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The Effects of Early Life History on Recruitment and Early Juvenile Survival of a Coral Reef Fish in the Florida Keys

Tauna Leigh Rankin

University of Miami, trankin@rsmas.miami.edu

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UNIVERSITY OF MIAMI

THE EFFECTS OF EARLY LIFE HISTORY ON RECRUITMENT AND EARLY
JUVENILE SURVIVAL OF A CORAL REEF FISH IN THE FLORIDA KEYS

By

Tauna Leigh Rankin

A DISSERTATION

Submitted to the Faculty
of the University of Miami
in partial fulfillment of the requirements for
the degree of Doctor of Philosophy

Coral Gables, Florida

May 2010

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Tauna Leigh Rankin

Approved:

Su Sponaugle, Ph.D.
Associate Professor of
Marine Biology & Fisheries

Terri A. Scandura, Ph.D.
Dean of the Graduate School

Robert K. Cowen, Ph.D.
Professor of Marine Biology
& Fisheries

Michael C. Schmale, Ph.D.
Professor of Marine Biology
& Fisheries

Dean A. Williams, Ph.D.
Assistant Professor of Biology
Texas Christian University

G. Todd Kellison, Ph.D.
Supervisory Research Biologist
NOAA Fisheries, Beaufort, NC

RANKIN, TAUNA LEIGH

(Ph.D., Marine Biology & Fisheries)

The Effects of Early Life History on
Recruitment and Early Juvenile Survival
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Processes that influence the early life stages of fishes can significantly impact population dynamics, yet they continue to be poorly understood. This dissertation examined relationships between the environment, early life history traits (ELHTs), behavior, and post-settlement survival for a coral reef fish, *Stegastes partitus*, in the upper Florida Keys, to elucidate how they influence juvenile demography. Otolith analysis of settlers and recruits coupled with environmental data revealed that *S. partitus* surviving the early juvenile period settled at larger sizes and grew slower post-settlement. Water temperature also influenced the ranges of these and other ELHTs as well as the intensity and direction of selective mortality processes acting on some of these traits (i.e., pelagic larval duration, mean larval growth). Otolith analysis was paired with behavioral observations of newly settled juvenile *S. partitus* in the field to reveal that the relationship between size-at-settlement, early juvenile growth and survival is behaviorally-mediated. Individuals that were larger at settlement were more active (i.e., spent less time sheltered, swam farther from shelters) and grew more slowly post-settlement. Likewise, slower juvenile growth was associated with greater activity, more conspecific aggression, and faster escape swimming speeds. A six-year time series of recruitment densities revealed substantial temporal (interannual, seasonal, lunar) and

spatial (by microhabitat, conspecific density) variability in recruitment which influenced the composition of recruits. For instance, larvae settling during the darkest phases of the moon were larger at settlement, but selective mortality processes during brighter periods removed more of the smallest settlers, resulting in juveniles with similar sizes-at-settlement regardless of when they arrived to the reef. Because recruitment strength and composition varied temporally, genetic markers (6 microsatellite and 1 mitochondrial loci) were used to determine if the genetic composition of monthly cohorts of settling larvae and juveniles also varies interannually, monthly, or across life stages. A lack of genetic structure suggested that *S. partitus* has a large effective population size and variation in ELHTs is not likely the result of successful spawning of a disproportionately small group of adults. As a whole, these results reveal processes associated with larval supply and post-settlement life that collectively shape juvenile demography.

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Chapter 1: General Introduction

Background

Understanding the early life history of marine organisms continues to be a central goal in marine ecology and biological oceanography. Most marine organisms (e.g., invertebrates, fishes) have complex life cycles with multiple ontogenetic shifts, and processes occurring during early life stages have been shown to significantly impact subsequent population dynamics (Hjort 1914, Houde 1987, Hellriegel 2000, De Roos et al. 2003). The early life history of fishes is characterized by large production of eggs and larvae that experience extremely high mortality rates. Additionally, variation in phenotypic traits, such as growth rate and size-at-age, allows for selective mortality processes to act on individuals during early-life stages (Sogard 1997). As a result, small changes in growth, stage duration, and mortality can yield large fluctuations in recruitment magnitude (Houde 1987).¹ Furthermore, for species, such as reef fishes, with planktonic larvae and relatively sedentary adult stages, the dispersal of eggs and larvae and post-settlement survival is a critical component of population replenishment and a primary determinant of patterns of population connectivity (Cowen et al. 2007, Pineda et al. 2007, Cowen and Sponaugle 2009). Therefore, population connectivity and other demographics are influenced by a diverse array of processes occurring during the early life stages.

The transport and delivery of pelagic larvae to suitable settlement habitat is essential to the completion of the life cycle for many reef fishes and largely determines the spatial scale of their population structure. Indeed, transport-related processes have been shown to directly influence recruitment (Milicich and Doherty 1994, Thorrold et al.

1994a, Sponaugle and Cowen 1996b, Kingsford and Finn 1997, Sponaugle et al. 2005, D'Alessandro et al. 2007). Most coral reef fish have a pelagic larval phase that lasts from days to weeks, which is enough time for dispersal distances on the order of 10s to 100s km based solely on passive transport by ocean currents (Roberts 1997). However, such circulation models fail to account for significant losses due to diffusion and mortality (Cowen et al. 2000). Furthermore, recent field evidence suggests that significant proportions of larvae may be retained in the vicinity or recruit back to natal reefs (Jones et al. 1999, Swearer et al. 1999, Jones et al. 2005). Larvae are not simply passive particles and may control their trajectory through behaviors such as vertical migration (Leis 1991, Paris and Cowen 2004) or horizontal swimming (Leis et al. 1996). Additionally, episodic physical features such as mesoscale eddies may aid in the retention of locally-spawned larvae (Lobel and Robinson 1986, Boehlert et al. 1992, Lee et al. 1994, Lee and Williams 1999). Such stochastic processes can introduce additional variation in the timing and magnitude of recruitment events (Meekan et al. 1993, Sponaugle and Cowen 1996b). For instance, passage of mesoscale eddies in the upper Florida Keys (FK) has been shown to deliver large pulses of larvae (Sponaugle et al. 2005) as well as advect them away from reefs (D'Alessandro et al. 2007).

Recruitment is often temporally and spatially variable and can be influenced by adult reproduction (Robertson et al. 1988, Meekan et al. 1993), pelagic processes (Shenker et al. 1993, Thorrold et al. 1994b, Paris and Cowen 2004, Sponaugle and Pinkard 2004b, Sponaugle et al. 2005, D'Alessandro et al. 2007, Shima and Swearer 2009), habitat selection (Sweatman 1985, Shima and Osenberg 2003), and post-settlement survival (Hixon and Beets 1993, Holbrook and Schmitt 2003, Almany and

Webster 2006). Spawning and/or settlement events are commonly synchronized to the lunar or tidal amplitude cycle (Robertson et al. 1988, Robertson et al. 1990, Robertson 1992, Sponaugle and Cowen 1996a, Kingsford and Finn 1997, D'Alessandro et al. 2007), which may have implications for survival. For instance, spawning during minimum amplitude tides may reduce offshore dispersal of larvae and increase nearshore retention closer to suitable settlement habitat and where nutrients are higher (Sponaugle and Pinkard 2004a). Furthermore, hatching and settlement of larvae during dark periods, particularly relatively moonless nights, can reduce the risk of predation as larvae leave their natal habitat or arrive at their juvenile environment (Johannes 1978, Victor 1986, Robertson et al. 1988). Patterns of larval supply may be maintained (Milicich et al. 1992, Sponaugle and Cowen 1996a) or obscured by post-settlement processes (Meekan et al. 1993, Sponaugle and Cowen 1996a, Schmitt and Holbrook 1999). Habitat selection at the time of settlement can create immediate spatial patterns of recruitment, and may also influence subsequent post-settlement processes. For instance, higher quality sites may support more settlers (Shima and Osenberg 2003) and/or may offer more refuges to protect against predation (Caley and St. John 1996, Almany 2004a).

Environmental factors, such as temperature and food abundance, influence growth during the early life of fishes (Houde 1989, Pepin 1991, Houde and Zastrow 1993) and can impact recruitment strength (Cushing 1990, Rutherford and Houde 1995, Wilson and Meekan 2002, Beaugrand et al. 2003, Bergenius et al. 2005). For poikilotherms, increases in water temperature typically induce metabolic rate increases and consequently higher growth rates (but see Munday et al. 2008). High metabolic rates require additional food intake, therefore starvation is expected to be more prevalent in warmer waters (Houde

1989). Temperature effects on growth and mortality of early stages of marine fishes are well-known for temperate species (Chambers and Leggett 1987, Houde 1989, Blaxter 1991, Pepin 1991, Rutherford and Houde 1995, Campana 1996, Otterlei et al. 1999). Far less research has been conducted in more temperature-stable tropical systems, in part because growth is assumed to be less variable (Houde 1989). However, recent studies provide evidence for temperature-mediated growth in several tropical species (McCormick and Molony 1995, Meekan et al. 2003, Green and Fisher 2004, Bergenius et al. 2005, Sponaugle et al. 2006). Temperature differences in seasonal environments can increase variability in growth rate (Raven and Geider 1988, Houde 1989, Sponaugle et al. 2006), size (Blaxter 1991, Atkinson 1994), condition (McCormick and Molony 1995), and stage duration (Harkey and Semlitsch 1988, Gillooly et al. 2002).

The significance of growth to young fish survival is delineated in the growth-mortality hypothesis (Anderson 1988), which contends that individuals that grow faster, attain larger sizes-at-age, or have reduced early life stage durations will experience enhanced survival. Faster growth results in larger individuals at a given age, which are less vulnerable to gape-limited predation ("bigger is better" mechanism; Miller et al. 1988, Leggett and Deblois 1994). Furthermore, faster growing individuals will spend less time at smaller sizes and therefore have lower probabilities of mortality than slower growing individuals ("growth-rate" mechanism; Ware 1975, Shepherd and Cushing 1980). Additionally, faster growing individuals may advance to the next life stage more rapidly, where predation and starvation pressures are expected to be diminished ("stage duration" mechanism; Houde 1987).

Growth-related processes can influence the magnitude and composition of recruitment pulses (Bergenius et al. 2002, Wilson and Meekan 2002). Furthermore, larval growth history can influence subsequent juvenile survival (Meekan and Fortier 1996, Qian and Pechenik 1998, Searcy and Sponaugle 2001, Shima and Findlay 2002, Vigliola and Meekan 2002, Marshall et al. 2003, McCormick and Hoey 2004, Raventos and Macpherson 2005a, Grorud-Colvert 2006). Otolith-based studies have revealed that larger size-at-hatching (Meekan and Fortier 1996, Vigliola and Meekan 2002, Raventos and Macpherson 2005a), faster larval growth rate (Meekan and Fortier 1996, Searcy and Sponaugle 2001, Shima and Findlay 2002, Raventos and Macpherson 2005a), shorter pelagic larval duration (Meekan and Fortier 1996, Shima and Findlay 2002), larger size-at-settlement (McCormick and Hoey 2004), higher condition at metamorphosis, and faster early juvenile growth (Searcy and Sponaugle 2001, Grorud-Colvert 2006, Sponaugle and Grorud-Colvert 2006) generally enhance survival of juvenile fishes. However, these trends in selective mortality are not pervasive. Patterns of selective mortality may not be maintained through time (Gagliano et al. 2007a) or occur in all populations of a species (e.g. *Thalassoma bifasciatum*; Carr and Hixon 1995, Searcy and Sponaugle 2001). Moreover, counter to the growth-mortality hypothesis, smaller sizes-at-settlement may enhance juvenile survival in some species of tropical marine fishes (Raventos and Macpherson 2005a, Grorud-Colvert 2006). Furthermore, the intensity of selection can vary in space and time to shape the distribution of traits in survivors. For instance, selective mortality may vary between seasons or years when individuals are exposed to different environmental conditions (Meekan and Fortier 1996, Sponaugle and Pinkard 2004b, Durieux et al. 2009). Additionally, the strength of selective mortality can

differ by habitat based on the abundances and suitability of refuges (Holbrook and Schmitt 2003) and densities of conspecifics and predators (Forrester and Steele 2004).

Physiological and/or behavioral trade-offs with accelerated growth can result in traits that are less than maximally optimal according to the growth-mortality hypothesis (Lima and Dill 1990, Arendt 1997, Sogard and Olla 2002). Rapid growth can result in physiological costs to development, tissue maintenance and repair, and, for fish, swimming capabilities (Arendt 1997), which have implications for ability to escape predation. Behaviorally, individuals may choose less optimal foraging habitats or strategies that lead to reduced food consumption/lower food quality, due to lower risks of predation or competition. For instance, smaller fish are more vulnerable to gape-limited predation and therefore may be more wary and shelter more often or for longer durations (Sogard 1997). However, smaller individuals also typically have lower fat reserves, higher weight-specific metabolic requirements, and larger drag coefficients and therefore may need to spend more time foraging than larger individuals (Wootton 1994, Krause et al. 1998). Additionally, amount of foraging activity or selection of foraging habitats influences subsequent growth rates, as well as exposure to predators (Lima and Dill 1990).

The vast number of processes that interact to influence recruitment dynamics of marine fishes confounds our understanding of the relative importance of each factor. To assess the major mechanisms driving observed demographic patterns, there is a need to examine these early life processes over multiple temporal and spatial scales and under natural conditions.

Study species

To fully explore the complexity of pre- and post-settlement processes influencing recruitment and juvenile survival, this dissertation focuses on one study species, the bicolor damselfish *Stegastes partitus*. *Stegastes partitus* is a zooplanktivorous fish common on spur and groove reefs throughout the Caribbean and Western Atlantic (Emery 1973, Lieske and Myers 1996), with highest densities in dead coral rubble piles at the reef base (pers. obs.). Adults spawn demersal eggs on a monthly basis throughout the year (Schmale 1981, Robertson et al. 1988), after which, the males guard the embryos for ~4 d until hatching (Robertson et al. 1988, Dorsey 1999). Larvae spend approximately 30 d in the plankton before settling to the reef and metamorphosing into juveniles overnight (Sponaugle and Cowen 1996a). The timing of settlement appears to be synchronized with lunar phase and peaks occur during the third quarter and/or new moon (Robertson et al. 1988, Sponaugle and Cowen 1996a, Dorsey 1999, D'Alessandro et al. 2007). Seasonal peaks in settlement to the FK typically occur during summer months (D'Alessandro et al. 2007).

Stegastes partitus is an ideal model species for studying processes affecting the early life history of coral reef fishes. They are common throughout the Caribbean and are integral to the trophic dynamics of the reef community (Randall 1967, Emery 1968). In addition to being abundant, they are easy to observe and collect at all life stages. Late-stage larvae are attracted to and readily collected in light traps. Juveniles settle at relatively large sizes (~ 10 mm) and maintain small territories and thus individuals can be located repeatedly for *in situ* observations.

Despite the advantages to studying the early life stages of *S. partitus*, little research has been conducted on selective mortality processes during the early life stages and how they are influenced by natural variability in growth-related early life history traits (ELHTs) and behavior. Certain ELHTs (e.g., larval growth, pelagic larval duration) have been shown to be related to settlement magnitude (Wilson and Meekan 2002, Bergenius et al. 2005) and spatial patterns of larval supply strength can be maintained by recruits (Sponaugle and Cowen 1996a, Grorud-Colvert and Sponaugle 2009). Furthermore, there's evidence that some ELHTs can vary spatially by juvenile habitat (Villegas-Hernandez et al. 2008) and juvenile condition and density of conspecifics can influence post-settlement survival (Tupper and Hunte 1994, Booth and Hixon 1999, Johnson 2008). Given the knowledge already acquired, there appears to be a large number of potential sources of variation in traits that can interact to influence selective mortality processes.

Study site

All the studies were carried out on coral reefs off the upper FK. The reefs of the FK are subtropical environments, with mean water temperatures varying seasonally from a low of 18°C in the winter to a high of 32°C in the summer. The reef tract is bathed by the Florida Current (FC), a major western boundary current. The FC is fed by two main sources: the Loop Current (LC) and the Antilles Current. The LC connects the Yucatan Current to the FC, which once it exits the Straits of Florida (SOF), becomes the Gulf Stream. The velocity of the FC through the SOF is seasonally variable, due wind and tidal cycles. Cyclonic frontal eddies that form along the boundaries of the LC and FC are the dominant mesoscale features in the southern SOF (Fratantoni et al. 1998) and larval

replenishment to the reefs has been hypothesized to be influenced by the formation and shedding of mesoscale eddies at the frontal boundary (Lee et al. 1994).

Objectives

The overall goal of this study was to determine if the composition of ELHTs varies with different environmental conditions, timing and location of settlement, and individual behavior and if so, how that affects selective mortality processes acting on the traits. The first objective was to examine how seasonal water temperature influences growth-related ELHTs and the intensity and direction of selective mortality processes acting on those traits. I sampled 16 monthly cohorts of settling larval and newly settled recruit *S. partitus*, 13 of which were tracked through time, and compared the distribution of otolith (ear stone)-derived ELHTs across seasons and through time (Chapter 2). Secondly, to determine if certain survival-related behaviors covary with ELHTs that are under the influence of selective mortality, I carried out field behavioral observations of both experimentally manipulated and naturally settled juvenile *S. partitus* (Chapter 3). Amount of sheltering, activity, and proximity to conspecifics were compared to otolith-derived measurements of size-at-settlement and mean juvenile growth to determine if they were correlated and could elucidate patterns in selective mortality. Third, I sought to identify temporal and spatial variation in recruitment and composition of ELHTs and determine how timing and location of settlement influences ELHTs and selective mortality processes. Monthly surveys and collections of newly recruited *S. partitus* were conducted over nearly six years in two habitats across six sites and combined with light trap catches of settlement stage larvae (Chapter 4). ELHTs were examined by size of recruitment events, lunar timing of settlement, habitat type, and density of conspecifics

and compared among age groups (settlement-stage larvae, 1-10 d post-settlement recruits, 11-28 d post-settlement juveniles). Lastly, to determine if genetic composition varies temporally with different settlement events as a result of differential transport or successful spawning of a small proportion of adults, and examine whether this variation is maintained or obscured through time, I compared six microsatellite loci and a part of the control I region of the mitochondrial genome among three monthly cohorts of settling larvae, newly settled recruits, and reproductively mature adults (Chapter 5).

Chapter 2: Temperature influences selective mortality during the early life stages of a coral reef fish

Background

Many organisms, including amphibians, insects, marine invertebrates, and fishes have complex life cycles with multiple ontogenetic shifts, characterized by changes in morphology, physiology, behavior, and/or habitat (Wilbur 1980). This life history confounds our understanding of the processes affecting population dynamics, because critical events may occur during any stage or cumulatively across stages (Wilbur 1980, Smith 1987, Phillips 2002). Metamorphosis from the larval to juvenile stage is thought to be a critical period characterized by a pronounced niche shift (e.g. from a pelagic to a benthic environment in marine organisms) and high rates of mortality (Wilbur 1980, Caselle 1999). Early life history traits (ELHTs), such as larval growth rate or stage duration, often vary among individuals due to differences in genetic makeup, maternal contributions, and/or environmental influences. This trait variation coupled with high mortality rates create conditions for selective processes to occur (Sogard 1997).

Temperature is well recognized in influencing metabolism and growth in poikilotherms (Atkinson 1994, Gillooly et al. 2001). Increases in environmental temperature result in metabolic rate increases and typically higher growth rates. Temperature differences in seasonal environments can increase variability of growth-related traits such as growth rate (Raven and Geider 1988, Houde 1989, Sponaugle et al. 2006), size (Blaxter 1991, Atkinson 1994), condition (McCormick and Molony 1995), and stage duration (Harkey and Semlitsch 1988, Gillooly et al. 2002). The consequences of such environmental influence can contribute to variation in survival (Pepin 1991,

Rutherford and Houde 1995, Qiu and Qian 1998) and recruitment magnitude (Rutherford and Houde 1995, Wilson and Meekan 2002, Bergenius et al. 2005).

The growth-mortality hypothesis (Anderson 1988) provides a theoretical framework for evaluating which traits may be selected for and whether consequences of performance based on larval traits propagate through to the juvenile stage (carry-over effects; Qian and Pechenik 1998, Searcy and Sponaugle 2001). It presumes that faster growing individuals, that are larger-at-age, or advance more quickly to the next stage, will preferentially survive. Faster growth results in larger individuals at a given age, which are less vulnerable to gape-limited predation ("bigger is better" mechanism; Anderson 1988, Miller et al. 1988). Furthermore, faster growing individuals will spend less time at smaller sizes and therefore have lower probabilities of mortality than slower growing individuals ("growth-rate" mechanism; Ware 1975). Additionally, faster growing individuals may develop and advance to the next life stage more rapidly, where predation and starvation pressures are expected to be diminished ("stage duration" mechanism; Houde 1987). Empirical evidence for larval experience influencing survival within a stage or even in subsequent stages is widely available for a number of taxa (amphibians, Goater 1994, fishes, Hare and Cowen 1997, polychaetes, Qian and Pechenik 1998, bryozoans, Wendt 1998, sponges, Maldonado and Young 1999, gastropods, Moran and Emlet 2001, crustaceans, Jarrett 2003, ascidians, Marshall et al. 2003, insects, De Block and Stoks 2005). Overall, larger size-at-hatching (Moran and Emlet 2001, Vigliola and Meekan 2002, Raventos and Macpherson 2005a), faster larval growth rate (Searcy and Sponaugle 2001, Takasuka et al. 2003), shorter stage duration (Meekan and Fortier 1996, Maldonado and Young 1999), larger size-at-metamorphosis (Semlitsch et al. 1988,

McCormick and Hoey 2004), higher condition-at-metamorphosis (Phillips 2002), and faster early juvenile growth (Searcy and Sponaugle 2001) generally enhance survival. However, these trends in selective mortality are not pervasive. Patterns of selective mortality may not be maintained through time (Gagliano et al. 2007a) or occur in all populations of a species (e.g. *Thalassoma bifasciatum*; Carr and Hixon 1995, Searcy and Sponaugle 2001). Additionally, some field and laboratory studies have provided evidence that, contrary to the growth-mortality hypothesis, faster growing and/or larger individuals can be more vulnerable to predation (Litvak and Leggett 1992, Pepin et al. 1992, Gagliano et al. 2007a). Thus, to maximize survival, behavioral or physiological trade-offs can result in less than maximally optimal traits (Lima and Dill 1990, Arendt 1997, Sogard and Olla 2002).

