was a marginally significant negative relationship (Linear regression, $R^2 = 0.69$, $p = 0.03$; Figure 3C) between average larval supply and settlement across locations. Based on these results we further investigated the relationship between settlement and the habitat characteristics.

Settlement and Habitat Characteristics

Relationship between settlement and tidal related factors

There was a weak non-significant positive correlation between average proportional settlement and elevation, a proxy for immersion time ($R = 0.56$, $p = 0.06$; Figure 4A), and no correlation between average proportional settlement and proximity to water ($R = -0.23$, $p = 0.47$; Figure 4B).

Temporal patterns of settlement and adults/habitat cover

Monthly-averaged settlement rate varied with time. Settlement was low during the winter to early spring months (December through March), with slight increases during summer and fall 2015. The highest settlement occurred in July to October 2016 (Figure 5A). Monthly-averaged percent free space was high during the winter to late spring months (December through May), decreased during the summer through September, before increasing again in the fall through the winter (Figure 5B). Monthly-averaged percent cover of live barnacles was highest during the summer months (June through August), but sharply decreased in September of both 2015 and 2016 (Figure 5C). The monthly-averaged percent cover of dead barnacles was low ($< 10\%$) during December 2014 to November 2016; but increased from September to November in both 2015 and 2016, corresponding to the periods of low percent cover of live barnacles (Figure 5C, 5D). Monthly-averaged percent cover of algae varied more than percent cover of dead barnacles; but was greatest in September of 2015 and 2016 (Figure 5E).

Relationship between settlement and free space

Of the habitat factors examined, variability in monthly-averaged *C. fissus* settlement was best explained by monthly-averaged percent free space. This model had the lowest AIC_c, and a 92% probability of being the correct model of all candidate models; given the evidence ratios > 10 , models with percent cover of live barnacles, percent cover of dead barnacles, and percent cover of algae were not deemed suitable (Table 6). *C. fissus* monthly-averaged settlement was significantly negatively correlated with monthly-averaged percent free space for

all settlement plates (range of R^2 values from 0.05 to 0.47, $p < 0.05$) except at locations 2, 4, 5, 10, and 11 (Figure 6), and when monthly settlement (log-transformed) and percent free space were averaged over all plates ($R^2 = 0.55$, $p < 0.001$; Figure 7).

Relationship between free space and live barnacle and algae cover

Percent free space was not related to percent cover of live barnacles ($R^2 = 0.05$, $p = 0.31$; Figure 8A) or percent cover of dead barnacles ($R^2 = 0.02$, $p = 0.46$; Figure 8B), but there was a negative relationship with percent cover of algae ($R^2 = 0.56$, $p < 0.001$; Figure 8C). Variability in monthly-averaged percent free space was best explained by the model that included percent cover of live barnacles and algae (62% probability of being the best model; Table 7). While the model including percent cover of live barnacles, dead barnacles, and algae had a 37% probability of being the best model, the evidence ratios < 2.0 for both these models provided insufficient evidence to suggest that one model was better than the other in explaining variability in percent free space. To further refine which explanatory variables best explained the variability in percent free space, we ranked the relative importance of possible explanatory variables. Percent cover of algae (100%) and percent cover of live barnacles (99.95%) had greater relative importance in explaining the variability in percent free space than percent cover of dead barnacles (37.04%; Table 8). Thus, we accepted the model including percent cover of live barnacles and algae as the best model explaining the variability in percent free space ($R^2 = 0.81$, $p < 0.001$).

Intra-site spatial patterns of settlement

C. fissus settlement varied within our site in the rocky intertidal. When settlement (average # per cm² d or proportion of settlers) was compared by plate for the time period that 12 plates were deployed, plates 3, 7, and 9 had the highest settlement, and plates 5 and 6, had the lowest settlement (Figure 9A). For the period that all 14 plates were deployed, plates 1 through 3, 7, and 9 had the highest settlement and plates 4 through 6 had the lowest settlement (Figure 9B). Further, there was a strong positive correlation between the proportion of *C. fissus* settlement on plates deployed in 2014 versus the proportion of settlement on plates deployed in 2015 ($R = 0.77$, $p = 0.002$; Figure 9C). There was a significant difference in settlement among plates at our site for both the 12-plate deployment period (Friedman's test: $\chi^2 = 19.67$, $p < 0.001$; Table 9) and 14-plate deployment period (Friedman's test: $\chi^2 = 22.36$, $p < 0.001$; Table 10). Multiple pairwise comparisons confirmed that plate 9 was ranked with the highest settlement and plate 6 was ranked with the lowest settlement, during both the 12-plate (Figure 10A) and 14-plate (Figure 10B) deployment periods. Settlement was also high at plate 3 (nearest the northern boundary of the settlement plate locations) during the 12-plate deployment period (Figure 10A, 10B). However, plate 2 was ranked with equally-high settlement as plate 3 during the 14-plate deployment period (Figure 10A, 10B).

