Chapter 1

General introduction

Several aspects of the natural history of the rocky intertidal barnacle can explain why it has long been exploited as an example of marine animal recruitment. The adult barnacle is sessile and does not move after the transition from the larval to the juvenile stage. Therefore, researchers can track the fate of individual barnacles in ways that would be difficult for non-sessile marine animals. Even among sessile animals, the barnacle is easiest to track because it grows on rocks in the rocky intertidal. A sizable portion of the rocky intertidal barnacle's day is spent in a pseudo-terrestrial environment, and whole populations of barnacles are accessible to scientists at regular intervals. Despite having this unique adult habitat, the barnacle has a lifecycle like most marine animals. Many marine animals have a dispersive larval stage, which was lost during the evolution of terrestrial life because distinct environmental features necessitated a different mode of reproduction (Steele 1985). The rocky intertidal barnacle is a model system for many other benthic marine organisms with the dispersive larval stage.

One of the greatest contributions to the field of marine ecology was the ability for barnacle ecologists to distinguish between settlers and post-metamorphic individuals (Connell 1985). Features that can be measured of settlers, such as their abundance are more closely representative of the dynamics during the larval period of the barnacle lifecycle, such as the supply of larvae. The precise definition of settlement is the first record of when an individual has attached to the benthic habitat. By this definition, after the first record of an individual settling, this individual is not considered a settler in

subsequent visits to the rocky intertidal, even if it is recorded once again in its earliest cyprid stage. Therefore, settlement at a given period of time carries specific information about the transition from the larval to the benthic phases in the marine animal lifecycle. In other recruitment systems, settlement cannot be measured as frequently or as reliably. The earliest stages recorded in other recruitment systems are generally post-metamorphic stages, which often are not considered settlers at all, but recruits due to their advanced stage of development.

I monitored settlement and survival of the barnacle, *Semibalanus balanoides*, at an intertidal site in Woods Hole called Gardiner beach. Barnacle recruitment at this site has been intensely monitored several years preceding my first field season including a preliminary study comparing this site to another one nearby in Woods Hole (Pineda, Riebensahm and Medeiros-Bergen, 2002), and a preliminary analysis of settlement and survival patterns on a daily frequency (Pineda, Starczak and Stueckle 2006). I heavily depended on the knowledge gained from these previous studies to create the spatial and temporal scales for my measurements. I sampled settlement at a daily frequency, because important variability in barnacle settlement occurs on this scale (Pineda 2000). I monitored rectangular surfaces 1.5 by 2 cm, because this was the minimum area that would have at least one recruit and could also be easily photographed using the macro setting of the digital camera that I used. There have been several occasions where people have recorded recruitment at these highly resolved scales, but the number of examples is growing larger (e.g. Wethey 1984; Raimondi 1990; Pineda, Starczak and Stueckle 2006) because this research is still yielding novel and sometimes astonishing results that are

changing our foundational concepts about connections between pelagic larval and benthic adult life stages of marine animals. An important recent advance was the unique information that settlement date provides about the survival of juveniles to the adult stage. My advisor and his co-authors defined a new concept for recruitment research, the recruitment window (Pineda, Starczak and Stueckle 2006). I collected data to resolve the recruitment window in three consecutive years; 2006, 2007 and 2008; and the analysis of the recruitment window has been the primary focus of my thesis. In chapter 2, a descriptive study of the 2006 recruitment window correlated variability in the recruitment window between quadrats at a site with patterns of settlement and recruit abundance. In chapter 4, I average among quadrats to describe whole site trends in the 2007 and 2008 recruitment windows.

Studies using post-settlement measures of intertidal barnacles reveal a rich set of both pre- and post- settlement factors influencing the recruitment of marine animals, and in particular they have focused on the transition during metamorphosis from the pelagic to the benthic stages. Raimondi (1991) tested a hierarchy of nested hypotheses, each carefully conceived to narrow the number of possible factors controlling the distribution of the rocky intertidal barnacle, *Chthamalus anisopoma*. Using measurements collected after settlement, he inferred that behaviors before and during settlement would explain the distribution of barnacles. In addition, he postulated a hypothesis on which behavioral mechanisms would produce linear and non-linear trends in the distribution of setters with increasing settler density. Jarrett and Pechenik (1997) measured the energy content of settlers through time. Though these measurements were made post-settlement, they

indicated sources of recruitment variability related to larval feeding conditions and larval duration in the competent cyprid stage. This variability in energy content described some degree of the juvenile growth in the adult habitat, indicating these pelagic experiences had lasting consequences in the benthic stages of the barnacle lifecycle. Miron, Boudreau and Bourget (1999) conducted a hybrid of these two approaches by inferring settlement behaviors that may be influenced by the energy content of settling larvae. Once again, these measurements were conducted only on post-settlement stages, though they relate to pre-settlement processes. The ability to measure settlement patterns with high fidelity allows inferences about which factors are most critical for affecting recruitment during the transition from the pelagic to the benthic stages.

There has been a historical and ongoing pursuit to reach backwards in the lifecycle of the intertidal barnacle before the stages of settlement to larval phases in the nearshore environment to explain the patterns of settlement that are observed. Hawkins and Hartnoll (1982) compared the settler abundance measured over four consecutive years, relating variability in settlement to factors such as variation in the spring diatom bloom and variability in wind conditions that would transport pelagic larvae onshore where they can touchdown on the adult habitat. Bertness et al. (1992) sought to make a link between measurements of larval abundances in the nearshore pelagic habitat with the measures of settlement in the rocky intertidal. Following up on this study Bertness, Gaines and Wahle (1996) linked settlement patterns in the rocky intertidal with larval abundances and wind induced transport in the pelagic environment. Attempts to make links between settlement patterns and pelagic based measurements continue to this day

(e.g. Jenkins 2003). Yet, planktonic measurements of barnacle larvae were not an objective of my graduate research. I found settlement measurements to impart enough information to study recruitment patterns and barnacle population dynamics.

The scope of this thesis encompasses findings that range over different timescales during the benthic phase of the barnacle lifecycle. At one extreme, the measurements reported in chapter 3 describe how high frequency physical forcing from wind is a source settlement variability. Though the link between wind and wave energy is well established (e.g. Tucker 1991), the fact that stochastic physical forcing may drive daily variability in settlement highlights how unpredictable recruitment patterns are on very short timescales. Chapter 4 investigates trends in temperature and this source of variability on recruitment. While high frequency variability also occurs in environmental temperature, the dominant period of variability is on timescales of a year with distinct periods of cold and warm conditions characterized by seasons that compose this cycle. I compare the recruitment patterns among years to assess how yearly differences in seasonal temperature can account for the recruitment patterns. Further, I employ an experimental approach to assess the role of seasonal changes in temperature on the periods of time when settlers can survive to adulthood. Despite the highly unpredictable nature of the physical forces like wind and temperature that affect recruitment of barnacles, the spatial variability in recruitment abundance may be quite predictable, as is demonstrated in chapter 2. Therefore, the findings of this thesis may help address an applied question in marine ecological research. Quotas for marine fisheries are calculated on a year to year basis to manage natural stocks of marine animals at

sustainable levels. The findings of this thesis indicate that standard measurements of marine animal settlement and the physical factors that drive recruitment can be useful in predicting the cohort's recruitment strength for the upcoming year. Since recruitment is an important factor in the fisheries assessments of sustainable yield, these predictions may allow enhanced fisheries management practices.

1.1 References

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