Where environments are heterogeneous and variable, not only will the range of traits exhibited by poikilotherms vary but the nature of their contributions to survival may change (Moran and Emlet 2001, Gagliano et al. 2007b, Durieux et al. 2009). I examined cohorts of a common reef fish settling to a subtropical reef system over a range of water temperatures to examine 1) how water temperature influences ELHTs and 2) whether selective loss of those traits over time changes in intensity or direction depending on temperature.

Materials and Methods

Study site and physical data sampling

The Florida Keys reef tract (FKRT) is bathed by the Florida Current (FC), a major western boundary current, with mean speeds of 1.6 m s^{-1} (Richardson et al. 1969) and daily and seasonally variable wind and tidal cycles. Cyclonic frontal eddies that form

along the boundaries of the Loop Current and FC are the dominant mesoscale features in the southern Straits of Florida (Fratantoni et al. 1998) and recirculation within eddies has been hypothesized to be a possible retention mechanism of both locally and upstream-spawned larvae in the FKRT (Lee et al. 1994, Lee and Williams 1999). Large multi-taxa pulses of settlement stage reef fishes have been shown to arrive to reefs during the passage of mesoscale eddies by the upper Florida Keys (FK; Sponaugle et al. 2005), but eddies also may advect larvae away from the FKRT (D'Alessandro et al. 2007).

Mean water temperature along the FKRT varies seasonally by approximately 10 °C and can significantly influence variation in ELHTs and recruitment strength (Sponaugle et al. 2006). Thus, to characterize the inshore environment of the FKRT, daily water temperature and current data were obtained from the National Underwater Research Center (NURC), which continuously records water temperature at 21 m depth at Conch Reef in the upper Florida Keys (FK; 24°59'N, 80°25' W). Additionally, SST and ocean color images of the FC, provided by the University of South Florida's Institute for Marine Remote Sensing (IMaRS), were used to describe the offshore environment and track the passage of mesoscale eddies.

Biological sampling

The bicolor damselfish *Stegastes partitus* is a common zooplanktivorous fish found throughout the FKRT, Bahamas, and Caribbean (Emery 1973). Juveniles and adults maintain benthic territories on spur and groove reefs and are found in highest densities within rubble at the reef base (pers. obs.). Adults spawn demersal eggs on a monthly basis throughout the year (Schmale 1981, Robertson et al. 1988), after which, the males guard the embryos for ~ 4 d until hatching (Robertson et al. 1988). Larvae

spend a mean of 30 d in the plankton before settling to the reef (Sponaugle and Cowen 1996a). Upon settlement, larvae metamorphose into juveniles overnight (pers. obs.). The timing of settlement appears to be synchronized with lunar phase, with pulses occurring during the third quarter and/or new moon (Robertson et al. 1988, Sponaugle and Cowen 1996a, D'Alessandro et al. 2007). Seasonal peaks in settlement to the FKRT typically occur during summer months (D'Alessandro et al. 2007). *Stegastes partitus* is an ideal model species for studying processes affecting the early life history of coral reef fishes because they are common throughout the Caribbean, are integral to the trophic dynamics of the reef community, are easy to observe and collect at all life stages, and have otoliths (ear stones) that provide a daily record of events occurring during early life.

To capture settlement-stage *S. partitus* larvae as they settled to the reef, light traps were deployed from June 2001 until January 2004 in conjunction with two other studies (Sponaugle et al. 2005, D'Alessandro et al. 2007). A total of three to six traps were deployed over a combination of four study sites located in the Florida Keys National Marine Sanctuary: French Reef (FR; 25°02.06' N, 80°21.00' W), Sand Island Reef (SI; 25°01.09' N, 80°22.08' W), Molasses Reef (MO; 25°00.74' N, 80°22.40' W), and Pickles Reef (PI; 24°59.23' N, 80°24.88' W). Larvae were used for analysis when sample sizes were sufficiently large ($n \geq 20$). Newly recruited *S. partitus* juveniles were censused and collected 3-5 d later at the same sites, with the exception of FR and MO, which are protected areas where benthic sampling was not permitted. Instead, recruits were collected just north of FR (NF; 25°02.53' N, 80°20.64' W) 3-5 d after larval collections at FR and MO. Recruit density was estimated by counting the number of newly recruited juveniles within ~ 20 randomly placed 5 × 1 m transects. Approximately 30 recruits were

collected by divers using hand nets and the anesthetic Quinaldine. Subsequent collections were made every 3-5 d thereafter for approximately two weeks, resulting in a total of three or four collections for each cohort (or group of fish settling at the same time; see below). All collected juveniles were immediately stored in 95% EtOH following collection to preserve their otoliths.

Otolith analysis

Prior to dissection, the standard length (SL) of each fish was measured to the nearest 0.01 mm by capturing an image of the fish with a Dage MTI digital video camera attached to a Leica MZ12 dissecting microscope and passing the image to a computer where it was analyzed using Image Pro Plus 4.5 image analysis software (Media Cybernetics). The otoliths of the collected fish were extracted and placed in a drop of medium viscosity immersion oil on a microscope slide to clear for a minimum of 30 d. Based on ease of reading, only the lapilli were examined (Sponaugle and Cowen 1996a). The clearest lapillus was chosen from each individual and viewed under 400× magnification through a Leica DMLB microscope equipped with a polarized filter between the first stage and light source. Similar to the SL protocol, the image was captured by a Dage MTI video camera and analyzed using Image Pro Plus 4.5 software. Each otolith was read once blind (no sample information available) and saved as a digital file. Images were re-examined blind to validate readings (Sponaugle and Pinkard 2004b). Otolith analysis was utilized to determine age (number of concentric increments), timing of hatching, timing of settlement, pelagic larval duration (PLD), larval and juvenile growth rates (increment widths), and size-at-age (otolith radius-at-each age, including settlement).

Data Analysis

Otolith analysis was used to back-calculate date of hatching and date of settlement. Only fish that settled within 14 d of each other were used in the analyses, resulting in 16 distinct cohorts. Utilizing the earliest hatch date and the earliest and latest settlement dates for each cohort, near-reef water temperature, chlorophyll a concentration, wind speed, alongshore and cross-shelf current velocity data, and all otolith-derived early life history traits (ELHTs; i.e. larval growth, PLD, size-at-settlement, juvenile growth) were averaged over the larval and juvenile periods separately.

Otolith-derived ELHTs were compared among cohorts using standard analysis of variance (ANOVA) techniques (SYSTAT version 11.0; Wilkinson 1992) where single measures were obtained for each individual fish. Where multiple measures were taken for each fish, such as otolith increment widths, only specific points (i.e. increments 1, 5, 10, 15, 20, 25, 27 d of larval life and 6 d post-emergence) were examined using separate ANOVA tests.

Canonical correspondence analysis was utilized to distinguish the relative importance of the various environmental factors in influencing ELHTs (CANOCO version 11.0; ter Braak and Smilauer 2002). Because of the known importance of temperature in influencing growth, the relationships among ELHTs and water temperature were further examined by comparing mean cohort-specific water temperature with mean cohort-specific larval growth over the entire larval period and during separate 5 d intervals, PLD, size-at-age, and size-at-settlement using least-squares regression techniques (SYSTAT version 11.0; Wilkinson 1992). Likewise, mean cohort-

specific juvenile growth over the first 6 d on the reef was regressed against the cohort-specific water temperature averaged over the juvenile period.

Because ELHTs have been demonstrated to influence recruitment magnitude (Bergenius et al. 2002, Wilson and Meekan 2002), which in turn can affect subsequent growth and survival (Booth 1995, White and Warner 2007), I examined the relationship between ELHTs and cohort density. Mean cohort-specific densities were regressed against the same mean cohort-specific ELHTs used in the regressions with temperature. Likewise, recruit densities were regressed against mean water temperature over the juvenile period.

Each cohort was further divided into four age groups: larvae, newly settled recruits (1-7 d post-settlement), intermediate juveniles (8-14 d post-settlement), and survivors (15-21 d post-settlement), which provided realistic timescales over which selective mortality could occur and resulted in sufficient sample sizes within the most age groups for each cohort. To determine whether mortality was selective with regard to any of the ELHTs, I compared the distribution of traits among age groups. If directional selection occurred for a given trait, there would be a shift in the distribution of that trait in the older age groups compared to younger age groups, or the initial population. Because temperature covaried with many of the traits, ELHTs were examined among age groups, with temperature as a covariate, using analysis of covariance (ANCOVA). For traits that could not be evaluated using ANCOVA (i.e. due to significant interactions between temperature and age group), monthly cohorts were divided into three seasonal groups by temperature (winter, spring, summer) and the traits were compared among age groups using general linear model (GLM) techniques. When significant differences were

detected, Tukey's post-hoc test was performed to identify which pair-wise differences were significant.

To determine whether growth trajectories of the different seasonal groups diverged through time, I examined daily growth by effect-coded season using repeated measures general linear model techniques (RM-GLM). To depict both linear and nonlinear forms of selective mortality, I estimated fitness functions using the cubic *b*-spline approach originated by Schluter (1988). This nonparametric method relates relative survival to quantitative traits without making any prior assumptions about the underlying model of selection. Age groups were coded as 0.25 (larvae), 0.5 (new recruits), 0.75 (intermediates), and 1 (survivors) to reflect relative fitness and used as poisson error terms in an iterative method of generalized linear models to estimate the splines. Because this method assumes that the initial group (larvae) has a fitness of zero (i.e. all individuals would be subject to mortality), the resulting surfaces are an underestimate of selective mortality. Therefore the method was adapted by Anderson (1995) and Sinclair et al. (2002) for two independent samples of a cohort, where $h(t)$ is the probability that a fish with a particular value of trait t at an initial age was caught in a sample of survivors, given that it was collected in one of the two samples. As per Sinclair et al. (2002), the initial group (larvae or new recruits) was coded as 1 and the survivor group as 3, and $h(t)$ estimated using a generalized additive model assuming a binomial error distribution and a logit link:

$$h(t) = e^u / (1 + e^u)$$

where u is a cubic *b*-spline smooth function of t , with a smoothing parameter λ chosen by generalized cross validation. The splines generated by the methods in Schluter (1988) and

Sinclair et al. (2002) were compared and the *b*-splines created using the fitness function developed by Schluter (1988) and the one adapted by Sinclair et al. (2002) were very similar in direction and shape. The main difference was in the estimated confidence bands. In many cases, they were wider using the adapted method because data was only included from the first sample taken and the last and information on the direction and intensity of selective mortality was lost from the intermediate age groups. However, because our data conforms to the assumptions of the function adapted by Sinclair et al. (2002), we are reporting those splines here (Fig. 2.4, 2.5).

Results

After removing fish that were too old or did not settle during the appropriate 14 d settlement windows, 1357 of 1682 aged fish were used in the analysis (Table 2.1). Sixteen monthly cohorts spanned June 2000 to November 2005, but only 13 were tracked through time (i.e. sampled in multiple collections and divided into age groups), and therefore included in the selective mortality analysis. The cohorts encountered mean water temperatures that ranged over 8.8 °C, encompassing nearly all of the seasonal variability in this region.

The CCA for six environmental variables and four ELHTs yielded a significant biplot based on a global permutation test (1000 permutations; $p < 0.01$; Fig. 2.1). The two axes explained ~ 36% of the variation in the ELHTs. However, when tested using forward selection and 1000 Monte Carlo permutations, near-reef water temperature averaged over the larval period was the only environmental variable included in the model because the addition of any other variable did not significantly improve the fit.

The ELHTs examined varied among all 16 cohorts (Table 2.1) and many were significantly related to temperature. Cohorts that recruited during the late-summer months (C, E, 3, 7) experienced faster mean larval growth rates than the cohorts that recruited during the winter (5, 6; Tukey: $p < 0.001-0.003$). While the relationship between mean growth (otolith increment width) over the entire larval period and temperature was marginally non-significant ($R^2 = 0.24$; $p = 0.053$), there was a significant positive relationship between early mean larval growth and mean water temperature (6-10 d: $R^2 = 0.40$; $p < 0.01$; Table 2.2). Likewise, size at 10, 15, 20, and 25 d of age was positively correlated with temperature. However, the relationship between size-at-settlement and temperature was negative ($R^2 = 0.31$; $p < 0.05$), likely due to the strong negative relationship between PLD and temperature ($R^2 = 0.62$, $p < 0.001$), since size-at-settlement is a function of growth rate and the number of days spent in the plankton. Larvae grew rapidly in warmer water, but settled sooner, resulting in small sizes-at-settlement. Mean near-reef water temperature explained 38% of the variation in mean juvenile growth over days 0-5 ($p < 0.05$). The seasonal forecast and hindcast larval growth trajectories demonstrate that summer *S. partitus* cohorts consistently grew faster than winter cohorts until day 27 of the larval period when warmer-water fish neared settlement, while cooler-water fish maintained more constant growth without settling (RM-GLM: $p < 0.01$; Fig. 2.2).

Density of new recruits varied from 0.00 to 0.63 recruits m^{-2} with a mean of 0.14 recruits m^{-2} . There were no significant correlations between recruit density and any of the ELHTs. A positive relationship between recruitment magnitude and mean water

temperature was significant once an outlier from the month with the largest recruitment event was removed ($R^2 = 0.44$; $p < 0.05$; Fig. 2.3).

In accordance with the growth-mortality hypothesis, individuals surviving up to three weeks on the reef were larger at the time of settlement regardless of temperature (Table 2.3, Fig. 2.4a). Contrary to the growth-mortality hypothesis, however, the survivor group also exhibited significantly slower growth over the first 6 d on the reef than the intermediates or the 6-7 d old recruits, once the extra variance due to differing water temperatures was controlled for (Table 2.4, Fig. 2.4b).

Since temperature interacted with larval growth and PLD to result in seasonal differences in selective mortality (Table 2.3), the monthly cohorts were grouped by season and the two traits reexamined by age group using GLM. During the winter months, survivors (i.e. those with higher fitness) exhibited faster mean larval growth than the intermediate group (Table 2.4, Fig. 2.5). Also in agreement with the growth-mortality hypothesis, there was a selective loss of individuals with longer PLDs during the coolest months (Table 2.4, Fig. 2.5). These trends were more or less maintained during the warm spring months, but changed sharply during the warmest months. During these summer months, individuals with shorter PLDs were selected against (Table 2.4, Fig. 2.5). The selective processes acting on larval growth rate were more complex. There was selection against faster growth during the beginning of the larval period (Days 1-5, $p < 0.01$; Table 2.4), but against slower growth towards the end of the phase (Days 20-25, $p < 0.001$; Table 2.4). This reversal may in part explain why there was no significant linear selective mortality evident in mean larval growth over the entire period ($p = 0.276$; Table

2.4), but the increased fitness of the fastest and slowest growers, as indicated by the *b*-spline, suggests that disruptive selection occurred (Fig. 2.5).

Discussion

Results of this study demonstrate that not only does temperature influence the ELHTs that are important to surviving the critical period of early juvenile life, but temperature can also influence how selective mortality processes act on those traits. Temperature influences growth-related ELHTs of a diversity of organisms, including daily growth rates, size-at-age, and length of development (Houde 1989, Blaxter 1991, McCormick and Molony 1995, Qiu and Qian 1998, Jarrett 2003, Meekan et al. 2003, Sponaugle et al. 2006) and selective mortality frequently acts on those traits (Goater 1994, Meekan and Fortier 1996, Qian and Pechenik 1998, Searcy and Sponaugle 2001, McCormick and Hoey 2004, Raventos and Macpherson 2005a, Gagliano et al. 2007a). However, there has been little evidence of a direct link between temperature and patterns of selective mortality (but see Gagliano et al. 2007b, Durieux et al. 2009). To my knowledge, the present study is the first to demonstrate that seasonal changes in water temperature not only influence the intensity of selective mortality, but can reverse the selective pressure on particular traits.

Temperature mediated traits and recruitment

ELHTs varied among the 16 damselfish cohorts examined in this study and a significant portion of the variation could be explained by temperature. Mean near-reef water temperature explained 62% of variation in PLD: larvae in warmer water spent less time in the plankton. Additionally, warmer water fish settled at smaller sizes, largely because they experienced a shorter larval duration. While there was no significant

relationship between larval growth and water temperature, early juvenile growth (averaged over the first 6 d) was faster during the summer compared to the winter ($R^2 = 0.38$; $p < 0.05$). In contrast, variation in water temperature explained 78% of the variation in larval growth of another common reef fish in the FK, *Thalassoma bifasciatum* (Sponaugle et al. 2006). One potential explanation for this difference is that growth and development are less variable in *S. partitus*: seasonal variation in larval growth (CV: 7.5) and PLD (CV: 10.3) of *S. partitus* was smaller than that for *T. bifasciatum* (CV: 10.3 and 15.9 respectively; Sponaugle and Grorud-Colvert 2006) in the same region, despite the fact that *S. partitus* recruits were sampled over a wider range of water temperatures (8.8 °C vs. 6.5 °C). Additionally, results of the CCA suggest that other unmeasured factors may play a role in shaping growth-related traits. For instance, Wilson and Meekan (2002) determined that water temperature, rainfall, and a component of the wind influenced larval growth of *S. partitus* collected over the reefs of San Blas.

Recruitment magnitude varied seasonally, but was unrelated to any of the ELHTs examined. Although the recruitment of reef fishes from other locations, such as Panama, is known to be related to growth or size-at-settlement (Bergenius et al. 2002, Wilson and Meekan 2002), differences in oceanography of the two systems make a comparison difficult. Stochastic physical processes (e.g. transient mesoscale eddies) are likely more prevalent in the FK and may disrupt fundamental biological relationships (Sponaugle et al. 2005). Recruit density did covary with water temperature, but the underlying mechanisms are unclear. Increased spawning output in warmer water is one possibility.

Patterns in selective mortality

Regardless of water temperature, larger *S. partitus* settlers preferentially survived the first 2-3 weeks on the reef. This is consistent with the ‘bigger-is-better’ component of the growth mortality hypothesis. Similar patterns have been detected for another pomacentrid, *Pomacentrus amboinensis*, on the Great Barrier Reef (GBR; McCormick and Hoey 2004). However, the opposite trend in selective mortality has been observed for other reef fishes (Sponaugle and Grorud-Colvert 2006), including *P. amboinensis* sampled in the same area of the GBR in a different year (Gagliano et al. 2007a).

Contrary to what is predicted by the growth-mortality hypothesis, *S. partitus* survivors experienced slower mean growth over the first 6 d post-settlement than the younger age groups. Very fast growth is known to be associated with reduced fitness in other taxa (Jennings et al. 1999, Olsson and Shine 2002, Arendt 2003, Alonso-Alvarez et al. 2007) and several potential trade-offs with accelerated growth explain why slower growth could be beneficial. Physiologically, rapid growth may be attained at the expense of development, tissue maintenance and repair, and, for fish, swimming capabilities (Arendt 1997). Compromise of these functions could result in reduced ability to escape predation. For instance, Sogard and Olla (2002) found that sablefish undergoing higher compensatory growth exhibited lower critical swimming speeds than fish with average growth rates. Potential behavioral trade-offs of faster growth are increased foraging activity or selection of foraging habitats which may expose individuals to greater risk of predation. While undergoing compensatory growth, juvenile coho salmon habituated to predators more quickly and were more likely to feed in risky food patches than continually fed conspecifics (Damsgard and Dill 1998). Likewise, fast growing Pacific

halibut exhibited increased swimming activity, relative to slower growers (Hurst et al. 2005). One potential explanation for the decoupling of size-at-settlement and juvenile growth in *S. partitus* is that larger settlers are less vulnerable to gape-limited predation, and may be able to quickly begin defending benthic territories. While larger settlers may still experience higher survival, the allocation of energy to territory defense may result in reduced juvenile growth, relative to smaller settlers.

Thalassoma bifasciatum juveniles, sampled on the same reefs as the present study, experienced the opposite trend in selective mortality for size-at-settlement and early juvenile growth (Sponaugle and Grorud-Colvert 2006). Individuals surviving the first two weeks on the reef were smaller at settlement, but of higher settlement condition. Survivors also grew more quickly during the first 3 d on the reef than the younger age groups. This indicates that selective mortality processes during early life are species-specific and likely related to life history strategies. For instance, *T. bifasciatum* has a longer and more variable larval duration followed by a protracted metamorphosis while buried under reef substrates, during which it does not feed. In comparison, *S. partitus* has a relatively short and less variable PLD and metamorphosis occurs within 24 h. For *T. bifasciatum*, it is possible that condition at the time of settlement is more important to surviving a lengthy metamorphosis than large size, whereas, larger *S. partitus* juveniles are less vulnerable to gape-limited predation they face immediately following settlement. Additionally, the methods of predator evasion utilized by these species differ, as *S. partitus* maintains small territories with refuges in which to shelter, while *T. bifasciatum* swims away to evade predators. These differences in life histories likely underlie the contrasting selective pressures exerted on them by predators.

The importance of size-at-settlement to survival of juvenile *S. partitus* illustrates how events occurring in one stage can carry over to influence survival during subsequent stages. Size-at-settlement is a function of larval growth and PLD and smaller sizes-at-settlement were consistently selected against during juvenile life in all seasons and years. The extent to which these carry-over effects continue to influence fitness in the adults that survive to contribute to the population could have important consequences for population dynamics.

Temperature induced changes in selective mortality

Patterns in selective mortality acting on larval growth rate and PLD changed with seasonal water temperature. In the cooler winter and spring months, individuals with slower larval growth rates and longer PLDs were selectively removed from the population, in accordance with the growth mortality hypothesis. However, during the summer months, there was a reversal in selection against individuals that spent shorter periods in the plankton. There was no significant directional selective mortality acting on larval growth during the warmest months, and some evidence that disruptive selection (i.e. loss of individuals with intermediate growth rates) occurred. Overall growth is faster (range shifts up) and two strategies that appear to enhance survival during the warmest months: faster larval growth or slower larval growth paired with a longer larval developmental period. Either extreme should result in larger sizes-at-settlement. Perhaps, as suggested for another reef fish, a minimum condition is required for settlement and this is attained more rapidly by fast growers as they store energy (lipids) at a faster rate, while slower growers must spend more days in the plankton accumulating lipids more slowly (Searcy and Sponaugle 2000).