DISCUSSION

Settlement processes and environmental factors influence early life history of benthic species, playing an important role in shaping populations (Fraschetti et

al. 2002). Many studies have investigated the influence of settlement processes and environmental factors on barnacle species' populations within the rocky intertidal (Farrell et al. 1991, Bertness et al. 1992, Olivier et al. 2000, Jenkins 2005, Pineda et al. 2010, Rivera et al. 2013). Specifically, some studies addressed the dependence of settlement rate on larval supply (Miron et al. 1995, Ross 2001, Pineda et al. 2010); however, processes influencing settlement habitat can also influence settlement rate (Gaines and Roughgarden 1985, Lewin 1986, Pineda 1994, Eckman 1996, Hoffmann et al. 2012). We examined the relationship between larval supply and settlement, and the influence of habitat elevation, proximity to water, and percent of available free space on settlement.

For both larval supply and settlement, *C. fissus* was the dominant species within our site in the spring-summer and therefore contributed most heavily to the adult populations, as previously observed in nearshore waters off La Jolla (Tapia and Pineda 2007, Hagerty et al. 2018). When comparing larval supply and settlement in the summer of 2014 relative to those measured in the summer of 2015, the rates of larval supply and settlement were higher in 2014 for each of the major categories of organisms collected: early stage nauplii, *Chthamalus fissus*, *Balanus glandula*, other species cyprids, and *Chthamalus fissus* metamorphs. The difference in the magnitude of values for 2014 versus 2015 may have been due to conditions being more conducive for larval transport, providing a larger availability of larvae within the water column in 2014. Other studies observed similar decreases in larval counts from 2014 to 2015 within the southern California coastal region (Basilio et al. 2017, Hagerty et al. 2018). Larval

decreases may have been due to the prominence of the warm blob event in San Diego towards the end of 2014 (Basilio et al. 2017, Pineda et al. in press), or El Niño in 2015 (McClatchie et al. 2016). Changes in sea surface temperature associated with El Niño can influence larval transport mechanisms (Tegner and Dayton 1991, Barth et al. 2007, Lot-Yat et al. 2011). Decreases in larval abundances may also be due to reduced levels of chlorophyll *a* (Paulay et al. 1985, Lo-Yat et al. 2011) or changes in local, small-scale hydrodynamics (Bertness et al. 1996, Jacinto and Cruz 2008) both resulting from El Niño conditions in 2015.

To understand the causes of the decreases in larval abundances it is important to consider the basal larval transport processes. Previous studies observed higher recruitment with discrete periods of upwelling in a variety of locations (Shanks et al. 2000, Iles et al. 2011, Rivera et al. 2013). In the intermittent time between upwelling periods (relaxation of upwelling-favorable winds) larvae might converge at a front (Roughgarden et al. 1991) which might be transported to shore through tidally generated internal waves (Shanks et al. 2009), that form at density gradients (Hagerty et al. 2018). Thus, a breakdown in larval transport may be due to El Niño's inhibition or delay of relaxation periods which may lead to decreases in primary productivity and settlement of benthic invertebrates (Lundquist et al. 2000, Barth et al. 2007). Therefore, the warming SST from 2014 to 2015 (Zaba and Rudnick 2016), leading into the El Niño period may have altered larval delivery to the shore resulting in a reduction in the larval pool (# of individuals available for settlement and subsequent recruitment).

Across the two years of observations (December of 2014 to December of 2016), settlement of *C. fissus* varied seasonally, with similar patterns to those documented in previous studies of higher settlement rates observed in the spring to summer than the fall to winter period (Pineda 1994, Tapía and Navarrete 2010). Settlement also decreased in the fall to winter months possibly due to seasonal or annual variation in the physical mechanisms that altered the delivery of larvae to shore decreasing the larval pool available for settlement (Broitman et al. 2005, Pineda et al. 2007, Menge et al. 2009, Menge et al. 2011, Hagerty et al. 2018).

Temporal fluctuations in larval supply corresponded across all traps; however, there were significant differences in settlement rate across plates per period within our site. Furthermore, the peaks in larval supply did not necessarily correspond with timing of peaks in settlement. The decoupling between larval supply and settlement time series could possibly indicate that the larval traps do not accurately represent the larval supply to our site. However, we used a known, tested trap design that previously collected barnacle cyprids in the rocky intertidal (Chen et al. 2013). Additionally, all traps exhibited similar patterns of larval supply, suggesting that they functioned similarly across our study site. Although we observed cases where larval supply was low, and settlement was high, these observations may potentially reflect a lag between the time larvae first arrive in the intertidal (larval supply) and when they find suitable habitat and settle (Swanson et al. 2007). However, this lag may also occur if larvae have an extended or variable competency period within the intertidal (McCormick et al. 2012, Rahman et al. 2014).

With low larval abundances observed in 2015 and our limitations in conducting a more robust time series analyses of larval supply and settlement, our assertion that there was a lack of relationship between larval supply and settlement based on the 2014 data. Variability in the relationship between settlement and larval supply was previously observed with some studies showing a negative correlation (Miron et al. 1995), positive correlation (Minchinton and Scheibling 1991, Ma 2005), negative or positive correlation dependent on larval delivery (Olivier et al. 2000), or no correlation (Satumanatpan and Keough 2001, Rilov et al. 2008) between larval supply and settlement. Given this variability and our own observations, we cannot definitively state that settlement may be predicted from larval supply. This decoupling between larval supply and settlement may be due to the environmental conditions experienced at settlement, including immersion time, proximity to water, and space available for settlement within the Bird Rock rocky intertidal.

Previous studies have utilized immersion time to standardize settlement rate (Jarrett 1997, Shanks 2009) and proximity to water's edge was suggested to influence settlement rate to a locality (Gaines et al. 1985). Although at some point elevation will matter (i.e. when settlement substrates are outside the water with respect to tidal changes), within the mid to high intertidal (i.e. where our settlement plates were distributed), we found minimal evidence that elevation was related to *C. fissus* settlement. Therefore, researchers should not assume immersion time (with respect to tidal cycle) linearly determines settlement rate, given the varying degree of correlation observed between these two variables

(Hatton 1938, Shanks 1986, Hills et al. 1998, Pineda 2000, Cruz et al. 2005).

Similarly, we found that proximity from the edge of the water did not have a direct influence on settlement. In the past, proximity to water was used to invoke a settlement shadow, that is, the first plates/rocks encountered by a parcel of water as the tide is rising might deplete larval supply to downstream plates (Gaines et al. 1985). However, based on the non-relationship between settlement and proximity to water, there was no evidence of a settlement shadow at our site.

We observed that with less free space there was higher settlement. This observation is opposite of the patterns observed by Gaines and Roughgarden (1985) who found more settlement with more free space and Jeffrey (2000) who found that substratum had no effect on barnacle settlement where adult density was low. The negative relationship between free space and settlement was observed at all settlement plates, indicative of a settlement intensification effect across our site (Bertness et al. 1992, Pineda 1994, Osman & Whitlatch 1995a, b, Pineda & Caswell 1997, Berntsson et al. 2004, Rilov et al. 2008, von der Meden et al. 2012). Similarly, Pineda (1994) observed an increase in *Chthamalus* spp. settlement when the amount of unsuitable surrounding habitat increased, minimizing the amount of free space available.

Given the diversity of habitat cover in the rocky intertidal, free space is a function of percent cover of adult barnacles and algae. We observed a negative relationship between settlement and live barnacles resulting in less settlement with high live barnacle cover. This relationship is opposite of what would be expected for typical gregarious larval barnacle settlement in response to recent

recruits, juveniles, or adults of conspecifics (Crisp & Knight-Jones 1953, Crisp & Meadows 1962, Chabot and Bourget 1988, Jeffery 2000, Matsumura & Qian 2014). Gregarious settlement can generally be facilitated by the ability of larvae to detect chemical cues and selectively settle based on the presence or absence of conspecific adults (Pawlik 1992, Scrosati and Ellrich 2017). The observed negative relationship between barnacle adults and settlers may be influenced by post-settlement mortality which results in a smaller adult barnacle population than the initial newly-settled population (Minchinton & Scheibling 1993). Settlement was positively related to algal cover. Overall, algal cover remained consistently low around 20%, only peaking in late summer through the fall. Previous research demonstrated the influence of algal cover (Jernakoff & Fairweather 1985) and its associated chemical cues (Walters et al. 1996) on limiting the suitable space available for benthic invertebrate settlement. Therefore, algal cover may have driven the intensification effect (Pineda 1994) where less space available due to algal coverage enhanced settlement. This study highlighted the influence of additional space occupiers (e.g., adult barnacles and algae) on the space available for settlement of *Chthamalus fissus* similar to previous studies such as Luckens (1975) and Beermann et al. (2013).

Within our site, there was a consistency in the ranking of settlement rate among plates from the time period using 12 plates to all 14 plates. For the 12-plate period, the plates with the lowest settlement rankings (plates 5 and 6) were near locations where habitat was less limiting and the locations where settlement rankings were highest (plates 3, 7, and 9) were where habitat was more limited.