Three recent studies have examined the influence of temperature on selective mortality: Gagliano et al. (2007b) determined, through the use of laboratory experiments, that egg size of the tropical damselfish *Pomacentrus amboinensis* was positively related to survival at control temperatures, but had no effect on survivorship at higher or lower temperatures. Likewise, wild caught silver-stripe round herring *Spratelloides gracilis* exhibited negative size-selective mortality and growth-selective mortality during the coolest month when their growth was the slowest (Durieux et al. 2009), yet selective mortality was not detected in any of the other cohorts. Grorud-Colvert and Sponaugle (*unpublished data*) similarly found that selection intensity on settlement condition in *T. bifasciatum* changed with temperature: During the coldest months there was strong selective mortality in favor of *T. bifasciatum* of higher condition, whereas, in the warmest month there was no significant directional selection. To my knowledge, however, the present study is the first to demonstrate that seasonal changes in water temperature can reverse the selective nature of mortality on particular traits, such as PLD. Thus, not only does temperature influence growth-related ELHTs, but also the direction and intensity of selective mortality acting on those traits. What is optimal for survival during one season may not be in others (Moran and Emler 2001, Durieux et al. 2009). This may explain why studies conducted over short periods of time have yielded contradictory results, and highlights the importance of research that encompasses seasonal variability. It is still unknown what the relative contribution to the adult population is from recruits arriving during the winter months compared to those settling during the summer. Although recruitment is lower in the winter, due to potentially stronger selective mortality, the

survivors could be particularly vigorous and may substantially contribute to the population.

In this study it is difficult to disentangle the direct effects of temperature from other factors that vary on a seasonal basis, including predator and prey composition and abundances (Pepin et al. 2003, Pepin 2004, Buckley and Durbin 2006). Enhanced prey abundances can positively influence growth rates and recruitment (Buckley and Durbin 2006), while predators can exert greater selective mortality pressures on fast-growing individuals that are entering their prey field (Pepin et al. 2003). I did not detect a strong relationship between growth-related traits and primary production (chlorophyll a concentration), but without measures of zooplankton prey and predator abundances, I cannot eliminate the interaction of these factors.

Taking into account ongoing global climate change, these results suggest that patterns in selective mortality may diverge from what currently exists. For instance, for *S. partitus* experiencing warmer temperatures, patterns in selective mortality acting on PLD reversed from selection against longer PLDs, to selection against shorter PLDs. While this suggests stabilizing selection over seasonal scales, in the context of long term climate change, one of these seasonal patterns may diminish in importance (i.e. selection against longer PLDs during cooler months). This situation is further complicated by the fact that PLD is negatively correlated with temperature. Under warmer conditions, PLD should be shorter, but selective mortality against short PLDs may result in lower fitness of a large portion of the settling cohort. The larger implications are that adaptive trends could change with increasing global temperatures, leading to the evolution of new early life strategies.

Table 2.1. Sixteen cohorts of *Stegastes partitus* used in temperature analysis, 13 of which were used in selective mortality analysis (divided into age groups). Mean LT and JT refer to near-reef water temperature (°C) averaged over the first hatch date to last settlement date (LT) and the first settlement date to last collection date (JT). Larvae (L) are settlement-stage larvae collected in light traps. Recruits (R) are juveniles from 1-7 d post-settlement; Intermediates (I), 8-14 d post-settlement; Survivors (S), 15-21 d post-settlement. Larval growth (LG) is mean otolith increment width over the entire pelagic larval duration (PLD); Juvenile growth (JG) is mean otolith increment width over the first 6 d post-settlement. Settlement size is otolith radius at the time of settlement.

Cohort	Settle Month-Yr	Mean		Number of	Total	LG (µm)	PLD (d)	Settlement Size (µm)	JG (µm)
		LT	JT						
5	Feb-03	20.6	21.2	18	18	7.8	29.2	234.3	4.6
6	Mar-03	21.0	21.3	14	14	7.8	29.9	239.1	4.7
9	Apr-05	22.9	23.9		14	8.0	29.6	244.1	4.8
8	Jan-04	23.9	23.4		19	7.8	30.2	228.6	
1	May-00	25.8	26.7	17	22	8.1	28.1	235.4	5.0
A	Jun-01	26.0	27.2	70	29	7.4	28.3	211.1	5.7
10	Oct-05	26.7	26.5		15	8.6	26.3	232.3	4.2
D	Jun-02	27.7	28.3	13	32	8.3	25.6	219.5	5.3
B	Jul-01	28.2	28.8	176	45	7.8	28.4	222.8	5.1
F	Jul-03	28.5	28.7	34	14	7.9	26.7	211.1	5.2
2	Jul-02	28.6	29.3	34	34	8.3	24.5	210.5	5.1
4	Oct-02	28.6	28.0		20	8.0	27.0	224.0	6.0
C	Aug-01	28.9	29.4	68	27	8.2	27.7	234.2	5.1
7	Aug-03	28.9	29.4		15	8.6	26.7	234.3	5.9
3	Sep-02	29.3	28.8		20	8.3	25.5	220.6	5.0
E	Aug-02	29.4	29.3	23	15	8.2	26.7	222.1	5.2

Table 2.2. Results of least-squares regressions between early life history traits and mean water temperature for 16 monthly cohorts of *Stegastes partitus*; * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

Trait		Relationship	R ²
Larval growth	entire period	+	0.24
	1-5 d	+	0.23
	6-10 d	+	0.40**
	11-15 d	+	0.30*
	16-20 d	+	0.18
	21-15 d		0.00
	1-5 d prior to settlement		0.02
PLD		-	0.62***
Size-at-age	5 d	+	0.23
	10 d	+	0.37*
	15 d	+	0.45**
	20 d	+	0.44**
	25 d	+	0.31*
	settlement	-	0.31*
Juvenile growth	entire period	+	0.24
	1-6 d	+	0.38*

Table 2.3. P-values of ANCOVA using *Stegastes partitus* otolith-derived traits (PLD, mean larval growth rate, size-at-settlement, mean juvenile growth rate over the first 6 d) as the dependent variables, age group (larvae, L; recruits, R; intermediate, I; survivors, S) as the factor, and mean water temperature over the larval period as the covariate. Where interactions were non-significant, Tukey tests revealed where traits varied significantly among age groups.

Trait	Interaction	Temp	Age Groups	Tukey
Larval growth	<0.001			
PLD	<0.001			
Size-at-settlement	0.221	0.369	<0.001	L < R < I < S
Juvenile growth 1-6	0.962	<0.001	<0.001	R > I > S

Table 2.4. Results of GLM, comparing *Stegastes partitus* otolith-derived traits (PLD and mean larval growth rate) among age groups (larvae, L; recruits, R; intermediate, I; survivors, S) for three different seasonal periods. Where significant relationships occurred, Tukey tests revealed where traits varied significantly among age groups.

Cohorts	Trait	P-value	Tukey
Winter	Larval growth	0.014	I < S
	PLD	0.023	I > S
Spring	Larval growth	<0.001	L < R, I, S
	PLD	<0.001	L > R, I
Summer	Larval growth	0.276	
	LG 1-5	0.005	L > R
	LG 6-10	0.002	L > R, R < I
	LG 11-15	0.005	L > R
	LG 16-20	0.282	NS
	LG 21-25	<0.001	L < R < I < S
	LG Last 5 d	<0.001	L < R < I < S
	LG 6-10 d prior	0.057	NS
PLD	<0.001	L < R, I < S	

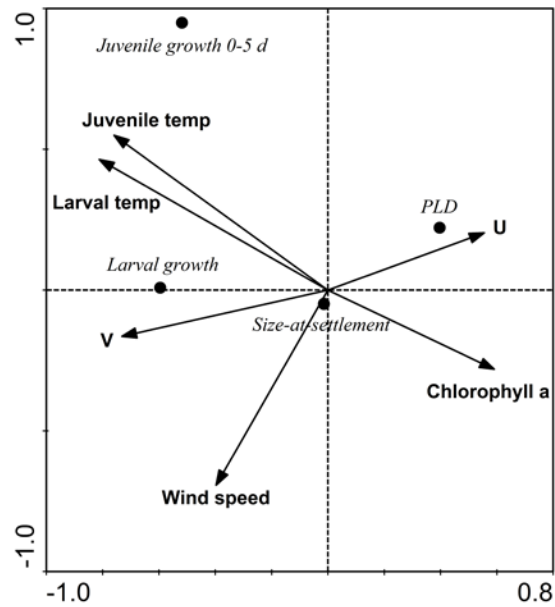


Figure 2.1. CCA ordination of *Stegastes partitus* early life history traits (mean larval growth, PLD, size-at-settlement, and mean juvenile growth during 0-5 d) and physical environmental factors (near-reef water temperature averaged over larval period and juvenile period, chlorophyll a concentration, wind speed, alongshore, and cross-self current velocity data).

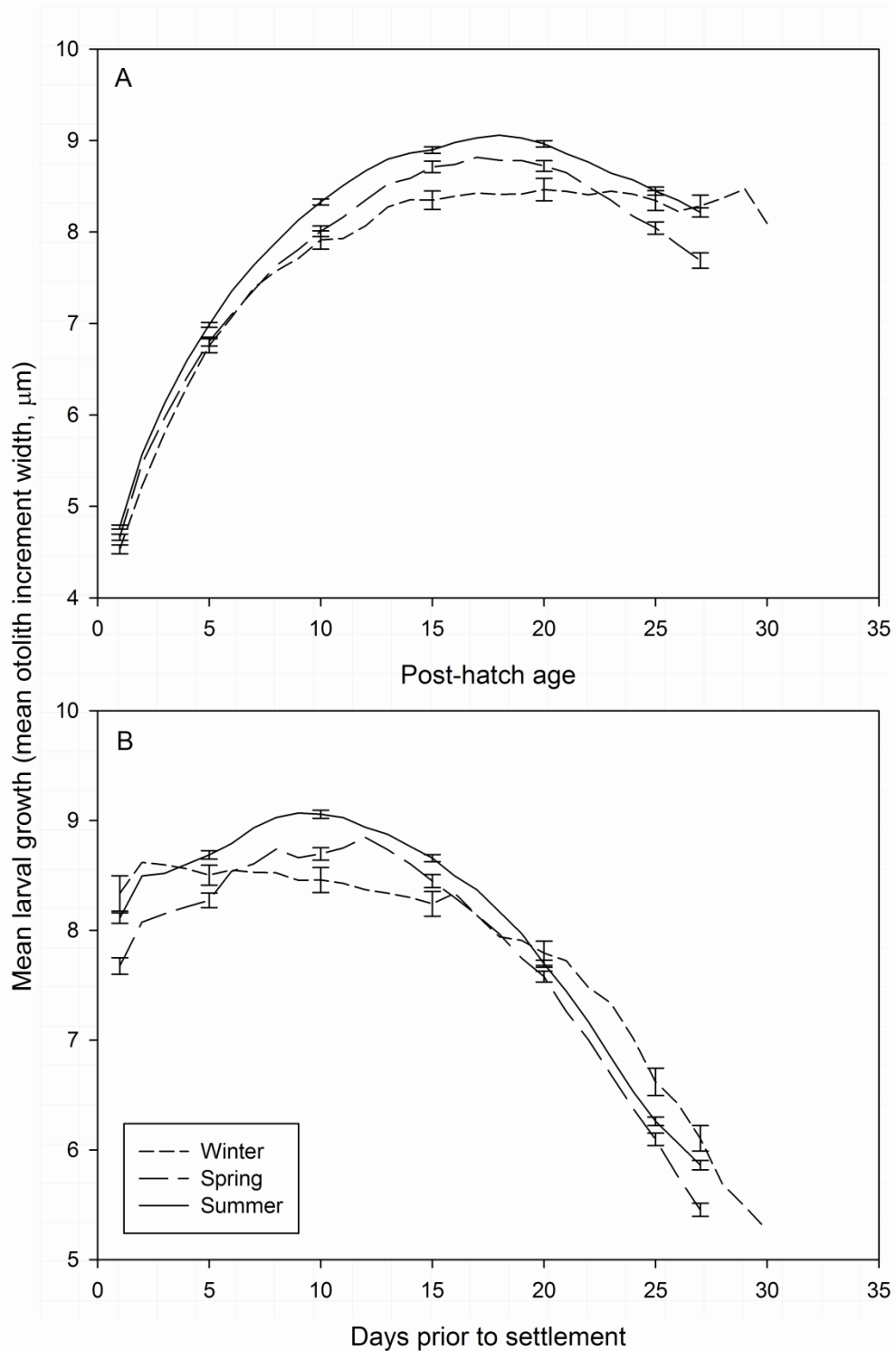


Figure 2.2. Otolith larval growth trajectories for *Stegastes partitus* settling during three different seasons. (A) Mean daily otolith increment widths from hatching until settlement. (B) Mean daily otolith increment widths hindcast from settlement until hatching. Representative SE bars are provided at increments 1, 5, 10, 15, 20, 25, and 27.

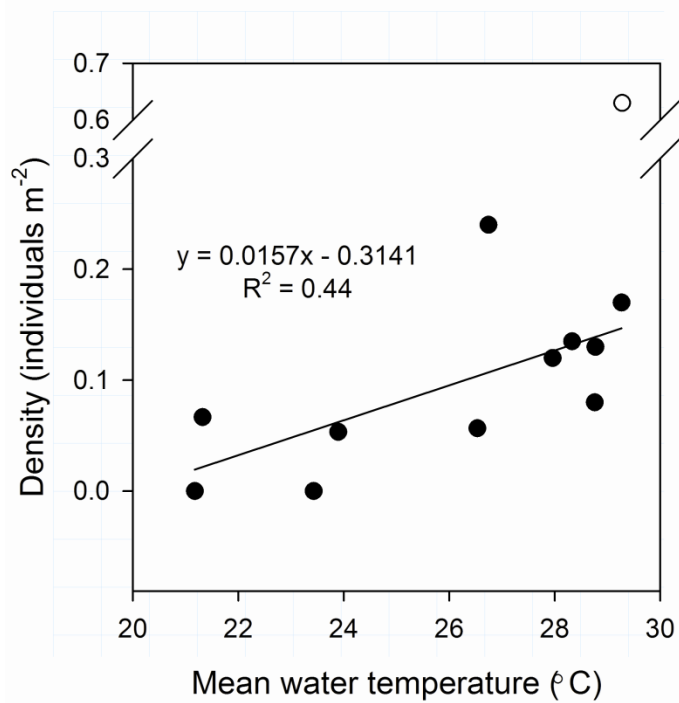


Figure 2.3. Relationship between new recruit density and mean water temperature over the juvenile period for all monthly cohorts of *Stegastes partitus* where recruit density was estimated. Relationship was significant when one outlier (o) was removed.

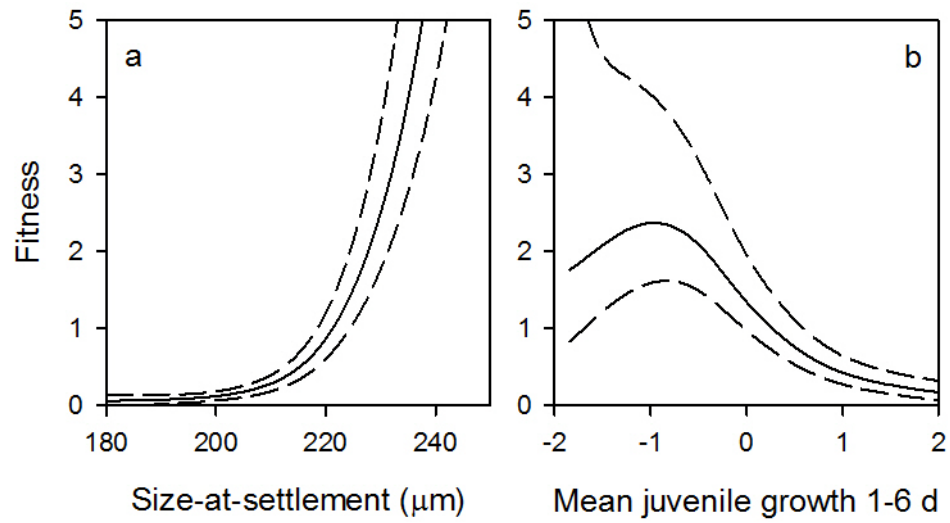


Figure 2.4. Intensity and shape (as cubic b -splines) of selective pressures acting on two otolith-derived traits, (a) mean size-at-settlement and (b) residuals of juvenile growth 1-6 d post-settlement regressed against seasonal water temperature, in 13 cohorts of *Stegastes partitus*.

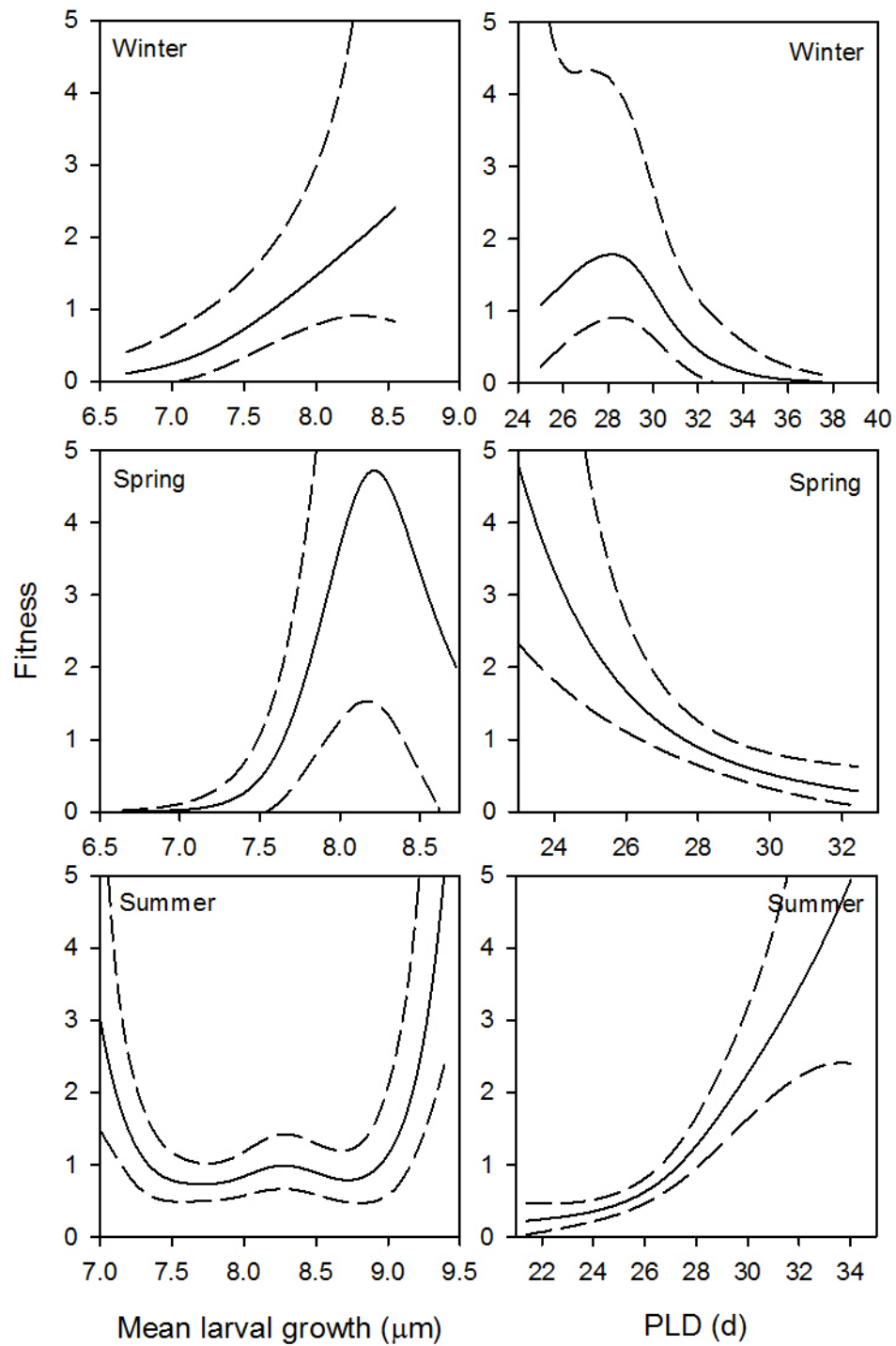


Figure 2.5. Intensity and shape (as cubic b -splines) of selective pressures acting on two otolith-derived traits, mean larval growth and PLD, in 13 cohorts of *Stegastes partitus* for 3 different seasonal periods, winter, spring, and summer.

Chapter 3: Influence of behavior on early juvenile growth and survival in a coral reef fish

Background

Predation is one of the major selective forces shaping the form and behavior of animals (Endler 1991, Lima 1998, Lind and Cresswell 2005). This is particularly true of the early life stages, which frequently endure high mortality rates due to predators (Sogard 1997, Houde 2002). Individuals with morphologies or behaviors that facilitate avoidance or escape from predators will have a greater probability of surviving to reproductive maturity and increasing their fitness.

The growth-mortality hypothesis (Anderson 1988) provides a theoretical framework for evaluating which traits may be selected against by predators. It contends that individuals that grow faster, attain larger sizes-at-age, or have reduced early life stage durations will experience enhanced survival. However, fast growth is known to be associated with reduced fitness in many taxa (Jennings et al. 1999, Olsson and Shine 2002, Arendt 2003, Alonso-Alvarez et al. 2007) and several potential trade-offs with accelerated growth may explain why slower growth could be beneficial. Physiologically, rapid growth may be attained at the expense of development, tissue maintenance and repair, and, for fish, swimming capabilities (Arendt 1997). Compromise of these functions could result in reduced ability to escape predation.

Behavior may also interact with these growth-related traits to influence survivorship. For instance, smaller fish are more vulnerable to gape-limited predation and therefore may be more wary and shelter more often or for longer durations (Sogard 1997). However, smaller individuals also typically have lower fat reserves, higher

weight-specific metabolic requirements, and larger drag coefficients and therefore may need to spend more time foraging than larger individuals (Wootton 1994, Krause et al. 1998). Likewise, amount of foraging activity or selection of foraging habitats influences subsequent growth rates, as well as exposure to predators (Lima and Dill 1990).

My previous research (Chapter 2) focused on identifying the growth-related traits important to the survival of young coral reef fishes. For a common reef fish, the bicolor damselfish *Stegastes partitus*, individuals surviving the first three weeks of life following settlement to the reef tend to be larger at settlement, but interestingly, grow more slowly during the first 6 d post-settlement (Chapter 2). The objective of the present study was to determine whether behavioral mechanisms underlie these unusual patterns in settlement size, growth rate, and survivorship.

My method for testing the hypothesis that survival-related behaviors covary with settlement size and juvenile growth was to combine behavioral observations of both experimentally manipulated and naturally settled juvenile *S. partitus* with otolith (ear stone)-derived measurements of size and growth. While otolith microstructure analysis is a common tool used to elucidate patterns in growth and mortality during the early life stages of fishes (e.g. Sogard 1997, Searcy and Sponaugle 2001), to my knowledge, it has not been utilized in conjunction with field observations to link behavior with growth. The advantage of this technique is the ability to back-calculate size and growth rates in order to compare these traits in the past and at the same point in time among individuals. In addition, age and timing of settlement can be determined and controlled for. Previous studies examining the influence of size and growth on risk-taking behaviors have created size or growth discrepancies by including fish of different ages (Dowling and Godin

2002, Brown and Braithwaite 2004, Fuiman et al. 2005), however, relationships between behavior and size or growth can be confounded by the differing levels of development and experience in different aged fish. Older individuals may have more experience with predators, and as a result, react differently to potential threats (McCormick and Holmes 2006). Developmental time can influence physiological capabilities, particularly during early life stages. I attempted to examine differences in behavior among fish that settled to a coral reef at the same time, therefore having the same level of development and experience with reef predators. I also compared experimentally manipulated fish with naturally settled individuals to determine if processes occurring during settlement can influence subsequent behavior.

Methods

Study species and site

The bicolor damselfish *Stegastes partitus* maintains benthic territories on spur and groove reefs in the Caribbean and Western Atlantic (Emery 1973), preferring dead coral rubble piles at the reef base (Chapter 4, pers. obs.). Adults are zooplanktivorous, but juveniles also consume benthic algae (Emery 1968). Adults are benthic brooders, with the males guarding the embryos for ~ 4 d until hatching (Robertson et al. 1988). Larvae have a pelagic larval duration of approximately one month (Sponaugle and Cowen 1996a), after which they find appropriate settlement habitat and metamorphose into juveniles overnight (pers. obs.). This transition is recorded in their otoliths. Additionally, daily deposition of material on otoliths provides a chronological record of size and growth. *Stegastes partitus* is an ideal model species for studying relationships among size, growth, and early juvenile behavior because they are abundant, easy to sample at both the

late larval (settlement) stage and as benthic juveniles, and they remain strongly site attached following settlement, facilitating repeated behavioral observations. The main predators on *S. partitus* juveniles are unknown, but barracuda (*Sphyraena barracuda*), bar jack (*Caranx ruber*), and cero (*Scomberomorus regalis*) have been observed preying on adults (Emery 1968). *Stegastes partitus* have also been found in the guts of trumpetfish (*Aulostomus maculatus*; Randall 1967). Gut contents indicate that *S. partitus* are not likely a common part of the diet of muraenids or other nocturnal fish (Randall 1967).

In the present study, late stage larvae were captured in light traps deployed from April 2008 to June 2009. Four to eight traps were deployed at three study sites located in the Florida Keys National Marine Sanctuary: North French Reef (NF; 25°02.53' N, 80°20.64' W), Sand Island Reef (SI; 25°01.09' N, 80°22.08' W), and Pickles Reef (PI; 24°59.23' N, 80°24.88' W).

Field manipulations

Fish were removed from the traps between 0700-0800 h and returned to the field station. They were kept overnight in a 114 l tank supplied with aerated seawater and coral rubble from the reef to allow for the completion of metamorphosis and acclimation to rubble substrate. The following morning, the standard length (SL) of each settler was measured to the nearest 0.5 mm. Individuals were paired by SL, such that one settler was ≥ 1.0 mm SL larger than the other. To enable individual identification, fish were injected in the dorsal musculature via a 30-gauge hypodermic needle with one of two colors of fluorescent elastomer (pink or green; randomized; as per Hoey and McCormick 2006). Following tagging, the pairs were transported back to the reefs in clear polyethylene bags

filled with seawater. Pairs were released onto randomly chosen 1 m² patches of rubble at Pickles or Sand Island reefs. A small, cylindrical wire cage (21 cm height by 23 cm diameter, 12 mm mesh size) was placed over fish pairs for a minimum of 2 h to protect them against predators while they acclimated to their new surroundings. Between 12-18 replicate pairs were established per experiment. Experiments were replicated a total of three times: once in August 2008, May 2009, and June 2009. Survival of tagged fish was monitored and recorded daily throughout each experiment. When an individual was missing, the surrounding area was searched to determine if the fish emigrated from its original location. Experiments were not terminated immediately once one fish of the pair was missing because additional days on the reef were necessary to measure juvenile growth. This was repeated every day until the end of the experiment (7 days). Because no emigrants were found, absence of experimentally established fish was interpreted as mortality.

Behavioral observations

Behavioral observations were conducted for every tagged fish each day between 1030 and 1430 h. This time interval was established as the peak period of activity for newly settled juvenile *S. partitus* in a pilot study and agrees with general feeding patterns established for the species (Myrberg 1972). Furthermore, boldness and aggression have been shown to be influenced by small within-day changes in water temperature in another damselfish *Pomacentrus moluccensis* (Biro et al. 2010). By restricting the time of day that observations were carried out, fluctuations in temperature were minimized.

To provide a comparison to the experimental trials, naturally settled juveniles were also observed. Depending on the number of divers available and the time in the

water, 11-32 observations were carried out each day. Both the experimental and natural observations have advantages and disadvantages. The benefit of establishing the fish at settlement is that their juvenile ages are controlled for. However, early post-settlement mortality is so high that many individuals will not survive the multi-day experimental trials, and thus their otoliths and the age and growth data they contain will be lost.

Observing naturally settled juveniles and collecting them immediately following a single observation ensures that all behavioral observations can be compared to otolith-derived traits, but juvenile age is unknown until otolith microstructure analysis, resulting in the exclusion of some individuals.

Each day of observations, a pair of divers would locate a pair of tagged or naturally settled juveniles and allow 2 min for the subject(s) to acclimate to their presence. The divers would then observe the subject(s) for 5 min, recording for each fish: (1) total time spent sheltered under rubble, (2) number of times shelter was sought, (3) maximum distance traveled horizontally and vertically from primary shelter, (4) density of conspecifics within a 7 m² area, and (5) closest distance to a conspecific. In addition to the above behaviors, in May and June 2009, divers also recorded for each fish: (6) number of bites taken on the substrate and in the water column, (7) number of times it chased or was chased by a conspecific, and (8) total time it spent chasing or being chased. At the end of each observation period, a model of a predator was used to elicit an escape response and this was videotaped at a frame rate of 30 s⁻¹ to estimate escape swimming speeds. Digital images were processed with VideoMach (Gromada v. 5.5.3) and analyzed in Image Pro Plus (Media Cybernetics v. 4.5). Habitat quality was assessed for each subject by estimating percent cover of live coral, macroalgae, hard bottom, rubble, and

sand, using a 2.25 m² quadrat placed with the subject's primary shelter in the center of the quadrat. A photograph of the quadrat was taken from directly above for future reference. Naturally-occurring juveniles were collected following a single observation period and stored in 95% EtOH to preserve their otoliths for microstructure analysis. For the experimental trials, all tagged survivors were collected on the seventh day, and stored in 95% EtOH.

Otolith analysis

Prior to dissection, the SL of each fish was measured to the nearest 0.01 mm by capturing an image of the fish with a Dage MTI digital video camera attached to a Leica MZ12 dissecting microscope and passing the image to a computer where it was analyzed in Image Pro Plus 4.5 image analysis software. The otoliths of the collected fish were extracted and placed in a drop of medium viscosity immersion oil on a microscope slide to clear for a minimum of 30 d. Based on ease of reading, only the lapilli were examined (Sponaugle and Cowen 1996a). The clearest lapillus was chosen from each individual and viewed under 400× magnification through a Leica DMLB microscope equipped with a polarized filter between the first stage and light source. Similar to the fish-measuring protocol, the image was captured by a Dage MTI video camera and analyzed using Image Pro Plus 4.5 software. Each otolith was read blind (i.e. no size or behavioral information available) by a single reader. Once all of the otoliths were read once, the process was repeated. If the difference in larval or juvenile ages between the two reads was < 5%, one of the two reads was chosen randomly as the final read. If the difference was ≥ 5%, the otolith was read a third time and the three reads compared. If the age of third read was < 5% different from either of the other two reads, the final read was chosen from one of the

closest values. If there was still a high discrepancy after the third read, the otolith was discarded. In total, three fish were rejected due to high variance among the three readings.

Data analysis

For naturally settled juveniles, otolith analysis was used to determine juvenile age (number of juvenile increments), juvenile growth rates (increment widths), and size-at-settlement (otolith radius-at-settlement). Only fish that were between 4-6 d old post-settlement were used in the analyses, to minimize the influence of age and experience on behaviors.

I previously demonstrated that temperature influences growth-related early life history traits in *S. partitus* (Chapter 2), thus to control for the influence of temperature among the three months of observations, values of the behavioral traits and the otolith-derived traits were standardized: the monthly mean was subtracted from the raw values and the difference was multiplied by 100 to get a percent deviation from the mean.

Relationships between behavioral traits and otolith-derived early history traits (i.e. size-at-settlement and mean juvenile growth) were examined using least-squares regression techniques, including individual linear regressions and forward stepwise multiple regressions (SYSTAT version 11.0; Wilkinson 1992). Where age covaried with behavioral traits in the naturally settled juveniles, behaviors were examined among early life history traits using analysis of covariance (ANCOVA). The relationship between age and behavior was detrended and the residuals were included in linear regressions with size-at-settlement and juvenile growth. To determine which behaviors or traits were most informative in explaining individual juvenile growth rates, I used regression tree analysis

(CART version 6; Fuiman et al. 2006). Briefly, this technique builds trees that predict the value of a dependent variable from a group of independent variables (i.e. behaviors) through recursive partitioning. The average sum of squares, averaged over all of the terminal nodes was used as goodness-of-fit statistic to build the model, and is reported as the proportion of reduction in error (PRE). I used a stopping criterion to stop growing the tree when nodes contained less than five percent of the total data. A pruning algorithm of 10-fold cross-validation was applied to produce a final tree that was a balance of complexity and reduction of sum of squares.

Results

From July 2008 until June of 2009, 206 observations were made on naturally settled juvenile *S. partitus*. Of those, 86 individuals ranged from 4-6 d old post-settlement and could thus be used in further analyses. Across the three experiments, 43 pairs of tagged settlers were established on the reef. One juvenile was positioned by itself in the May experiment, because its partner was injured en route to the site. Across all experiments, there was 44.8% survivorship over the length of the trial (7 d post-settlement). The August experiment had the highest survivorship (62.5%; Table 3.1) and the May experiment had the lowest (25.9%). Most of the mortality occurred over the first 24 hr, before the first observations were made, therefore few behaviors and no age/growth data were recorded for fish that did not survive the experimental trials and this precluded comparisons of behaviors between survivors and non-survivors. Within each trial, there was a trend in size-selective mortality, whereby larger settlers tended to preferentially survive, however it was marginally non-significant in any individual experiment or after standardizing each SL by the monthly mean and combining all the

experiments (t-test; $p = 0.066$). When the June experiment was excluded, however, the survivors of the combined August and May experiments were significantly larger than the non-survivors (t-test; $p = 0.017$).

For naturally settled juveniles, the relationship between mean juvenile growth rate and size-at-settlement was not significant for all months of observations considered together. However, for fish observed in 2008, individuals with larger settlement sizes had significantly slower juvenile growth rates ($R^2 = 0.09$, $p = 0.017$; Fig. 3.1a). Likewise, there was a significant negative relationship between mean juvenile growth and size-at-settlement across the three experiments ($R^2 = 0.15$, $p = 0.015$; Fig. 3.1b).

Comparison of behaviors and traits individually revealed several significant relationships. For naturally settled juveniles, individuals that were larger at settlement tended to spend less time sheltering within the rubble and traveled farther horizontally from the rubble piles (Table 3.2; Fig. 3.2a, c). Similarly, individuals with slower mean juvenile growth rates spent less time sheltered and swam higher in the water column (Table 3.2; Fig. 3.2b, d). The experiments yielded similar results: larger settlers sheltered less and traveled farther away from their shelters (Fig. 3.3a, c). Individuals exhibiting slower juvenile growth rates also traveled shorter horizontal distances away from their shelters and were closer to neighboring conspecifics (once two outliers were removed; Fig. 3.3b, d).

There were no significant relationships between the number of bites taken and size-at-settlement or juvenile growth. Other behaviors observed in 2009 included the number of times and total time spent chasing or being chased by conspecifics, but these events were relatively rare during May because the subjects spent most of the time in

shelters. In June, there were more interactions, most of which were the result of larger conspecifics chasing the subjects. There was no significant relationship between the number of times each subject was chased and their size-at-settlement, but individuals that were chased more often experienced slower juvenile growth ($R^2 = 0.28$; $p = 0.028$). This negative relationship strengthened once individuals with no interactions were removed ($R^2 = 0.57$; $p = 0.019$; Fig. 3.4). The similarly negative relationship between juvenile growth and total time spent being chased was marginally non-significant ($R^2 = 0.23$; $p = 0.052$). Most of the chases lasted < 1 s and divers measured the time with a stopwatch, therefore time spent being chased was not measured as accurately as the number of times that a chase occurred. Escape or burst swimming speed was also measured for experimental fish in June, revealing a negative relationship between juvenile growth and swimming speed ($R^2 = 0.27$; $p = 0.038$; Fig. 3.5).

Both naturally settled and experimental juveniles were examined using a forward stepwise multiple regression with mean juvenile growth rate as the dependent variable and behaviors, conspecific densities, distance to nearest conspecific, and size-at-settlement as independent variables. The multiple regression for the naturally settled juveniles resulted in shelter time as the only independent variable included in the model because the addition of any of the other behaviors or traits did not significantly improve the fit. For the experimental fish, a multiple regression including size-at-settlement and distance to nearest conspecific explained over 21% of the variation in juvenile growth.

The regression tree for the naturally settled individuals explained $\sim 30\%$ of variance in juvenile growth-rate (Fig. 3.6). The first terminal node was defined by high distances traveled in the water column. The 43 juveniles that swam higher than 102% of

the mean (standardized value) were divided into two groups based on shelter time. Individuals that spent less time sheltering exhibited a lower mean juvenile growth rate. The regression tree for the experimental fish explained ~ 45% of variance in juvenile growth rate (Fig. 3.7). The first node was defined by proximity to conspecifics. Individuals with a distance to nearest conspecific < 31 cm were divided into two groups based on maximum horizontal distance. Individuals that traveled farther from their shelters ($> 135\%$ of the mean) also grew more slowly.

Discussion

Results of this study demonstrate that selective mortality processes during early juvenile life can be behaviorally mediated. Size-at-settlement and early juvenile growth influence survival and several key behaviors (interactions with conspecifics, swimming capabilities, sheltering, and distance traveled) underlie these relationships.

Influence of size-at-settlement on behavior

Juvenile *S. partitus* that were larger at settlement spent less time in rubble shelters and traveled farther horizontally from those shelters both among naturally settled and experimentally manipulated fish. This suggests that larger settlers had a greater propensity to take risks (were bolder), which has implications for fitness (i.e. survival and reproduction; Budaev 1997, Brown and Braithwaite 2004). Bolder individuals may be more likely to discover novel habitats or food sources. Several studies have found that larger individuals tend to be less bold (i.e. take longer to emerge from shelter; Dowling and Godin 2002, Brown and Braithwaite 2004), however, these experiments manipulated size by using different aged individuals. In addition to being larger, older fish would also have greater experience with predators, which may result in warier behavior. In the

present study, I controlled for age to minimize any confounding influence on behavior. With experiences being equal, larger individuals should be less vulnerable to gape-limited predation (Anderson 1988, Miller et al. 1988, Sogard 1997) and should therefore have the benefit of greater activity. Another difference between the studies is that fish in my experiments were allowed to acclimate for a minimum of 18 hr before being observed for the first time, whereas the previous studies tested individuals in novel environments. Boldness may differ in novel environments compared to habitats to which individuals have acclimatized.

Another explanation for the observed patterns between behavior and settlement size may relate to life history strategy. Larval supply and juvenile recruitment of coral reef fishes, including this species, occur in multi-day pulses (D'Alessandro et al. 2007, Grorud-Colvert and Sponaugle 2009). Upon settlement, *S. partitus* must locate and maintain small territories, which are important for acquiring food, shelter, and eventually mates. Individuals that settle early within a pulse may need to defend their new territories and establish dominance over successive settlers to maximize fitness. Empirical research has demonstrated that prior residents can reduce recruitment of several species of reef fish (Shulman et al. 1983, Almany 2004b). Although I observed relatively few instances where a juvenile subject chased another conspecific, when it occurred, the subject was larger than the fish it was chasing. Similar patterns in aggressive behaviors have been observed in young red drum *Sciaenops ocellatus* (Nakayama et al. 2009).

Influence of behavior on early juvenile growth

In most cases, the individuals that settled at larger sizes experienced slower subsequent growth. Additionally, individuals that spent less time sheltering and traveled

higher in the water column exhibited slower juvenile growth rates, suggesting greater activity levels in slower growing juveniles. With increased activity, there is a greater potential for increased foraging and food consumption. However, I did not observe a difference in bite rates between fast and slow growers. Therefore, the most parsimonious explanation is that greater levels of activity resulted in greater energy expenditure, and subsequently, slower growth rates. Consistent with this hypothesis, I also observed that slower growing juveniles were chased more often by conspecifics. A similar relationship between juvenile growth and intraspecific chasing was observed for this species in the Bahamas (Johnson 2008). In the present study, there were only sufficient data collected during the June experiment to detect this relationship, however, distance to nearest conspecific was collected throughout all of the experiments and there was a significant positive relationship between growth and proximity to conspecifics. The fact that proximity to conspecifics influences growth rate suggests that competition and/or agonistic interactions are greater among close neighbors. As *S. partitus* is primarily planktivorous, conspecifics were not likely directly excluding the subjects from access to food, and this is corroborated by the lack of a relationship between bite rate and juvenile growth. Instead, and as the chasing data suggest, closer proximity to neighbors likely results in more agonistic interactions. Agonistic behavior, such as chasing, can be physiologically costly (Briffa and Sneddon 2007) due to build-up of lactic acid, production and release of stress hormones (Wilson et al. 1990, Briffa and Sneddon 2007), injury, and energy expenditure (Neat et al. 1998).

An alternative, though not mutually exclusive, explanation for the observed variation in growth rates is that a greater amount of energy was allocated for alternative

purposes in slower growers. For instance, rapid growth can be sacrificed in exchange for development, tissue maintenance and repair, and swimming capabilities (Arendt 1997). I observed that slower growers exhibited faster burst swimming speeds following a simulated predator attack. Trade-offs between growth and swimming performance have been observed in other teleosts (Kolok and Oris 1995, Billerbeck et al. 2001, Sogard and Olla 2002) and amphibians (Arendt 2003), although a relationship between growth rate and routine swimming speed was not detected in larval red drum (Fuiman et al. 2005). However, Fuiman et al. (2005) compared younger, faster growing larvae to older, slower growing individuals reared in captivity and did not examine burst swimming speed.

Additional trade-offs can exist between condition (i.e. lipid reserves) and accelerated growth (Johansen et al. 2001, Sogard and Spencer 2004). For instance, Johnson (2008) observed that high condition *S. partitus* juveniles placed in high densities grew more slowly than low condition juveniles in the same densities and attributed this reduction in growth to more agonistic interactions among high condition individuals. Condition has been demonstrated to influence behavior and survival in other species as well. A recent study that manipulated condition in bluehead wrasse *Thalassoma bifasciatum* found that higher condition juveniles exhibited faster escape swimming speeds and less risk-taking behavior under simulated predator threat (Grorud-Colvert and Sponaugle 2006). In another damselfish *Pomacentrus moluccensis*, higher condition fish were more aggressively dominant than lower condition fish, and despite their higher aggression, experienced lower predation mortality (Booth and Beretta 2004). I did not measure condition in this experiment, but condition often covaries with size (Henderson et al. 1988, Thompson et al. 1991, Schultz and Conover 1997) and I observed that

individuals with larger settlement sizes exhibited greater activity, slower juvenile growth, and higher survival (Chapter 2).

Behavioral implications for survival

Identifying the behaviors that are most influential to juvenile growth and that explain patterns of selective mortality acting on growth rates is challenging. Ideally, one would compare the behaviors and growth-related traits of individuals that did not survive the week-long experimental trials with those that did to examine patterns in behavior growth and survival. Unfortunately, when individuals did not survive until collection, I lost a portion of the data, i.e. the otolith-derived size and growth data. Additionally, the majority of the subjects that did not survive the duration of the experiment disappeared within the first 24 h. This left me with a sample size of non-survivors that was too small to compare behaviors. Nonetheless, there was enough variability in the behavior and growth-related traits among survivors to flush out relationships among them.

The results from the naturally settled and the experimentally-manipulated juveniles were somewhat different from, but broadly consistent with each other. Results of the simple linear regressions revealed significant positive relationships between juvenile growth and time spent sheltered in both the natural and experimental populations. However, the multiple regression for the experimental fish indicated that settlement size and distance to nearest neighbor were more important in explaining the variation in growth rate and the inclusion of shelter time did not explain any additional variance, whereas, the multiple regression for the naturally settled juveniles included only shelter time. Essentially, relationships between behavior and size and growth were

consistent, but the relative importance of different traits varied among the experimental and natural fish.