Based on the high settlement at plate 3 and the knowledge that moving from north to south habitat was less limiting with increasing cobbles available, we added plates 1 and 2 to the north end of our site during the 14-plate period. We observed high settlement at plates 1 and 2 in addition to plates 3, 7, and 9. These increases in settlement with less free space at locations 1, 2, and 3 were further evidence of the intensification effect, similar to Pineda and Caswell (1997). Locations 7 and 9 however, had consistently high settlement when compared to both larval supply and habitat characteristics, despite not being in locations where available adult habitat was limiting. This suggests that other factors in addition to the intensification effect may have influenced settlement dynamics at some locations within our site. These factors may include the microhydrodynamic conditions around settlement substrate and larval behavior during settlement. Previous studies have demonstrated that the ability of larvae to settle is dependent on the scaling of small-scale hydrodynamics and how these may or may not impede the detection of conspecifics (Wright and Boxshall 1999, Crimaldi et al. 2002). Thus, within the Bird Rock rocky intertidal, settlement at ~ 1-month temporal time scales may be influenced by small-scale benthic processes such as habitat cover, small scale hydrodynamics, and larval behavior at settlement. To extend our understanding of the influence of small-scale processes in shaping settlement dynamics at our site we need to quantify the temporal duration of competency for *C. fissus* and characterize the location of arrival of larvae within our rocky intertidal site. To investigate these two-components we must consider the role of hydrodynamics (Pineda 1991, Bertness et al. 1996, Jacinto and Cruz 2008, Rilov

et al. 2008) in influencing the early larval behavior (Crisp 1955, Haury et al. 1982, Miron et al. 1996, Wright and Boxshall 1999, Crimaldi et al. 2002, Kent et al. 2003) of barnacles which ultimately leads to settlement (Hawkins and Hartnoll 1982).

Conclusions

Within our site, there was evidence of decoupling between larval supply and settlement. One possible explanation for this decoupling is that habitat characteristics or availability of free space influenced *C. fissus* settlement. Availability of free space was determined by live barnacle and algal cover. However, it is possible that additional microhydrodynamic features, such as micro-eddies (Crimaldi et al. 2002, Koehl 2007) and aspects of larval behavior (Crisp 1974, Miron et al. 1996, and Kent et al. 2003) also influence barnacle larval supply and settlement. Therefore, invoking just larval supply or larval transport processes to explain settlement rate is misleading; variability in substrate availability can further explain settlement rate dynamics. Investigating the influence of habitat on settlement patterns within coastal ecosystems is important to understand the settlement processes shaping benthic invertebrate populations. Some studies have acknowledged settlement intensification on reflective beaches; but have mainly focused on the influence of surf-zone hydrodynamics on settlement at reflective versus dissipative beaches (Shanks et al. 2017, Morgan et al. 2018). The role of intensification and other habitat or environmental factors must be considered to fully understand the post-settlement processes and environmental factors that help shape rocky intertidal communities.

CHAPTER 2 TABLES AND FIGURES

Table 1. *Chthamalus fissus* sampling dates for settlement (D = daily, W = weekly, or both, depending on the accessibility of the site) and surveys of adult populations and habitat (M = monthly) from April 2014 to December 2016.

Month	2014	2015	2016
January		D, W, M	W, M
February		W, M	W, M
March		W, M	W, M
April	D	D, W, M	D, W, M
May	D	D, M	D, M
June	D	D, M	D, M
July	D	D, M	D, M
August		D, W, M	D, M
September		D, W, M	D, M
October	D	D, M	D, M
November	D	D, M	D, M
December	D, M	D, W, M	D, M

Table 2. Averages ($\pm$ SE) and proportions of barnacle larvae (out of each sub-category nauplii, cyprids, and settlement species) collected in larval traps (measure of larval supply) and on settlement plates (measure of settlement) during summer 2014 and summer 2015.

Group	Summer 2014		Summer 2015	
	Averages $\pm$ SE	Proportions	Averages $\pm$ SE	Proportions
<i>Trap (counts/day)</i>				
Nauplii Early Stage	5.05 ($\pm$ 0.96)	0.993	0.91 ($\pm$ 0.07)	0.991
Nauplii Late Stage	0.03 ($\pm$ 0.02)	0.006	0.01 ($\pm$ 0.006)	0.016
Cyprid <i>Chthamalus fissus</i>	4.75 ($\pm$ 1.04)	0.979	0.13 ($\pm$ 0.02)	0.902
Cyprid <i>Balanus glandula</i>	0.02 ($\pm$ 0.01)	0.005	0.003 ($\pm$ 0.003)	0.024
Cyprid 'Other'	0.07 ($\pm$ 0.02)	0.015	0.01 ($\pm$ 0.006)	0.073
<i>Settlement (# cm²/day)</i>				
<i>Chthamalus fissus</i>	160.29 ($\pm$ 17.86)	0.99	22.58 ($\pm$ 4.43)	0.99
<i>Balanus glandula</i>	0.005 ($\pm$ 0.002)	0.001	0.001 ($\pm$ 0.0008)	0.001

Table 3. Average rank for settlement, by location for 2014 (June 16th - July 16th, 2014) using Nemenyi's procedure / two-tailed test. The locations with similar ranks are grouped as A-C.