I used regression trees to include more relationships among the behaviors and traits. One advantage of regression tree analysis is that predictors may be considered in the model more than once (i.e. at each node), which means that prediction can occur even when the independent and dependent variables are not monotonically related (Fuiman et al. 2006). Therefore, the regression trees result in a more complex representation of the mechanisms at work. The regression tree for the experimental group suggests that distance to nearest conspecific has the greatest predictive power for juvenile growth, followed by maximum horizontal distance from shelter, whereas maximum vertical distance explains the most variation in growth for the natural group. It is important to note that I was not able to include observations on chasing and escape swimming speeds since these were not collected for all individuals, and therefore their relative importance is unknown. It is unclear why there were differences in relative importance of particular behaviors between the experimentally manipulated and naturally settled juveniles. There are a suite of behaviors that can influence growth and survival and behavioral correlations can develop from experiences with predators (Bell and Sih 2007). It is possible that differences in the settlement experiences among the experimental and naturally settled fish manifested into subtle differences in behavior and growth, but this is speculation. Despite the differences in how the experimental and naturally settled individuals were established in their juvenile habitat, fundamental relationships between growth and behavior were consistent. Thus, although the relative importance of behavioral traits is unclear, the broad agreement in the relationships between particular

behaviors and growth characteristics indicate that patterns of growth and selective mortality are likely behaviorally mediated.

Combined, these behavioral relationships indicate that juvenile growth of *S. partitus* is more influenced by energy expenditure than food intake. Larger settlers are less vulnerable to gape-limited predation and can allocate more energy to defending territories, development, tissue maintenance, and condition than smaller settlers which must grow quickly to narrow their predator fields (i.e. compensatory growth; Metcalfe and Monaghan 2001, Sogard and Olla 2002, Ali et al. 2003, Alvarez and Metcalfe 2007). Of the behaviors observed, swimming ability may have the greatest impact on predator escape (Fuiman et al. 2006). Proximity to conspecifics can also have implications for survival. *Stegastes partitus* maintains small territories on the reef and surrounding rubble and adults of several species of damselfishes have been shown to increase settlement (Sweatman 1983, Lecchini et al. 2007) and post-settlement survivorship of conspecifics (Almany 2003). Because I did not observe any of the predation events, I cannot establish a direct cause-effect relationship between behaviors, slower juvenile growth, and survival. However, coupled with the evidence that juveniles with larger sizes-at-settlement and slower juvenile growth rates have higher survivorship (Chapter 2) these results demonstrate that selective mortality during the early juvenile phase of *S. partitus* is behaviorally mediated.

Table 3.1. Characteristics of three *in situ* behavioral experiments using bicolor damselfish (*Stegastes partitus*). ‘Established’ refers to numbers of individuals released at the beginning of the experiment. ‘Survivors’ were those that survived the full 7 d experiment. Descriptive information includes the percent survivorship and the SL at the time of release of individuals that did not survive the entire length of the experiment (non-survivors) and those that did (survivors). The trend of survivors possessing larger SL at the time of release was non-significant for each experiment.

Month	Established	Survivors	% Survival	Non-survivor SL	Survivor SL
Aug-08	24	15	62.5	11.5	12.3
May-09	27	7	25.9	10.9	11.5
Jun-09	36	17	47.2	10.8	11.0

Table 3.2. Summary results for ANCOVA for *Stegastes partitus* behavioral traits (time spent sheltering, maximum vertical distance traveled, and maximum horizontal distance traveled) as the dependent variables, settlement size and juvenile growth as the independent variables, and juvenile age as the covariate. Significant results with independent variables are in bold. Significant effects of the covariate are italicized.

Effect	Shelter time			Max vertical distance			Max horizontal distance		
	<i>df</i>	<i>F</i>	<i>P</i>	<i>df</i>	<i>F</i>	<i>P</i>	<i>df</i>	<i>F</i>	<i>P</i>
Age	3, 82	4.462	<i>0.034</i>	3, 82	3.065	<i>0.016</i>	3, 82	2.336	0.959
Settlement size	1, 84	4.175	0.046	1, 84	0.041	0.746	1, 84	4.720	0.034
Settlement size × Age	3, 82	3.338	0.302	3, 82	2.065	0.720	3, 82	1.677	0.533
Age	3, 82	5.245	<i>0.038</i>	3, 82	5.859	<i>0.021</i>	3, 82	0.009	0.930
Juvenile growth	1, 84	5.586	0.020	1, 84	5.346	0.024	1, 84	0.011	0.932
Juv growth × Age	3, 82	3.93	0.199	3, 82	3.895	0.761	3, 82	0.011	0.895

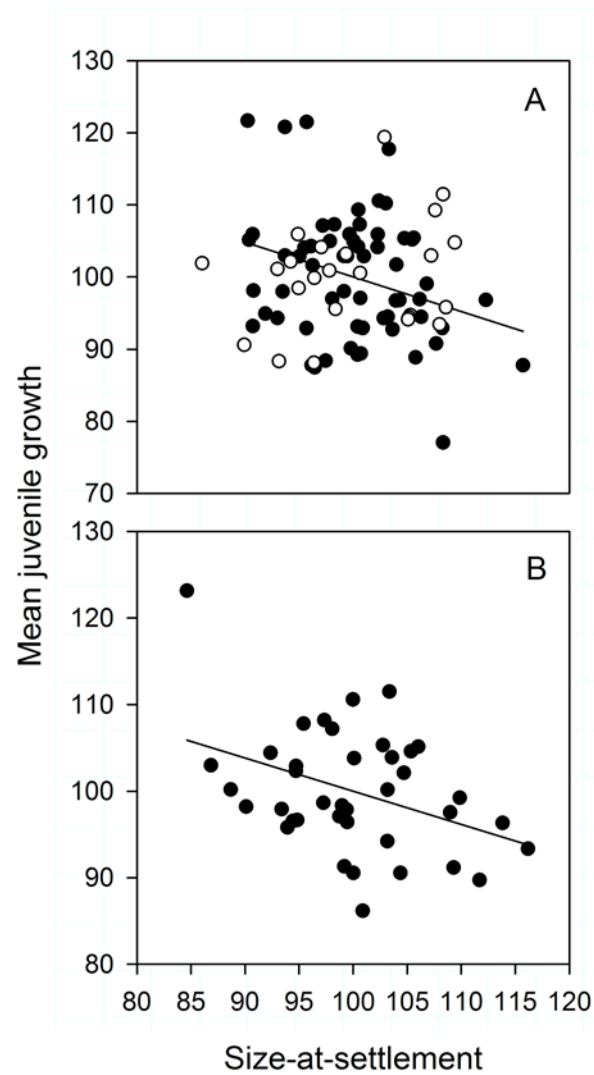


Figure 3.1. *Stegastes partitus*. Mean juvenile growth-rate as a function of size-at-settlement for (A) naturally settled juveniles and (B) experimentally manipulated individuals. Least squares regression of all naturally settled individuals was not significant, but it was significant for the individuals collected in 2008 (closed circles; $R^2 = 0.09$, $p = 0.017$). The regression for the experimental fish was also significant ($R^2 = 0.15$, $p = 0.015$).

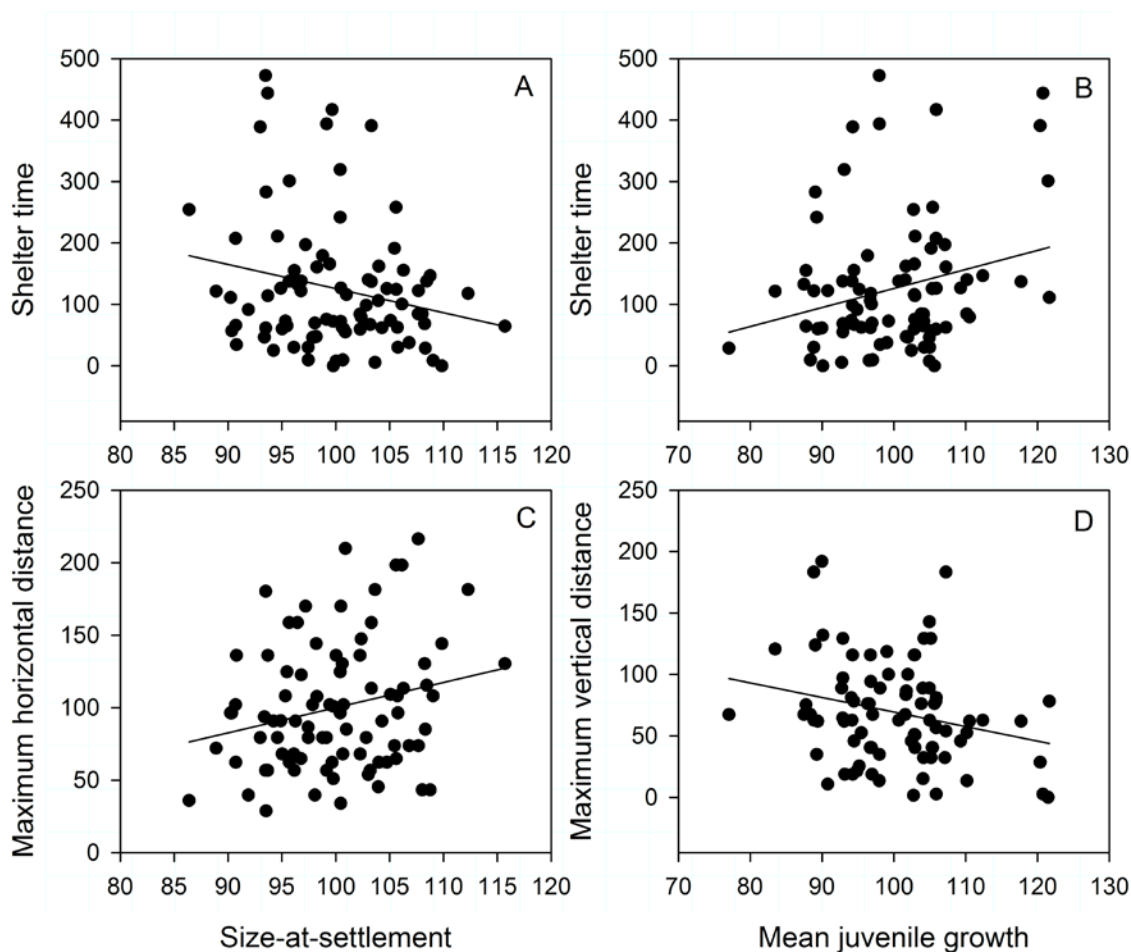


Figure 3.2. *Stegastes partitus*. Relationships among standardized values of behavioral and growth-related traits in naturally settled juveniles: Least squares regression revealed a significant difference in shelter time with (A) size-at-settlement ($R^2 = 0.05$, $p = 0.044$) and (B) mean juvenile growth ($R^2 = 0.06$, $p = 0.020$) after detrending for age ($F_{1,84} = 4.64$, $p = 0.034$ and $F_{1,84} = 6.17$, $p = 0.015$ respectively). Maximum horizontal distance traveled from shelter differed with (C) size-at-settlement ($R^2 = 0.05$, $p = 0.033$) without an effect of age. Maximum vertical distance traveled in the water column varied with (D) juvenile growth ($R^2 = 0.06$, $p = 0.023$) after detrending for age ($F_{1,84} = 6.09$, $p = 0.016$). While juvenile growth was considered to be dependent on behavioral traits, it was plotted here as the independent variable for ease of comparison with size-at-settlement.

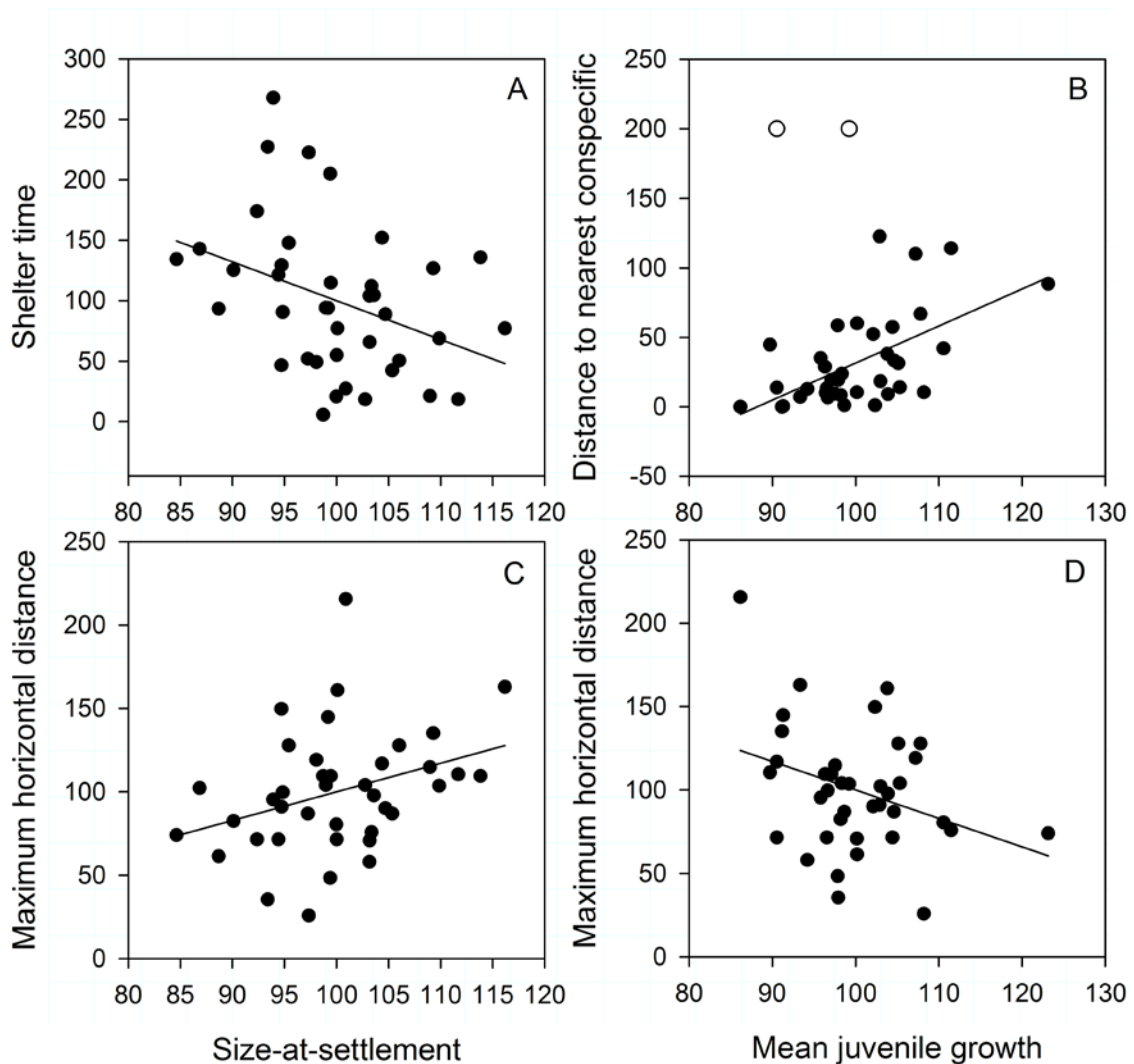


Figure 3.3. *Stegastes partitus*. Relationships among standardized values of behavioral and growth-related traits in experimentally manipulated juveniles: Least squares regression revealed a significant difference in (A) shelter time with size-at-settlement ($R^2 = 0.14$, $p = 0.021$). (B) Distance to nearest conspecific varied significantly with juvenile growth ($R^2 = 0.33$, $p < 0.001$) once two individuals with no conspecifics within a 7 m² radius were removed (open circles). Maximum horizontal distance traveled from shelter differed with (C) size-at-settlement ($R^2 = 0.11$, $p = 0.037$) and (D) mean juvenile growth ($R^2 = 0.11$, $p = 0.039$). While juvenile growth was considered to be dependent on behavioral traits, it was plotted here as the independent variable for ease of comparison with size-at-settlement.

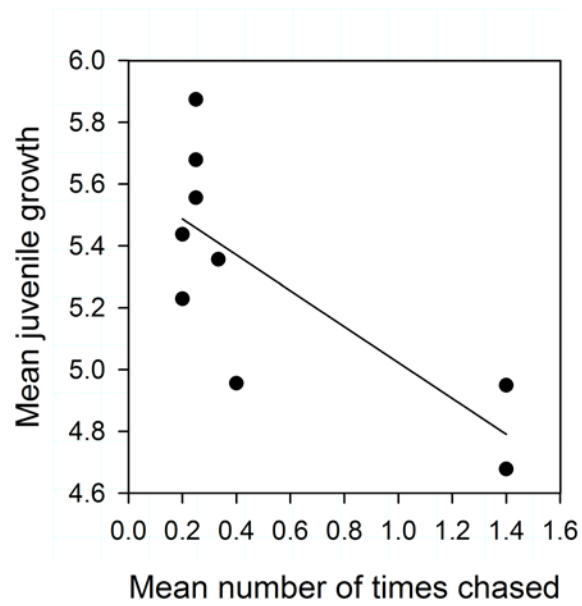


Figure 3.4. *Stegastes partitus*. Mean juvenile growth as a function of mean number of times a subject was chased during daily 5 min observations over 7 d. Line is least squares regression ($R^2 = 0.57$, $p = 0.019$).

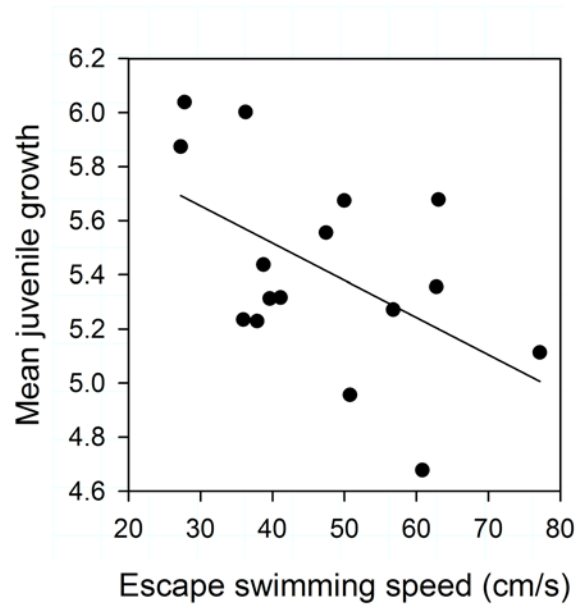


Figure 3.5. *Stegastes partitus*. Mean juvenile growth as a function of burst swimming speed. Line is least squares regression ($R^2 = 0.27$, $p = 0.038$).

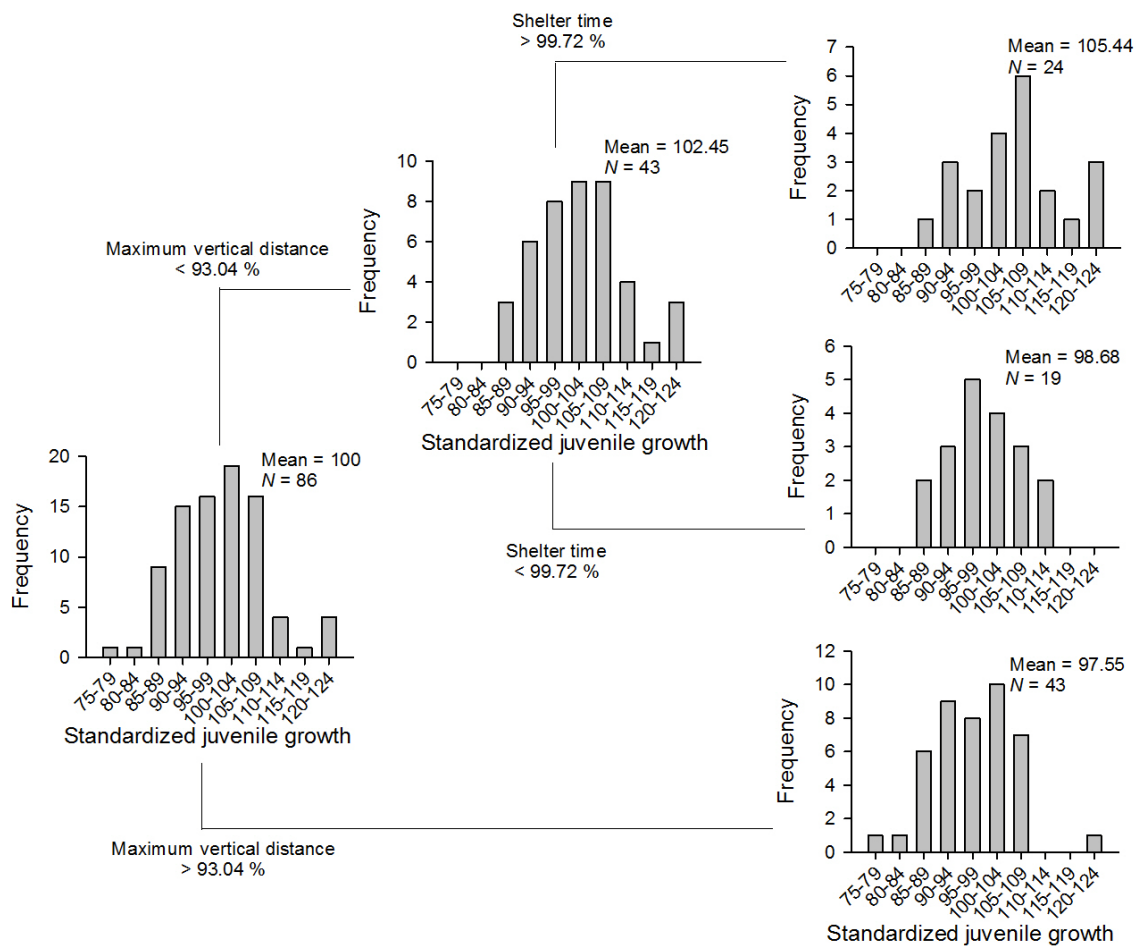


Figure 3.6. Regression tree for predicting juvenile growth for naturally settled *Stegastes partitus*. Each group of juveniles is subdivided according to the value of a behavioral trait until a terminal node is reached. Mean values refer to standardized juvenile growth.

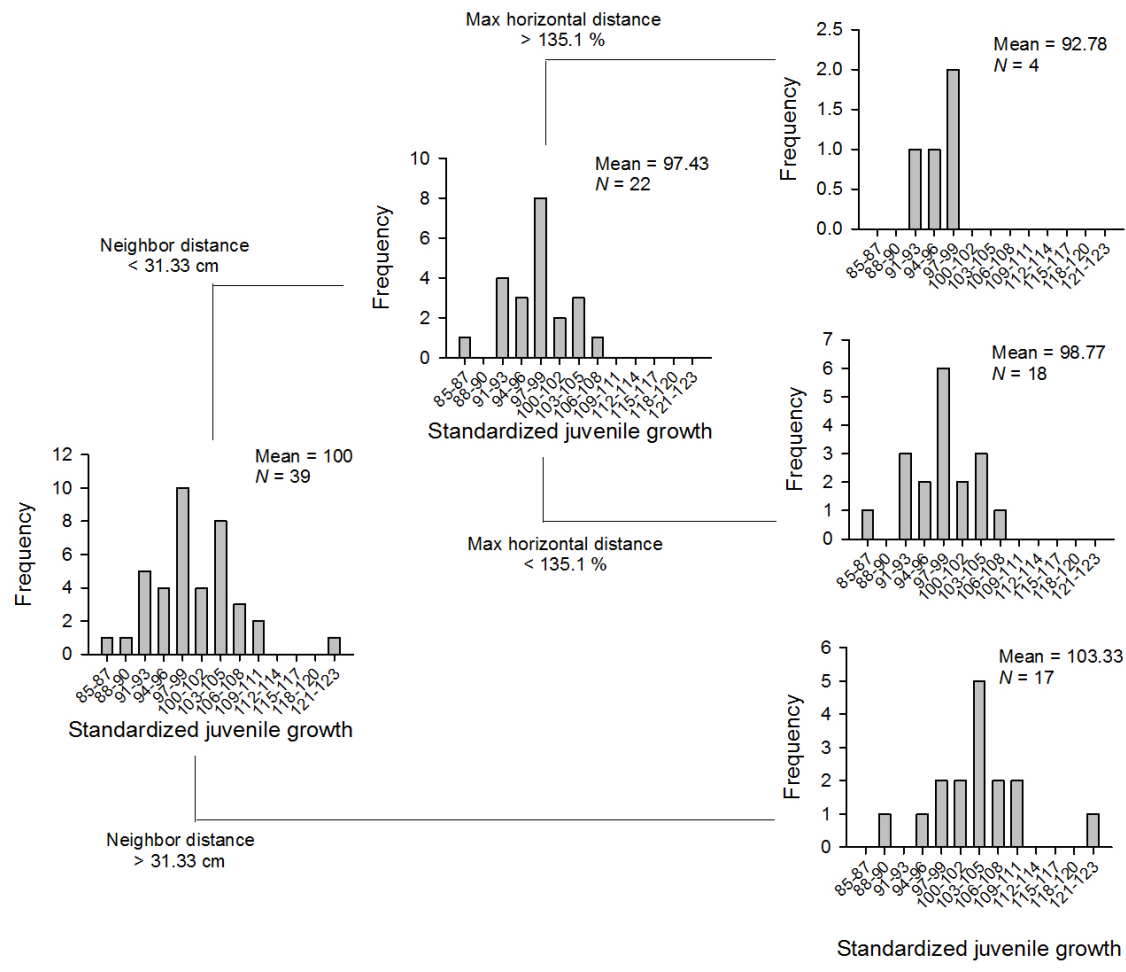


Figure 3.7. Regression tree for predicting juvenile growth for experimentally manipulated *Stegastes partitus*. Each group of juveniles is subdivided according to the value of a behavioral trait until a terminal node is reached. Mean values refer to standardized juvenile growth.

Chapter 4: Temporal and spatial patterns of early life history traits and their influence on settlement and post-settlement processes

Background

Understanding the mechanisms that drive variability in population dynamics is a fundamental goal of ecology. Most marine organisms have complex life cycles with multiple ontogenetic shifts, and processes during the early life stages can influence population dynamics. For taxa such as many coral reef fishes, which are demersal as juveniles and adults but possess a planktonic larval phase, population replenishment can be highly variable in space and time (Victor 1983, Sale et al. 1984, Robertson et al. 1988) and patterns in settlement and post-settlement processes can strongly influence population size and distribution (Victor 1983, Doherty 1991, Doherty and Fowler 1994, Caley et al. 1996, Caselle 1999).

Temporal fluctuations in settlement include daily, monthly, seasonal, and interannual variability. Many species of reef fish exhibit seasonal variation in larval settlement and recruitment with changes in temperature and other environmental variables (Bergenius et al. 2005, Sponaugle et al. 2006, D'Alessandro et al. 2007, Chapter 2). Lunar and tidal amplitude synchrony of settlement is common in various taxa (Robertson 1992, Acosta et al. 1997, Kingsford and Finn 1997, D'Alessandro et al. 2007). Settlement and recruitment can also vary spatially with distance from shore (D'Alessandro et al. 2007), by depth, habitat quality (Ohman et al. 1998), and composition of residents (e.g. predators, competitors; Almany 2004b). The mechanisms that drive these patterns can occur during larval production or pelagic life and can be physical (i.e. wind, currents, storm events, and other oceanographic features) or

biological (timing of spawning, parental contribution, food availability, predator abundance, growth, and behavior). For instance, environmental factors have been significantly correlated with settlement intensity and recruitment magnitude, including wind components (Raventos and Macpherson 2005b), solar radiation and rainfall (Bergenius et al. 2005), lunar illumination and tidal amplitude (Reyns and Sponaugle 1999, Valles et al. 2009), and water temperature (Rutherford and Houde 1995, Sponaugle et al. 2006, Chapter 2). Additionally, oceanographic features, such as passage of mesoscale eddies in the upper Florida Keys, have been shown to deliver large pulses of larvae (Sponaugle et al. 2005) as well as advect them away from reefs (D'Alessandro et al. 2007).

Growth-related traits, such as larval growth and size-at-settlement, also vary in space and time and have been linked to settlement magnitude (Bergenius et al. 2002, Wilson and Meekan 2002, Macpherson and Raventos 2005). Further, these traits can carry over to influence post-settlement mortality and impact recruitment success and subsequent juvenile survival (Searcy and Sponaugle 2001, McCormick and Hoey 2004, Chapter 2). For many species, faster larval growth (Searcy and Sponaugle 2001, Takasuka et al. 2003, Chapter 2), shorter larval duration (Meekan and Fortier 1996), larger size-at-settlement (McCormick and Hoey 2004), or higher condition-at-settlement (Searcy and Sponaugle 2001, Sponaugle and Grorud-Colvert 2006, Hamilton et al. 2008) confers a survival advantage.

The magnitude of mortality may vary with timing and location of settlement. For instance, many species of reef fish settle during the darker phases of the lunar cycle (Robertson et al. 1988, Robertson 1992, Sponaugle and Cowen 1996a, D'Alessandro et

al. 2007), and it is hypothesized that they do so to escape stronger predation during brighter periods (Johannes 1978, Williams 1983, Victor 1986, Robertson et al. 1988). Presence of conspecifics has been shown to enhance post-settlement survival in some species (Almany 2003), but high densities of conspecifics can also increase mortality of recruits (Tupper and Hunte 1994, Johnson 2008). Some habitats may support more recruits (Shima and Osenberg 2003) due to greater or higher quality food sources (Nemeth 1997), the presence of more suitable refuges (Nemeth 1998), or fewer predators (Caley 1993, Holbrook and Schmitt 2003). Selective mortality pressures may vary under these circumstances. If early life history traits also vary with timing or location of settlement, selective mortality processes may be further complicated.

While reproduction has been shown to be an important influence on timing of settlement and recruitment (Meekan et al. 1993, Dorsey 1999), recent evidence suggests that the pelagic environment may play a greater role in shaping larval quality (Sponaugle and Pinkard 2004b, Sponaugle et al. 2006, Shima and Swearer 2009) and success. However, it is still unclear under what circumstances pre- or post-settlement processes are relatively more important in influencing juvenile and adult demography (Doherty 1991, Hixon 1998). In some instances, recruitment is well correlated with larval supply (Victor 1986, Milicich et al. 1992), while others suggest that post-settlement processes (e.g., prior residents, immigration, and emigration) are sufficiently dominant that patterns of supply are obscured (Schmitt and Holbrook 1996). In some locations, the relative importance of pre- and post-settlement processes may be species-specific (Sponaugle and Cowen 1996a).

Here, I examined spatial and temporal variation in recruitment for a common coral reef fish and tested whether this variation was correlated with certain growth-related traits. Specifically, I explored whether traits varied with the magnitude and lunar timing of settlement, recruitment habitat, and density of conspecifics, due to variability in larval supply and/or post-settlement processes. I expected that larval quality (i.e. growth-related early life history traits) would vary with timing and location of settlement, but that post-settlement processes might act to obscure this variation by selecting against less optimal traits.

Materials and Methods

Study site and physical data sampling

The Florida Keys reef tract (FKRT) is bordered by the seasonally variable Florida Current (FC). Cyclonic frontal eddies that form along the boundaries of the Loop Current and FC are the dominant mesoscale features in the southern Straits of Florida (Fratantoni et al. 1998) and recirculation within eddies has been hypothesized to be a possible retention mechanism of both locally and upstream-spawned larvae in the FKRT (Lee et al. 1994, Lee and Williams 1999).

Mean water temperature in the FKRT varies seasonally by approximately 10 °C and can significantly influence variation in ELHTs and recruitment strength (Sponaugle et al. 2006, Chapter 2). Thus, to characterize the inshore environment of the FKRT and control for temperature effects, daily water temperatures were obtained from the National Underwater Research Center (NURC), which continuously records water temperature at 21 m depth at Conch Reef in the upper Florida Keys (FK; 24°59' N, 80°25' W).

Biological sampling

The bicolor damselfish *Stegastes partitus* is common throughout the Caribbean (Lieske and Myers 1996). Adults are highly territorial and spawn demersal eggs on a monthly basis throughout the year (Schmale 1981, Robertson et al. 1988), after which, the males guard the embryos for ~ 4 d until hatching (Robertson et al. 1988). Larvae spend a mean of 30 d in the plankton before settling to the reef and metamorphosing into juveniles overnight (Sponaugle and Cowen 1996a). Juveniles and adults maintain benthic territories on spur and groove reefs and are found in highest densities in areas of high current flow and within dead coral rubble piles (Emery 1973, Nemeth 1998). The timing of settlement appears to be synchronized with lunar phase, with pulses occurring during the third quarter and/or new moon (Robertson et al. 1988, Sponaugle and Cowen 1996a, D'Alessandro et al. 2007). Seasonal peaks in settlement to the FK typically occur during summer months (D'Alessandro et al. 2007). *Stegastes partitus* is an ideal model species for studying processes affecting the early life history of coral reef fishes because they are common throughout the Caribbean, are integral to the trophic dynamics of the reef community (Randall 1967, Emery 1968), are easy to observe and collect at all life stages, and have otoliths (ear stones) that provide a daily record of events occurring during early life.

Newly recruited *S. partitus* juveniles were censused monthly on six different reefs within the Florida Keys National Marine Sanctuary offshore of Key Largo, Florida, for 65 months from April 2003 until August 2008. The census was timed to coincide with the full moon, which is known to be a period of low settlement. Four of the reefs are part of the bank reef tract ~ 10 km offshore: French Reef (FR; 25°02.06' N, 80°21.00' W), Sand

Island Reef (SI; 25°01.09' N, 80°22.08' W), Molasses Reef (MO; 25°00.74' N, 80°22.40' W), and Pickles Reef (PI; 24°59.23' N, 80°24.88' W), two of which are sanctuary protected areas (MO, and FR; Fig. 4.1). The other two sites, Triangles (TR; 25°01.153'N, 80°26.272'W) and White Banks (WB; 25°02.609'N, 80°22.133'W), are inshore patch reefs (Fig. 4.1). Recruitment density was estimated for two habitats within the bank reef sites, the reef itself and dead coral rubble at the base of the reef, by counting the number of newly recruited juveniles within 15 randomly placed 5 × 1 m transects in each habitat. Within the two inshore patch reefs (TR and WB), only reef habitat was surveyed due to the lack of coral rubble habitats surrounding the reef. At SI, PI, TR, and WB, all censused recruits were collected by divers using hand nets and the anesthetic Quinaldine. Because FR and MO are sanctuary protected areas, benthic sampling was not permitted. Additional collections were made at the non-sanctuary protected sites, after each survey, off of the transects during 2007 and 2008 to supplement sample sizes. All collected juveniles were immediately stored in 95% EtOH following collection to preserve their otoliths.

Settlement-stage *S. partitus* larvae that were collected in light traps at FR, SI, MO, and PI from June 2001 until January 2004, as part of two other studies (Sponaugle et al. 2005, D'Alessandro et al. 2007), were utilized to compare differences in growth-related traits and magnitude of supply with the data from recruits.

Otolith analysis

Prior to dissection, the standard length (SL) of each fish was measured to the nearest 0.01 mm by capturing an image of the fish with a Dage MTI digital video camera attached to a Leica MZ12 dissecting microscope and passing the image to a computer

where it was analyzed using Image Pro Plus 4.5 image analysis software (Media Cybernetics). The otoliths of the collected fish were extracted using standard dissecting techniques and placed in a drop of medium viscosity immersion oil on a microscope slide to clear for a minimum of 30 d. Based on ease of reading, only the lapilli were examined (Sponaugle and Cowen 1996a). The clearest lapillus was chosen from each individual and viewed under 400× magnification through a Leica DMLB microscope equipped with a polarized filter between the first stage and light source. Similar to the SL protocol, the image was captured by a Dage MTI video camera and analyzed using Image Pro Plus 4.5 software. Each otolith was read once blind (i.e. without sample information available) and saved as a digital file. Every 5th individual was measured a second time (sensu Baumann et al. 2003). The images of the remaining 656 fish were examined to determine if there was any ambiguity in the placement of the increments and an additional 161 fish were aged a second time, resulting in a total of 325 fish aged twice. Otoliths were rejected where the difference between the first and second reads was > 5%, resulting in six exclusions. Otolith analysis was utilized to determine post-settlement age (number of concentric increments after settlement mark), pelagic larval duration (PLD; number of concentric increments from the primordium to the settlement mark), larval and juvenile growth rates (increment widths), and size-at-age (otolith radius-at-each age, including settlement).

Data analysis

Otolith analysis was used to back-calculate date of hatching (collection date minus PLD and post-settlement age) and date of settlement (collection date minus post-settlement age). Spawning dates were calculated by subtracting 4 d from the hatch dates,

for average egg development (Robertson et al. 1988). Daily settlement magnitude was estimated from the monthly measures of recruit density coupled with the settlement dates of the collected fish and adjusted for estimated mortality with age (*sensu* Houde 2002). Mortality was estimated by fitting a function (equation: $y = 0.0671x^2 - 5.0165x + 89.763$; where x = juvenile age in day, and y = number of recruits) to the age frequency distribution of all 9+ day old recruits (Fig. 4.2). Only these older recruits were used because younger fish were underrepresented in the samples due to the timing of sampling (during the full moon, which is known to be a low settlement period) and the fact that older recruits do not shelter as much. The mortality function was then used to adjust the number of settlers per day based on the age of the recruits that settled on that day.

Lunar and tidal periodicity in settlement and spawning

Lunar day of settlement was assigned for each aged fish (day 1 corresponding to the new moon; day 8 corresponding to the first quarter; day 15 corresponding to the full moon; day 23 corresponding to the third quarter). Each fish was also assigned a tidal amplitude day (day 1 corresponding to the maximum tidal amplitude closest to the new moon). These data were collapsed into a single lunar and maximum tidal amplitude cycle. Rayleigh tests were utilized to determine if light trap catches or settlement magnitude were uniformly distributed across the lunar or tidal amplitude cycles (Zar 1999). When data were non-randomly distributed, the mean lunar or tidal amplitude day about which the data were centered was calculated.

Variation in early life history traits by lunar phase of settlement and over time

Aged fish were also divided into three age groups: larvae (all settlement-stage larvae collected from 2001-2004 light traps), newly settled recruits (1-10 d old), and

juveniles (11-28 d old). To determine if the composition of growth-related traits varied with lunar timing of settlement, otolith derived traits were compared among lunar phases by age group using Kruskal-Wallis procedures (SYSTAT version 11.0; Wilkinson 1992), followed by post-hoc non-parametric multiple comparison tests (Zar 1999). For this and all subsequent analyses, individuals were classified into four groups by lunar phase which included each moon phase and 3-4 d on either side of the phase (first quarter moon: days 5-11, full moon: days 12-18, third quarter moon: days 19-26, new moon: 27-4). To determine whether patterns of selective mortality varied with lunar phase, I compared the traits among age groups by lunar phase in the same manner. If directional selection occurred for a given trait, there would be a shift in the distribution of that trait in the older juveniles compared to younger recruits or larvae, and between recruits and larvae.

Previous results demonstrated that temperature can influence the intensity and direction of selective mortality acting on some early life history traits (i.e. larval growth and PLD; Chapter 2). Additionally, during early life history, many traits are known to covary with temperature and these traits can influence recruitment magnitude (Bergenius et al. 2002, Wilson and Meekan 2002). To minimize the effect of temperature I divided monthly cohorts into three categories by temperature (< 25 °C, 25 to < 28 °C, and > 28 °), which also corresponded roughly with season. Over 65% of the recruits collected were from the warmest temperature group and therefore comparisons of traits with other processes (i.e. settlement magnitude, lunar phase of settlement, location of settlement, and age group) were confined to individuals that settled during the warmest months.

Variation in early life history traits by settlement habitat

Variable habitat quality (i.e. food abundance and quality, substrate suitability) and habitat-specific differential predation pressure may lead to preferential habitat selection by larvae and/or differential survival of recruits (Shima and Osenberg 2003). To examine whether early life history traits vary by microhabitat choice, traits were examined for larvae and recruits in reef and rubble habitats using Kruskal-Wallis procedures (SYSTAT version 11.0; Wilkinson 1992), followed by post-hoc non-parametric multiple comparison tests (Zar 1999). To control for the influence of settlement magnitude on early life history traits, I compared the mean values of the traits between reef crest and rubble habitats only for the warmest temperatures when recruitment was relatively large.

Variation in early life history traits with recruitment magnitude

To determine if recruitment magnitude reflects variation in larval supply, light trap catches from 2003-2004 were compared with recruitment magnitude over the same period using least-squares regression techniques (SYSTAT version 11.0; Wilkinson 1992). To determine if composition of growth-related traits varies with recruitment magnitude, recruit density was divided into two groups: small events where monthly recruitment was $\leq 10\%$ of the seasonal total, and large events where monthly settlement was $> 10\%$ of the seasonal total. The 10% criterion was selected a posteriori based on the distribution of the data into apparent categories. Early life history traits were compared between large and small events similarly to the method for lunar phase of settlement and settlement microhabitat, first by comparing within settlement-stage larvae collected from 2003-2004 (where I had measures of settlement magnitude) then within the 1-10 d old recruits over the same time period.

Influence of older conspecifics on recruitment magnitude and early life history traits

The density of conspecifics may make an area more or less favorable for larvae settling, or juveniles surviving, therefore recruit density was also regressed against juvenile (2-3 mm SL), intermediate (3-5 mm SL), and adult (> 5 mm SL) conspecific densities to determine if recruitment magnitude is related to densities of conspecifics. The growth-related traits were also regressed against adult conspecific density to determine if composition of traits is related to presence of adult conspecifics.

Results

Interannual and monthly variation in recruitment magnitude

Over six years, *Stegastes partitus* recruitment varied on both an interannual and monthly basis (Fig. 4.3). Because monthly sampling began in April 2003 and ended in August 2008, I limited interannual comparisons of recruitment magnitude to April through August of each year. This also eliminated the three months (March 2005, December 2007, and March 2008) when sampling was not possible due to weather conditions. Annual *S. partitus* recruitment was similar for most years, with the exception of 2004, which was three-fold to over six-fold less than the other five years, and 2008, which had the highest magnitude. Examining monthly differences, the highest mean recruitment across years was during July and August (Table 4.1). The coefficients of variation (CV) were relatively high for all months, indicating high interannual variability, but July and August were on the lower end of the spectrum (1.59 and 1.48 respectively; Table 4.1). The month with the lowest mean recruitment magnitude across years and the largest CV was February (0.17 individuals per 75 m² and 4.23 respectively).

Spatial patterns in recruitment magnitude

Recruitment magnitude varied almost 12-fold between the four reef crest habitats along the bank reef tract and the two inshore patch reefs, with recruitment to the patch reefs being consistently lower. When recruitment to the rubble habitats around the base of the reefs was included, the difference increased to 29-fold, because there was high recruitment to the rubble surrounding the offshore reefs, but no recruitment to the seagrass surrounding the inshore patch reefs. Within the offshore reefs, recruitment was three-fold greater in the rubble habitat compared the reef habitat. Offshore recruitment to the protected sites (FR and MO) did not differ significantly from recruitment to the unprotected sites (PI and SI; t-test, $p = 0.469$).

Lunar and tidal periodicity in settlement and spawning

Within months, back-calculated settlement was strongly periodic (Fig. 4.4). For the aged individuals, there was a significant peak in settlement on day 2 of the lunar cycle (one day after the new moon; Table 4.2, Fig. 4.5a). After adjusting for recruitment magnitude (density) and post-settlement mortality, the peak in settlement shifted to day 29 (one day before the new moon) and there was greater representation of juveniles that settled around the third quarter moon (days 19-26; Table 4.2, Fig. 4.5b). This corresponds more closely to light trap catches of settlement-stage larvae from 2003-2004, where the mean peak in settlement was calculated to be on day 27, due to averaging two peaks: one on days 22-23 and another on days 1-2 (the third quarter and new moons respectively; Table 4.2, Fig. 4.5c). The maximum tidal amplitude cycle is tightly coupled with the lunar cycle in Florida, but specific timing of maximum amplitude tides with lunar phase shifts seasonally (Fig. 4.4). Settlement of juveniles corrected for post-settlement mortality

peaked on day 1 of the maximum tidal amplitude cycle (Table 4.2, Fig. 4.6). This typically corresponds to one of the two peaks in tidal amplitude each month, though not always the largest one. The fact that settlement is not bimodal further suggests that lunar phase plays a more dominant role or interacts substantially with tidal amplitude.

Back-calculation of spawning day for aged juveniles revealed a peak in successful spawning on day 1 of the lunar cycle, corresponding to the new moon (Table 4.2, Fig. 4.7a). Using the adjusted values of settlement intensity as above, the distribution remained non-random with a mean peak in spawning around day 26 (Table 4.2, Fig. 4.7b), largely due to an increase in spawning contribution on day 20. This again corresponds more closely to the spawning distribution back-calculated from the light-trap larvae (Table 4.2, Fig. 4.7c), which peaked on day 20.