Location	Average of Ranks	Groups		
8	2.145	A		
14	2.371	A		
12	3.016	A	B	
3	4.145		B	C
7	4.387			C
9	4.935			C

Table 4. Average rank for settlement, by location for 2015a (April 24th - June 5th, 2015) using Nemenyi's procedure / two-tailed test. The locations with similar ranks are grouped as A-D.

Location	Average of Ranks	Groups			
12	1.791	A			
8	2.744	A	B		
14	3.302		B	C	
3	3.907			C	D
9	4.512				D
7	4.744				D

Table 5. Average rank for settlement, by location for 2015b (June 6th - August 2nd, 2015) using Nemenyi's procedure / two-tailed test. The locations with similar ranks are grouped as A and B.

Location	Average of ranks	Groups
12	2.448	A
14	2.612	A
1	2.983	A
2	4.069	B
7	4.216	B
9	4.672	B

Table 6. Results of model selection using information theoretic criteria to quantify the relationship between monthly-averaged settlement of *Chthamalus fissus* and percent cover of live barnacles, dead barnacles, free space, and algae, n = 21 months.

Table values were calculated from regression analysis on models that included monthly-averaged log-transformed settlement of *C. fissus* as the response variable, and monthly-averaged percent cover of live barnacles and free space and hyperbolic arcsin-transformed percent cover of dead barnacles and algae as explanatory variables.

K is number of explanatory variables included in model + 1, AIC_c is second-order corrected AIC for sample size < 40 .

ΔAIC_c is the difference between AIC_c of each model and the model with lowest AIC_c . *Weights* are Akaike weight of evidence (probability) that model is best approximating model in a given set of candidate models. *Evidence Ratio* is evidence supporting best approximating model.

*Model with lowest AIC_c against which all other models are compared.

Explanatory Variable (% cover)	K	AIC_c	ΔAIC_c	Weights	Evidence Ratio
Live Barnacles	2	12.034	16.4445	0.0003	3722.9591
Dead Barnacles	2	5.057	9.4676	0.0081	113.7259
Free Space	2	-4.410	0	0.9242	1*
Algae	2	0.826	5.2365	0.0674	13.7115

Table 7. Results of model selection using information theoretic criteria to quantify the relationship between monthly-averaged percent free space and percent cover of live barnacles, dead barnacles, and algae, $n = 21$ months.

Table values were calculated from regression analysis on models that included monthly-averaged percent free space as the response variable, and monthly-averaged percent cover of live barnacles and hyperbolic arcsin-transformed percent cover of dead barnacles and algae as explanatory variables.

K is number of explanatory variables included in model + 1, AIC_c is second-order corrected AIC for sample size < 40 .

ΔAIC_c is the difference between AIC_c of each model and the model with lowest AIC_c . *Weights* are Akaike weight of evidence (probability) that model is best approximating model in a given set of candidate models. *Evidence Ratio* is evidence supporting best approximating model.

*Model with lowest AIC_c against which all other models are compared.

Explanatory Variable (% cover)	K	AIC_c	ΔAIC_c	Weights	Evidence Ratio
Live Barnacles	2	125.495	31.5426	8.90E-08	7069670.020
Dead Barnacles	2	126.034	32.0820	6.79E-08	9258099.934
Algae	2	109.081	15.1291	0.000361	1928.643
Live Barnacles, Dead Barnacles	3	124.492	30.5394	1.46E-07	4280974.374
Live Barnacles, Algae	3	93.952	0	0.629241	1*
Dead Barnacles, Algae	3	110.434	16.4815	0.000163	3792.358
Live Barnacles, Dead Barnacles, Algae	4	95.013	1.0606	0.370267	1.699*

Table 8. Ranked relative importance of factors explaining the variability in percent free space from the Akaike weights in Table 7, n = 21 months.

Explanatory Variable	Relative importance	% importance
Algae	1.0000	100.00
Live Barnacles	0.9995	99.95
Dead Barnacles	0.3704	37.04

Table 9. Significance values (values with a $p < 0.05$ are in bold) comparing *C. fissus* settlement across plate pairs for plates 3-14 (April 24th, 2014 to June 5th, 2015, $n = 217$ days per plate) using a multiple pairwise comparison Nemenyi's two-tailed test.