Traits by lunar phase of settlement

Early life history traits varied among fish settling on different lunar phases for all three age groups examined. Larvae settling to the reef on the third quarter and new moons experienced faster larval growth and were larger at settlement than larvae arriving on the first and full moons (Table 4.3, Fig. 4.8). Furthermore, the new moon settlers spent significantly less time in the plankton than larvae settling on the other moon phases (Table 4.3, Fig. 4.8). Recruits that spent 1-10 d on the reef had fairly similar traits among the different lunar phases of settlement, with the exception that third and full moon settlers had the slowest larval growth and the new moon settlers, the fastest larval growth. In addition, juvenile growth during the first 2 d was fastest for third quarter moon settlers (Fig. 4.9). By 11-28 d post-settlement, juveniles that settled on the third quarter and new

moons had longer PLDs and faster early post-settlement growth than first and full moon settlers (Table 4.3, Fig. 4.9).

Variation in traits over time

Across all lunar phases of settlement, there was a shift with age from smaller sizes-at-settlement and faster juvenile growth to larger sizes-at-settlement and slower juvenile growth (Table 4.4, Figs. 4.8 and 4.9). Shifts in traits over time were less consistent for the other two early life history traits. There was a shift from slower to faster larval growth with age for individuals that settled during the first and full moons, but the opposite trend for the third quarter and new moon settlers (Table 4.4, Fig. 4.8). Likewise, the PLD of new moon settlers increased with age, while PLD of first and full moon settlers decreased over time. In many cases, the shift in traits between the larvae and 1-10 d old juveniles was most pronounced for the first and full moon settlers (e.g. size-at-settlement; Fig. 4.8).

Variation in traits with settlement magnitude

Early life history traits were much more variable during smaller settlement events than larger ones, which precluded a significant linear relationship between monthly settlement magnitude and any of the individual traits. To examine whether early life history traits varied with settlement magnitude at the time of settlement and if the patterns changed due to selective post-settlement mortality, larval traits were examined relative to settlement magnitude and then compared to the trait distributions of recruits. Monthly settlement magnitude of the collected recruits was significantly correlated with light trap catches of larvae in 2003 and 2004 ($R^2 = 0.42$, $p < 0.05$; Fig. 4.10), suggesting that post-settlement processes did not remove all of the variation introduced during larval supply.

Larvae that settled to the reef during large events had significantly slower larval growth, longer PLDs, and larger sizes-at-settlement than those that arrived during small events (Fig. 4.11). Comparing the traits of the 1-10 d old recruits revealed consistent trends between large and small events, but these only remained significant for PLD ($p = 0.032$; Fig. 4.12b).

Variation in early life history traits by settlement habitat

Comparisons of mean traits among microhabitats revealed that individuals that settled to the reef had significantly faster larval growth and were significantly larger at settlement ($p = 0.003$ and 0.004 respectively; Fig. 4.13c). When comparing these habitat-specific patterns among age groups, larval growth rates differed between habitats for younger recruits (1-10 d; $p = 0.049$), but not for older juveniles (11-28 d; Fig. 4.14a). In contrast, differences in settlement size by habitat were not significant in 1-10 d old recruits, but were significant in the older age group ($p = 0.020$; Fig. 4.14c).

Influence of older conspecifics

Monthly recruit density was positively correlated with the density of > 1 mo. old juvenile conspecifics (2-3 cm SL; $R^2 = 0.83$, $p < 0.001$; Fig. 4.15a). This positive relationship was maintained when only cohorts settling during the warmest temperatures were examined ($R^2 = 0.45$, $p = 0.025$). There was also a positive correlation between recruit density and density of intermediate age conspecifics (3-5 cm SL; $R^2 = 0.042$, $p = 0.034$; Fig. 4.15b). The trend between recruit density and adult conspecific density was negative, but non-significant ($R^2 = 0.17$, $p = 0.120$; Fig. 4.15c). However, there were significant positive correlations between larval growth ($R^2 = 0.56$, $p = 0.021$) and size-at-settlement ($R^2 = 0.54$, $p = 0.023$) of recruits with adult density (Fig. 4.16). There was a

slightly negative, but non-significant ($R^2 = 0.17$, $p = 0.262$) trend between early juvenile growth and adult conspecific density.

Discussion

Results of this nearly six year time series indicate that there is interannual, monthly (seasonal), and lunar periodicity in the settlement and recruitment of the common reef fish, *Stegastes partitus*, to the upper Florida Keys. Such patterns have been demonstrated for *S. partitus* settling to other locations (Robertson et al. 1988, Robertson 1992, Sponaugle and Cowen 1996a), as well as in a shorter study of larval supply in the Florida Keys (D'Alessandro et al. 2007). Similar settlement/recruitment patterns have been shown to be related to particular early life history traits (Bergenius et al. 2002, Wilson and Meekan 2002) in Panama. Certain early life history traits not only influence recruitment magnitude, but also juvenile survival of *S. partitus* (Chapter 2). Here I tested whether traits vary with the timing and location of settlement and whether post-settlement selection of traits similarly varies over time and space. Results demonstrate that early life history traits can differ with magnitude of recruitment, lunar timing of settlement, settlement habitat, and density of conspecifics. Further, post-settlement processes interact with the timing and location of settlement to influence the suite of traits of surviving juveniles.

Spatial patterns in recruitment and early life history traits

Recruitment to offshore bank reefs of the upper Florida Keys was 12-fold higher than to the inshore patch reefs. This may be due, in part, to differences in physical processes that influence larval transport, and depletion of larvae as they cross the reef crest (D'Alessandro et al. 2007), however, there is also evidence that habitat in the inshore

patch reefs is less optimal than along the offshore bank reefs for this species (Nemeth 1997). *Stegastes partitus* juveniles in the backreef/patch reef habitat around both St. Croix and Jamaica grew more slowly and took twice as long to reach adult size than those on the forereefs and this was attributed to decreased planktonic food availability and increased competition for space inshore (Nemeth 1997). Figueira et al. (2008) similarly observed elevated growth rates and asymptotic sizes of *S. partitus* in forereef habitats compared to backreefs in the Florida Keys. However, they did not detect a difference in food availability between habitats and they attributed the differences in growth to reduced competition and greater mortality on the fore reef. In addition to cross-shelf differences, I observed a three-fold greater abundance of recruits in coral rubble than on the reef crest. Due to the reduction of wave action in the back reef and lower abundance of branching coral species (e.g. *Acropora* sp. and *Porites* sp.), there is relatively little coral rubble surrounding the inshore patch reefs. Nemeth (1997, 1998) observed greater mortality of *S. partitus* juveniles on *Montastrea annularis* boulder coral than *Porites porites* rubble piles, suggesting that mortality may be greater and possibly more selective in backreef habitats that lack coral rubble piles.

I did not collect enough recruits across the two patch reef sites, Triangles and White Banks, to compare traits of recruits to those habitats with those that settled along the fore reef. However, I did compare growth-related early life history traits among individuals that settled on the reef crest versus surrounding rubble on the offshore bank reefs. Individuals that settled on the reef crest had faster larval growth rates and were larger at settlement than those in rubble habitats. When fish were divided by age, younger recruits (1-10 d post-settlement) exhibited differences in larval growth, but not size-at-

settlement between habitats. In contrast, the older juveniles (11-28 d) differed in size-at-settlement, but not larval growth. These results suggest that the observed variation in larval growth between habitats may be due to differential habitat selection during settlement by larvae of different condition (Marshall and Keough 2003, Botello and Krug 2006) or the result of selective mortality occurring shortly after settlement (i.e. before the recruits were collected; Bonin et al. 2009). Variation in settlement sizes between habitats, however, appears to be entirely due to differences in selective mortality. Previous results demonstrated that selective mortality acts during the first few weeks of settlement to favor survivors with faster larval growth and larger mean sizes-of settlement in *S. partitus* (Chapter 2). As these are larval traits, they are not directly influenced by the difference in quality of post-settlement habitats, but instead appear to carry-over and influence survivorship under selective predation. Consistent with Nemeth (1998) and the fact that lower overall abundances of recruits were found in the reef habitats, selective mortality appears to be higher in the reef habitats.

Temporal patterns in early life history traits with settlement

Monthly recruitment consistently peaked during the summer months, especially in July and August, but there was also significant interannual variability. This is consistent with patterns of larval supply in this region (D'Alessandro et al. 2007). Examination of growth-related traits in settlement-stage larvae in relation to settlement magnitude revealed that individuals arriving in larger pulses had slower larval growth, longer PLDs, and were larger at settlement. Young recruits (1-10 d post-settlement) maintained these trends in traits, but the differences remained significant only for PLD. Positive correlations between larval growth and settlement intensity have been documented for *S.*

partitus across seasons in San Blas, Panama (Wilson and Meekan 2002), but temperature-related influences on traits were not controlled for as was done in the present study by only examining monthly cohorts that settled during the warmest months. When I examined traits by settlement magnitude across seasonal temperatures, individuals from larger settlement events exhibited faster larval growth than those that settled during small events, however within the peak recruitment season during the warmest months, the pattern was reversed. It is unclear why individuals settling during large pulses would have slower larval growth. Recruitment magnitude can be correlated to production (Meekan et al. 1993) and greater production may be due to more individuals spawning or larger individual clutch sizes. There are known trade-offs between clutch size and egg size (LobonCervia et al. 1997) or oxygen availability (Lee and Strathmann 1998), which can influence subsequent larval performance (Ware 1975), but not necessarily result in greater post-settlement mortality (Gagliano et al. 2007a). Alternatively, large recruitment events may signal a period of reduced mortality and/or selective mortality in the plankton, therefore allowing more individuals with slower larval growth rates to survive to settlement. Growth in the plankton is not generally thought to be density dependent, but if larvae are transported in aggregations, there may be an opportunity for density-dependence to operate (Shepherd and Cushing 1980). Regardless of the mechanism, individuals with slower larval growth, arriving in the larger pulses, were removed from juvenile population so that differences in larval growth with recruitment strength disappeared. In contrast, size-at-settlement is consistently an important trait for recruitment and juvenile survival (Chapters 2 and 3), and large settlement sizes are attained through either fast larval growth or longer PLDs. With regard to settlement

pulses, variation in size-at-settlement appears to be driven more by time spent in the plankton.

Back-calculated settlement dates revealed a peak in settlement around the new moon. This settlement record, however, is based on the otolith analysis of juveniles that survived a period of post-settlement mortality. By adjusting for estimated mortality, the peak in lunar settlement shifted from one day following the new moon to two days prior to the new moon, with relatively more individuals settling around the third quarter moon (days 19-26). This is consistent with the light trap catches of settlement-stage larvae collected during a portion of the time I measured recruitment. Patterns of recruitment for *S. partitus* in other Caribbean locations are somewhat variable, but generally peak around the third quarter (Sponaugle and Cowen 1996a) and new moons (Robertson et al. 1988, Robertson 1992). The pattern that I observed appears to be the result of greater settlement magnitude around the third quarter moon, but preferential survival of individuals settling around the new moon. The adaptive implications of settling on the new moon is avoidance of visual predators (Johannes 1978, Victor 1991); however, if this was the single most important cue, the majority of settlement would occur during this time in all geographic locations. Lunar timing of settlement may be constrained by timing of larval production and relatively fixed development (Robertson et al. 1988), although pelagic processes certainly introduce variation that may obscure patterns in production (Robertson et al. 1988, Robertson et al. 1993, Cowen 2002). For instance, variation in larval transport to settlement habitat can result in variability in settlement during the dark half of the lunar cycle from the third quarter to new moon, encompassing minimum amplitude tides as well. A longer time series of larval supply of *S. partitus* in the upper

Florida Keys during 2002-2003 indicates that settlement in this area may in fact be bimodal, peaking during the quarter moons and minimum amplitude tides (D'Alessandro et al. 2007), but immediate differential survival may obscure this signal in surviving recruits. However, this bimodal pattern of settlement was largely driven by settlement pulses in 2002 that differed slightly from 2003, in that more pulses peaked around the first quarter moon. So, there also can be interannual variability in lunar timing of settlement.

Growth-related traits varied among lunar phases of settlement. Larvae settling to the reef during the dark portion of the lunar cycle, around the third and new moon, were larger, faster growing, and spent less time in the plankton than larvae that settled during the brighter portion of the lunar cycle, around the first quarter and full moons. Therefore the larvae settling during the dark phases of the moon are not only less susceptible to visual predation (Victor 1991), they are arriving with more optimal traits (Anderson 1988). This may be because their larval periods were better synchronized with their food source. It has been shown in other subtropical environments, that zooplankton abundance in the epipelagic layer peaks just before the new moon (Hernandez-Leon et al. 2002), coinciding with the timing of hatching for numerous species (Hernandez-Leon 2008), including *S. partitus* (Dorsey 1999). An increase in prey items around the new moon could be beneficial for larvae at first feeding as well as just prior to settlement. Those larvae that do not synchronize with their prey source may be forced to remain in the plankton until they develop fully or reach a minimum size, and settle during less optimal times (i.e. first quarter and full moons). Delay of settlement has been shown to result in striking declines in larval condition in invertebrate taxa with non-feeding larval stages or

specific diet requirements (Marshall and Keough 2003, Botello and Krug 2006).

Although *S. partitus* are feeding during their larval stage, they have a relatively invariant PLD, which suggests that there may be less flexibility in settlement timing and deviations from the optimum result in sacrifices to larval quality.

Most of the observed differences in traits among larvae settling during different lunar phases were not retained in the juveniles. However, the new moon settlers that survived the first 10d post-settlement continued to have faster larval growth than most of the other settlers (difference from 1st quarter moon settlers was non-significant). Patterns were less variable among lunar phases for size-at-settlement: selective mortality rapidly removed individuals with the smallest settlement sizes regardless of lunar timing of settlement. Indeed, most post-settlement mortality is thought to occur within the first 2 d of settlement (Almany and Webster 2006). During some lunar phases, large size-at-settlement was associated with fast larval growth (dark phases), while individuals settling during other phases achieved larger settlement sizes through long PLDs (light phases). Thus, selective mortality patterns on larval growth and PLD were opposite between dark and light phases of the moon. Another interesting difference between individuals that settled during the darker portion of the lunar cycle versus those settling during the brighter periods was that there was a greater shift in mean size-at-settlement between the larval and juvenile stage for the first quarter and full moon settlers. This suggests stronger selective removal of small settlers. Furthermore, third quarter and new moon settlers that survived to 11-28 d post-settlement exhibited faster early juvenile growth rates than those settling on the first quarter and full moons, when only the third quarter moon settlers exhibited significantly faster early juvenile growth 2-10 d post-settlement. Previously, I

demonstrated that selective mortality processes act on early juvenile growth to remove individuals with faster juvenile growth rates (Chapter 2). Results of the present study indicate that selection against this trait is not as strong for fish settling during more optimal times of the lunar cycle. Despite the advantage to settling during the dark phases of the moon, some exceptional individuals that settle during less optimal times are maintained in the population. This may explain why there remains variability in timing settlement for this species and many others (Robertson 1992, Sponaugle and Pinkard 2004a, D'Alessandro et al. 2007).

It is important to note that I used a cross-sectional approach, rather than a longitudinal sampling design, to compare traits of different aged fish, and detect patterns in selective mortality. There are disadvantages to this method, as neither time of hatching nor settlement was controlled for and individuals may have been exposed to different environmental features that were unmeasured, but contributed to differences in traits with age. That being said, cross-sectional approaches have been used before to examine selective mortality processes (Hawn et al. 2005) and results of the present study are consistent with findings using a longitudinal sampling design (Chapter 2).

Another caveat to this study is that monthly sampling limited the sample sizes of different aged juveniles that settled during different lunar phases. Despite these constraints, I observed significant differences among both lunar phases and age groups. The direction of selective mortality varied by lunar phase for larval growth and PLD, but was consistent among lunar phases for size-at-settlement and early juvenile growth, albeit weaker for individuals that settled during the third quarter and new moons and arrived with more optimal traits.

Density-dependent effects

For the warmest months from 2007-2008, monthly *S. partitus* recruit density was strongly positively correlated with the density of > 1 mo old juvenile conspecifics (2-3 cm SL). This is consistent with a pattern of monthly pulses in settlement following one another, but could also indicate enhanced recruitment as a result of the presence of conspecifics. Further evidence that the presence of conspecifics can enhance recruitment is provided by a positive relationship between recruit density and density of intermediate-sized conspecifics (3-5 cm SL), which should be at least several months old and could have settled during a different season. Presence of conspecifics can enhance reef fish settlement (Sweatman 1983, Lecchini et al. 2007) or inhibit it (Steele et al. 1998, Almany 2003). Interestingly, the relationship between recruit density and adult conspecific density was not significant, and if anything, appeared negative. The presence of conspecifics may signal high quality habitat, but *S. partitus* is a highly territorial species and reproductively mature adults may aggressively deter settlement of potential competitors. Younger conspecifics may not be as disturbed by new settlers or as effective in removing them. While recruitment magnitude was not significantly correlated with adult conspecific density, some early life history traits of recruits were. Larval growth and sizes-at-settlement were greater for recruits surrounded by higher densities of adult conspecifics. Since these traits are related to enhanced survival (Chapter 2), it is possible that only the best performers can survive high densities of adult conspecifics, and in fact high densities of conspecifics have been associated with elevated mortality of juveniles of this species (Tupper and Hunte 1994, Johnson 2008). These are coarse comparisons, but the fact that significant relationships were detected implies that density of conspecifics

has an important influence on early life history traits and post-settlement processes. Presence of conspecifics may initially serve as a cue for settlement, but the aggressive nature of adult *S. partitus* may also prevent all except the strongest recruits from remaining within high densities of adults. Previous work documented that recruits in close proximity to conspecifics exhibited slower juvenile growth (Chapter 3), a trait associated with enhanced survival (Chapter 2). A similar, negative, but non-significant trend was evident in the present study between early juvenile growth and adult conspecific density.

Conclusions

Results of this study demonstrate that early life history traits interact with both temporal and spatial patterns of settlement and recruitment to influence reef fish juvenile demography. The distribution of early life history traits of settlers is related to both timing and location of settlement. Post-settlement processes may maintain that variation or obscure it. Individuals settling during optimal times (i.e. new moon, large pulses) arrive with better traits, such as larger sizes-at-settlement. Large settlement sizes can be achieved by faster growth or longer PLD and it appears that both scenarios are used by *S. partitus*. Fish settling on the new moon achieved larger settlement sizes through faster larval growth, but larvae settling during larger events spent more days growing in the plankton. Regardless of the mechanism, most of the variation in traits among individuals that settled during different lunar phases and settlement magnitudes was not maintained in the juveniles over time. Selective mortality processes acted consistently in the same direction on some traits (size-at-settlement, early juvenile growth) regardless of the

timing of settlement to produce survivors with similar traits, although, the intensity of selective loss of less advantageous traits varied depending on lunar phase of settlement.

Early life history traits also varied as a function of choice of settlement habitat. Individuals settling on reef habitat and/or within high densities of adult conspecifics were larger at settlement compared to those in rubble habitat or within low densities of adults. Because the microhabitat preferences of settling larvae could not be determined from my method of sampling (light traps), I cannot completely disentangle the relative importance of pre- and post-settlement processes in creating these spatial patterns. However, the fact that 1-10 d old recruits did not vary in settlement sizes between reef and rubble habitats, but the 11-28 d olds did indicates that selective loss of the smallest settlers occurred post-settlement and was strongest in reef habitats. Therefore, differences in early life history traits due to lunar timing of settlement are not maintained throughout the early juvenile phase, due to vastly different selective pressures acting on individuals settling during different lunar phases, but variation in traits among post-settlement habitats are preserved. The resulting patterns of density and composition of ELHTs are the product of very different selective mortality processes acting over multiple temporal and spatial scales. Therefore, for *S. partitus*, and probably other species with similar life histories, timing and location of settlement shape juvenile demography.

Table 4.1. Monthly variability in recruitment of *Stegastes partitus*. Mean is the mean number of recruits per 300 m², SD is the standard deviation, and CV is the coefficient of variation.

Month	Mean (# 300 m⁻²)	SD	CV
January	0.31	0.79	2.53
February	0.17	0.73	4.23
March	0.29	0.80	2.72
April	1.70	3.11	1.83
May	3.39	7.00	2.07
June	4.55	6.91	1.52
July	5.39	8.58	1.59
August	6.57	9.73	1.48
September	2.64	3.16	1.20
October	1.19	2.66	2.23
November	2.02	3.21	1.59
December	0.25	0.61	2.43

Table 4.2. Rayleigh statistics for lunar and tidal amplitude synchrony in settlement and successful spawning of *Stegastes partitus* in the upper Florida Keys. All tests were significant at < 0.001 . Z is the Rayleigh test statistic; Day is the mean peak in lunar or maximum tidal amplitude calculated from mean vector angle; s is the mean angular deviation; Day 1 is the new moon.

	n	Z	Day	s
Lunar settlement				
Aged recruits	786	134.5	2	5.0
Recruits adj. for mortality	1429	142.0	29	5.4
Settlement-stage larvae	415	64.1	27	5.1
Tidal settlement				
Recruits adj. for mortality	1383	161.6	1	5.3
Lunar spawning				
Aged recruits	788	89.0	1	5.3
Recruits adj. for mortality	1433	86.4	26	5.7
Settlement-stage larvae	196	21.7	21	5.3

Table 4.3. Results of Kruskal-Wallis tests, comparing *Stegastes partitus* early life history traits among different phases of lunar settlement (first quarter, 1ST; full moon, FULL; third quarter, 3RD, and new moon, NEW) for three age groups (larvae, L; recruits, R; 1-10 d post-settlement recruits; juveniles, J; 11-28 d post-settlement juveniles).