	3	4	5	6	7	8	9	10	11	12	13	14
3	1	< 0.001	< 0.001	< 0.001	0.999	< 0.001	0.990	0.019	< 0.001	< 0.001	< 0.001	< 0.001
4	-	1	0.006	0.001	< 0.001	0.847	< 0.001	0.015	0.759	0.563	1.000	1.000
5	-	-	1	1.000	< 0.001	0.571	< 0.001	< 0.001	< 0.001	0.852	0.024	0.015
6	-	-	-	1	< 0.001	0.155	< 0.001	< 0.001	< 0.001	0.385	0.002	0.001
7	-	-	-	-	1	< 0.001	0.658	0.217	0.001	< 0.001	< 0.001	< 0.001
8	-	-	-	-	-	1	< 0.001	< 0.001	0.017	1.000	0.969	0.940
9	-	-	-	-	-	-	1	0.000	< 0.001	< 0.001	< 0.001	< 0.001
10	-	-	-	-	-	-	-	1	0.832	< 0.001	0.004	0.006
11	-	-	-	-	-	-	-	-	1	0.003	0.498	0.593
12	-	-	-	-	-	-	-	-	-	1	0.813	0.733
13	-	-	-	-	-	-	-	-	-	-	1	1.000
14	-	-	-	-	-	-	-	-	-	-	-	1

Table 10. The significance values (values with a $p < 0.05$ are in bold) comparing *C. fissus* settlement across plate pairs for plates 1-14 (June 6th, 2015 to December 15th, 2015, $n = 156$ days per plate) using a multiple pairwise comparison Nemenyi's two-tailed test

	1	2	3	4	5	6	7	8	9	10	11	12	13	14
1	1	0.131	0.281	0.244	0.102	0.003	0.346	0.104	0.006	1.000	0.773	0.296	0.321	0.359
2	-	1	1.000	< 0.001	< 0.001	< 0.001	1.000	< 0.001	0.999	0.011	< 0.001	< 0.001	< 0.001	< 0.001
3	-	-	1	< 0.001	< 0.001	< 0.001	1.000	< 0.001	0.990	0.033	0.000	< 0.001	< 0.001	< 0.001
4	-	-	-	1	1.000	0.977	< 0.001	1.000	< 0.001	0.790	1.000	1.000	1.000	1.000
5	-	-	-	-	1	0.998	< 0.001	1.000	< 0.001	0.541	0.997	1.000	1.000	1.000
6	-	-	-	-	-	1	< 0.001	0.998	< 0.001	0.049	0.616	0.961	0.953	0.937
7	-	-	-	-	-	-	1	< 0.001	0.980	0.046	0.001	< 0.001	< 0.001	< 0.001
8	-	-	-	-	-	-	-	1	< 0.001	0.546	0.997	1.000	1.000	1.000
9	-	-	-	-	-	-	-	-	1	0.000	< 0.001	< 0.001	< 0.001	< 0.001
10	-	-	-	-	-	-	-	-	-	1	0.996	0.842	0.862	0.889
11	-	-	-	-	-	-	-	-	-	-	1	1.000	1.000	1.000
12	-	-	-	-	-	-	-	-	-	-	-	1	1.000	1.000
13	-	-	-	-	-	-	-	-	-	-	-	-	1	1.000
14	-	-	-	-	-	-	-	-	-	-	-	-	-	1

Figure 1. (A) Study site in Bird Rock, La Jolla, CA, USA ($32^{\circ} 48' 33''$ N, $117^{\circ} 16' 07''$ W) (Google Earth 2016). (B) Large white boxes and numbers indicate locations within the intertidal where paired larval traps (in blue) and settlement plates (in orange) were deployed during summer 2014 and 2015. (C) Numbers indicate *Chthamalus fissus* settlement plate deployment locations on boulders (in orange) and where adult surveys (in red) were conducted December 2014 to December 2016.

A.

B.

Larval Supply

Settlement

C.

Settlement

Adults

Figure 2. Time series for *Chthamalus fissus* larval supply (# cyprids / trap) for (A): 2014, (B): 2015a, (C): 2015b and for *Chthamalus fissus* settlement (# settlers / cm²d) for (D): 2014, (E): 2015a, (F): 2015b. Please note 2014 included June 16th, 2014 to July 16th, 2014; 2015a included April 24th, 2015 to June 5th, 2015; and 2015b included June 6th, 2015 to August 2nd, 2015.

Figure 3. Average $\log(x+1)$ transformed *Chthamalus fissus* larval supply (# cyprids / trap) versus average $\log(x+1)$ *Chthamalus fissus* settlement (# settlers / cm^2d) by location for (A) 2014 (June 6th, 2014 to July 16th, 2014), (B) 2015a (April 24th, 2015 to June 5th, 2015), (C) 2015b (June 6th, 2015 to August 2nd, 2015). The error bars have been excluded for ease of visualization and the adjusted R^2 values are given for each period, along with the associated p-value when it is significant.

Figure 4. Average proportion of settlement of *Chthamalus fissus* from 2014-2016 by plate with respect to elevation (A) and distance to water (B). Only dates when 12 plates were deployed were used, points are labeled by plate

Figure 5. Monthly-averaged *Chthamalus fissus* settlement (A); and monthly-averaged percent free space (B), percent cover of live barnacles (C), percent cover of dead barnacles (D), and percent cover of algae (E) from December 2014 to December 2016. Panels A-E included $\pm$ SE for $n = 14$ plates across 24 months. May 2015, September 2015, and May 2016 were excluded from panel A due to incomplete settlement data, $n = 21$ months.

Figure 6. Monthly-averaged *Chthamalus fissus* settlement versus monthly-averaged percent free space for each settlement plate (numbers 1-14) from December 2014 to December 2016, n = 21 months.

Figure 7. Log-transformed monthly-averaged (over all plates) *Chthamalus fissus* settlement compared to monthly-averaged percent free space (over all plates), n = 21 months ($p \ll 0.001$).

Figure 8. Monthly-averaged percent free space compared to monthly-averaged percent cover of live barnacles (A); hyperbolic arcsin-transformed percent cover of dead barnacles (B); and hyperbolic arcsin-transformed percent cover of algae (C), $n = 21$ months. Panels B and C zoomed in on the x-axis for ease of visualization

Figure 9. Average *Chthamalus fissus* settlement $\pm$ SE (A), and average proportion of settlement $\pm$ SE (B) for each plate grouped by dates where 12 plates (April 24th, 2014 to June 5th, 2015, n = 217 days per plate) and 14 plates (June 6th, 2015 to December 15th, 2015, n = 156 days per plate) were deployed. The correlation between average proportion of settlement $\pm$ SE per plate in 2014 (n = 173 days per plate) versus in 2015 (n = 200 days per plate) (C). The black point is to distinguish between two overlapping points. Plates 1 and 2 were omitted to compare plates during the same time interval.

Figure 10. Average rank of *Chthamalus fissus* settlement for 12 plates (n = 217 days per plate) (A), and 14 plates (n = 156 days per plate) (B) ordered from smallest to largest values. The arrows indicate which plates were similar, according to pairwise comparisons using Nemenyi's multiple comparison test.

CHAPTER 3:

General Thesis Conclusions and Future Directions

Through our two-year project, we concluded that the environment of the rocky intertidal plays a prominent role in shaping the processes that result in *Chthamalus fissus* settlement. Therefore, when studying the settlement of benthic invertebrate populations, the habitat dynamics (e.g., available space, hydrodynamics) and larval behavior must be considered. It is important to consider the role each factor plays in shaping settlement to have a holistic understanding of how benthic invertebrate populations develop. A mix of short- (monthly to seasonal scale) to long-term studies (yearly scale) must continue to allow for observations of the process of settlement and the factors which influence this process across small (rocky intertidal localities) to larger (regions) spatial scales through time.

In taking this multi-scaled approach, researchers will further understand the environmental dynamics that result in alterations to settlement patterns. Some studies such as Valencia-Gasti and Ladah (2016) observed settlement on a local (~1 km scale), and found that, despite homogenous patterns of larval transport and subsequent settlement, slight spatial changes in settlement may have resulted from variations in geomorphology and bathymetry influencing the differences in larval transport to sites in close proximity. Other studies have highlighted at scales of ~100m, spatial variability in settlement that may also be influenced by larval searching behavior and the availability of space, in addition to temporal variability influenced by differences in the larval pool due to variations in

transport mechanisms across time (Pineda 1994). There have been studies that focused on settlement and recruitment variation from a meso-scale (regional) to small-scale (locality). Such studies include Lagos et al. (2005) who found that *Chthamalus* species' settlement variation was correlated with indices (SST) related to changes in transport (topographically modified upwelling) at a regional or meso-scale. Other studies have investigated the influence of climatic factors on recruitment from regional to ocean basin scales across long-term time series (Menge et al. 2011). Across a 20-year period, Menge et al. (2011) observed that upwelling and climatic events explained ~40% of the variation in recruitment across a regional scale (~250 km), with the additional variation explained by local processes (~ 1 km to 100s of m) relating to transport and post-settlement factors. These examples indicate that a multitude of factors shape the settlement and ultimate recruitment of benthic invertebrate populations. Therefore, these factors must all be considered with regards to the weight of their influence in formulating the mosaic of settlement processes which shape benthic invertebrate populations within specific coastal communities.

Following the life history stages of *C. fissus* across multiple spatial scales begins to resolve the influences on settlement during larval development. To gain a fundamental understanding of the connection between offshore larval development in the coastal ocean to onshore juvenile and adult benthic populations requires investigating the biological and physical processes that shape larval dispersal and settlement (Cowen and Sponaugle 2009). The processes which warrant investigation following our study include mechanisms of larval

transport leading to dispersal, hydrodynamic conditions, and larval searching behavior during settlement, and post-settlement mortality. To understand the influence of these processes on settlement, the reproductive connectivity of a population, defined as the exchange of individuals that ultimately reproduce, must be observed to understand the minimum number of recruits a population requires to ecologically sustain itself across time (Pineda et al. 2007). For example, high recruitment has been observed (Hughes et al. 2000) when the proportion of reproductive *Acropora* spp. individuals was close to 100%. Additionally, where *Mytilus* spp. were tracked through an elemental tracer, they were found closer (~20-30 km) to their original spawning site than initially expected (Becker et al. 2007). These types of studies allowed researchers to examine the interactions between life history stages that connect a population. Extending our study would allow for the examination of barnacle reproductive patterns that supply new recruits to sustain populations within intertidal communities as well as the biological and physical factors which influence these patterns.

To further my study, investigating the reproductive connectivity of *C. fissus* populations within Bird Rock may help inform the spatial boundaries of local populations from their nearshore development to onshore settlement. By informing these spatial boundaries around the reproductive connectivity of benthic invertebrate populations, more effective management of coastal ecosystems with precious resources (e.g., locations for sustainable local fisheries and ecotourism) is possible (Roberts 1997, Becker et al. 2007). The potential to implement spatial boundaries has been highlighted in Gerber et al. (2011), which

describes the conceptual framework for considering the influence of dispersal and other factors on demographic models which inform the spatial dynamics of a population. This framework for creating spatial boundaries based on the spatial dynamics of populations is one consideration for coastal management or protection (Sale et al. 2005). Managing marine protected areas (MPAs) requires an ecosystem-based management approach (Halpern et al. 2010). Often MPAs are structured with central regions where removal of any physical or biological components is prohibited and surrounding these regions are buffer zones where removal of these components is permitted (Long et al. 2015, DiFranco et al. 2016). The idea of ecosystem-based management is the allowance of the regulated use of buffer zones within MPAs for socio-economic sustainable activities following specific guidelines which satisfy conservation aims and allow for local economies (i.e. tourism and fisheries) and coastal ecosystems to both be sustained long-term (Long et al. 2015, DiFranco et al. 2016). By maintaining strict enforcement of ecosystem-based management, restrictions of no-take and buffer zones within MPAs, coastal regions with high productivity and biodiversity can be better protected from external, anthropogenically-related threats (Jones et al. 2007). Therefore, to maintain a healthier longevity of coastal ecosystems (e.g., rocky intertidal, coral reef, and seagrass communities), the larval transport and dispersal patterns of populations with planktonic larvae must be considered to understand the boundaries of population connectivity to establish MPAs.

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APPENDICES

APPENDIX A. Field deployment of larval traps paired with settlement traps.

Technical display and dimensions of larval traps including segmented funnel
ending in 100 μm sieve.

APPENDIX A

APPENDIX B. Elevations (with respect to MLLW) for both the larval supply traps and the settlement plates across pairings used throughout the timeline of sampling.

APPENDIX B

Pair Label	Trap Elevation	Plate Elevation
1	0.382	0.429
2	0.385	0.482
3	0.385	0.583
7	0.398	0.444
8	0.432	0.322
9	0.411	0.410
12	0.426	0.408
14	0.422	0.479

APPENDIX C. Field deployment of the settlement plates. Dimensions and specifications of plates where individuals were counted along the seam of each of the 3 grooves. Examples of the individuals sampled are pictured from right to left: *Chthamalus fissus* metamorphs, cyprids, and *Balanus glandula* metamorphs.

APPENDIX C

APPENDIX D. Set-up for adult population / habitat surveys which included sampling a quadrat at each of the 14 plate locations, then through transect, random selection, we sampled three additional quadrats north, west, and east of each plate rock to quantify the % cover categories listed.

APPENDIX D

APPENDIX E. Initial exploration of the interaction between measures of intertidal hydrodynamics (significant wave height and sediment volume) and its interaction with larval supply either by Spring-Summer period (2014 vs. 2015) or sample period (2014, 2015a, and 2015b).

APPENDIX E

APPENDIX F. Initial figure to analyze the potential interaction between significant wave height and sediment volume to understand the role of microhydrodynamics in larval transport which further shapes benthic invertebrate (i.e. barnacle: *Chthamalus fissus*) settlement within the rocky intertidal.

APPENDIX F