Traits	LARVAE		1-10 d		11-28 d	
	<i>P</i>	post-hoc	<i>P</i>	post-hoc	<i>P</i>	post-hoc
Larval growth	< 0.001	1st, full < 3rd, new	0.008	3rd < 1st, new; full < new	0.113	
PLD	< 0.001	1st, full, 3rd > new	0.962		0.003	1st < 3rd, new
Size-at-settlement	< 0.001	1st, full < 3rd, new	0.886		0.124	
Juvenile growth 1-2 d			0.004	1st, full, new < 3rd	0.004	1st, full < 3rd, new

Table 4.4. Results of Kruskal-Wallis tests, comparing *Stegastes partitus* early life history traits among age groups (larvae, L; recruits, R; 1-10 d post-settlement recruits; juveniles, J; 11-28 d post-settlement) for different phases of lunar settlement (first quarter, 1st; full moon, FULL; third quarter, 3rd; and new moon, NEW).

Traits	1 st		FULL		3 rd		NEW	
	<i>P</i>	post-hoc	<i>P</i>	post-hoc	<i>P</i>	post-hoc	<i>P</i>	post-hoc
Larval growth	< 0.001	L < R, J	0.015	L < R, J	0.044	L, J > R	< 0.001	L > R, J
PLD	0.016	L > R, J	0.045	L < R	0.125		< 0.001	L < R < J
Size-at-settlement	< 0.001	L < R < J	< 0.001	L < R, J	< 0.001	L < R < J	< 0.001	L < R, J
Juvenile growth 1-2 d	< 0.001	R > J	< 0.001	R > J	0.001	R > J	0.006	R > J

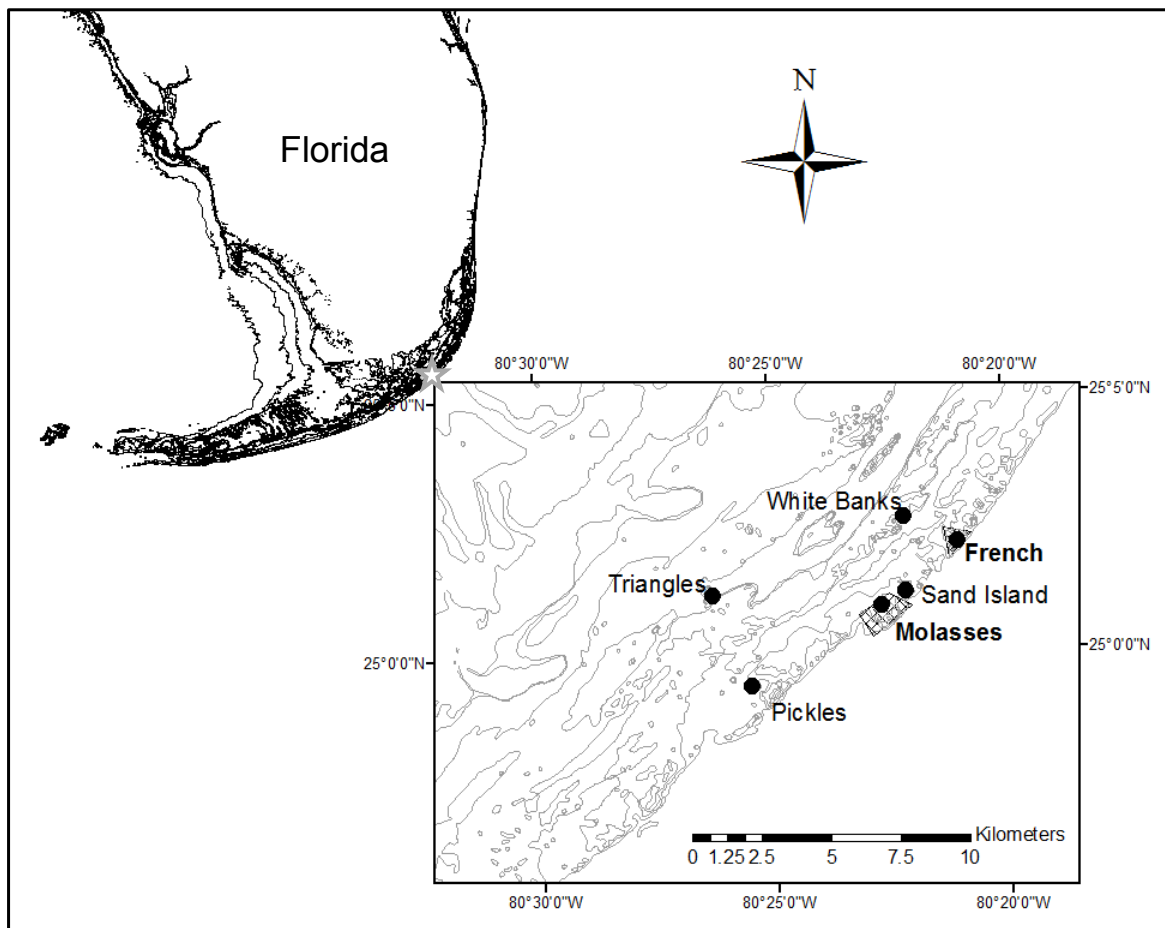


Figure 4.1. Map of the upper Florida Keys with sampling sites for light trap deployment and recruit surveys and collection.

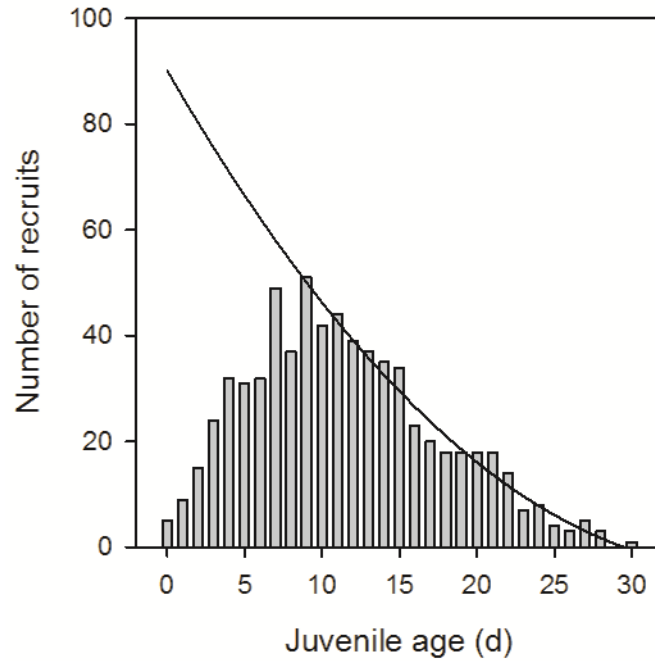


Figure 4.2. Juvenile age distribution of *Stegastes partitus* recruits in the upper Florida Keys (bars) with a function ($y = 0.0671x^2 - 5.0165x + 89.763$) fitted to the slope of the 9+ day old recruits (line) to estimate mortality.

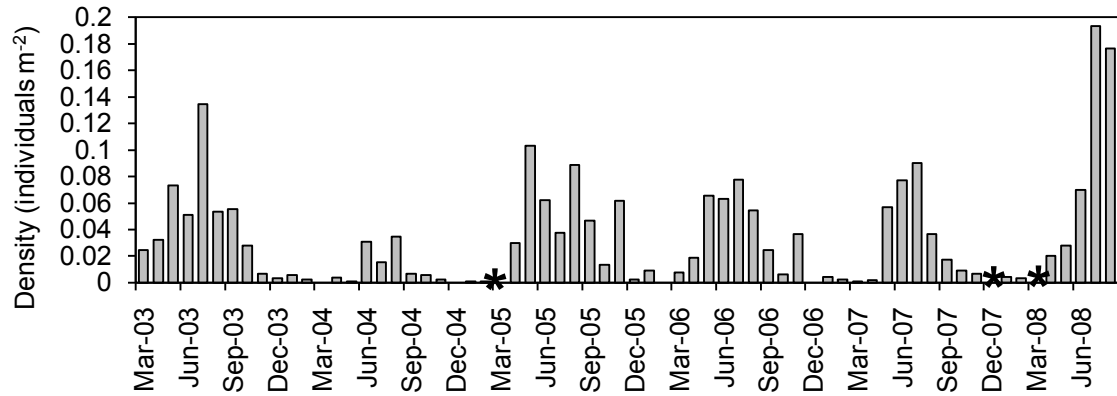
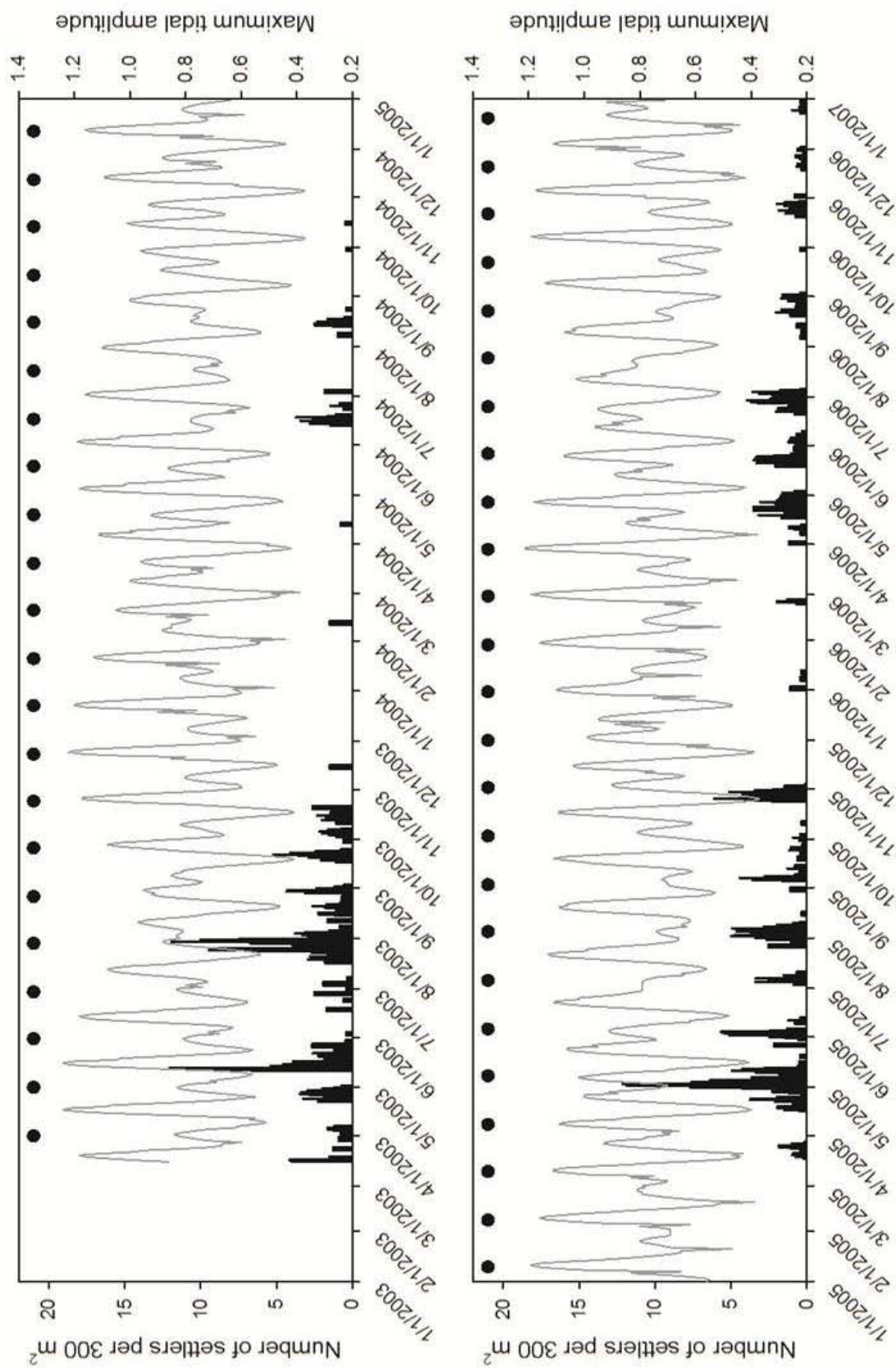


Figure 4.3. Monthly recruitment of *Stegastes partitus* in reef and rubble habitats across four Florida Keys sites: Pickles, Molasses, Sand Island, and French Reefs. Asterisks indicate months when sampling did not take place.

Figure 4.4. Daily back-calculated settlement of *Stegastes partitus* in reef and rubble habitat at Pickles and Sand Island Reefs combined (bars). Timing of settlement of

collected recruits was adjusted for monthly density estimates and estimated post-settlement mortality. Maximum tidal amplitude is indicated by a line, and new moons by solid circles. Asterisks indicate months when sampling did not take place.



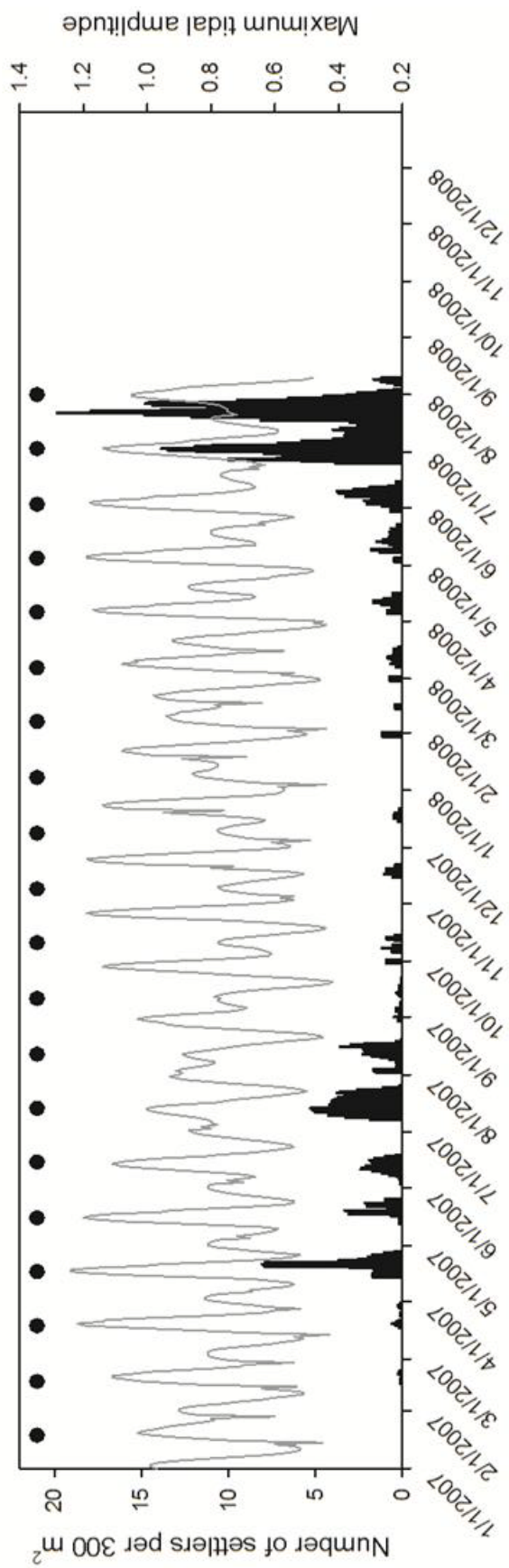
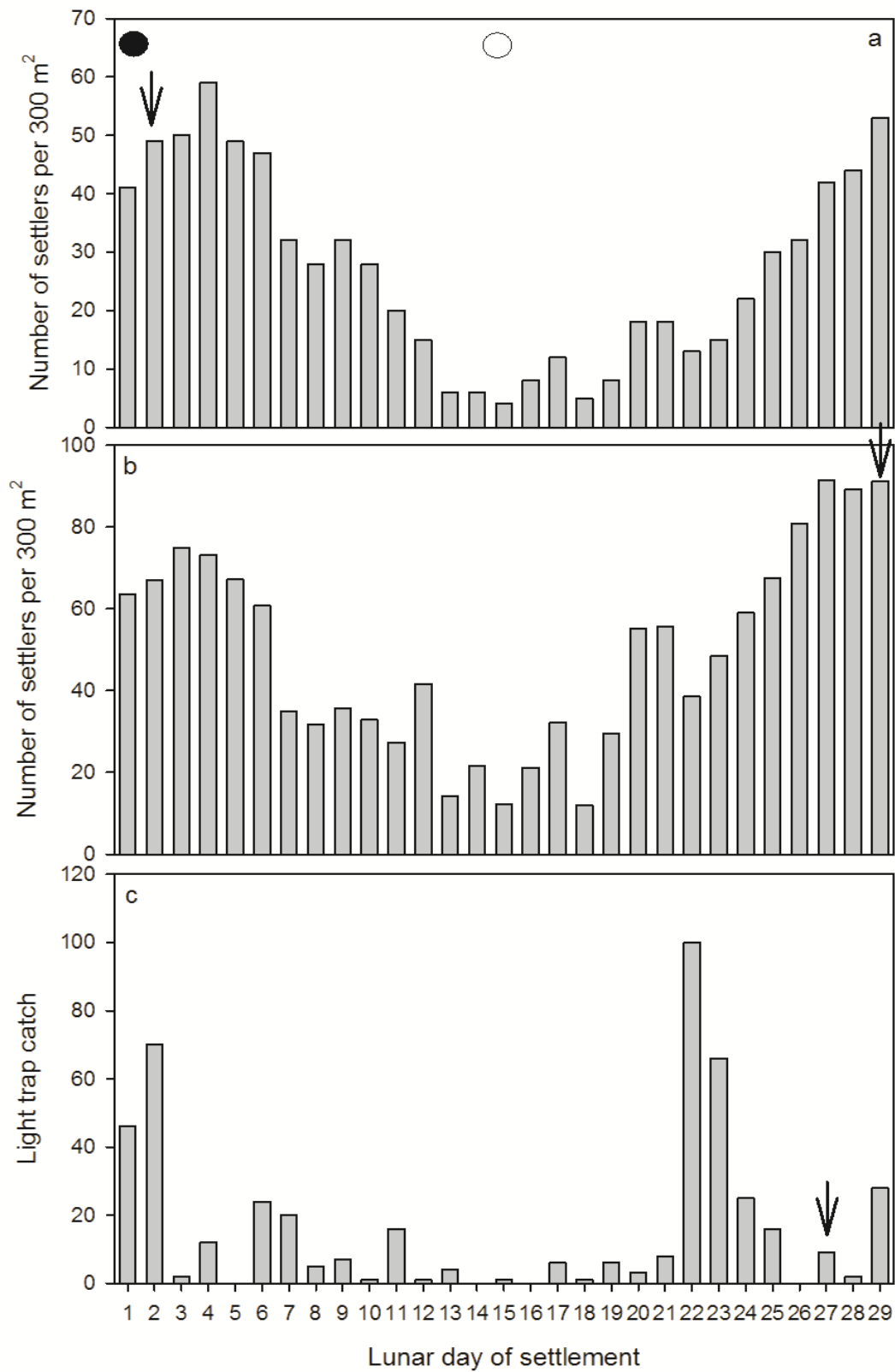


Figure 4.5. Back-calculated lunar settlement of *Stegastes partitus* recruits (a) collected from April 2003 to August 2008, and (b) adjusted for recruitment magnitude (density) and mortality. (c) Total number of late-stage larvae collected in light traps from May 2003 to January 2004 plotted over a single lunar cycle. Day 1 = new moon. Arrow indicates mean day about which settlement peaked.



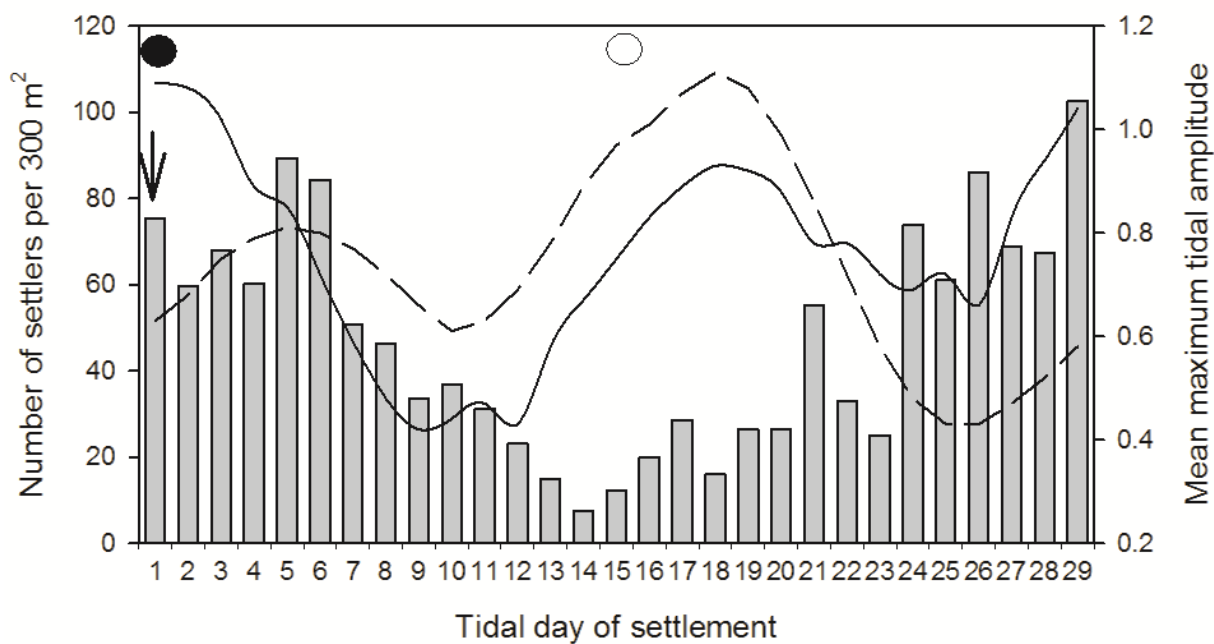


Figure 4.6. Back-calculated settlement of *Stegastes partitus* recruits collected from April 2003 to August 2008, adjusted for recruitment magnitude (density) and mortality, plotted over a single maximum tidal amplitude cycle. Two sample maximum tidal amplitude cycles plotted for representative days when maximum occurred in conjunction with the new moon (solid line) and the full moon (dashed line). New moon indicated by a solid circle and full moon by an open circle.

Figure 4.7. Back-calculated timing of successful spawning by *Stegastes partitus* for (a) recruits collected from April 2003 to August 2008, and (b) adjusted for recruitment magnitude (density) and mortality. (c) Back-calculated timing of successful spawning of settlement-stage larvae collected in light traps from May 2003 to January 2004 plotted over a single lunar cycle.

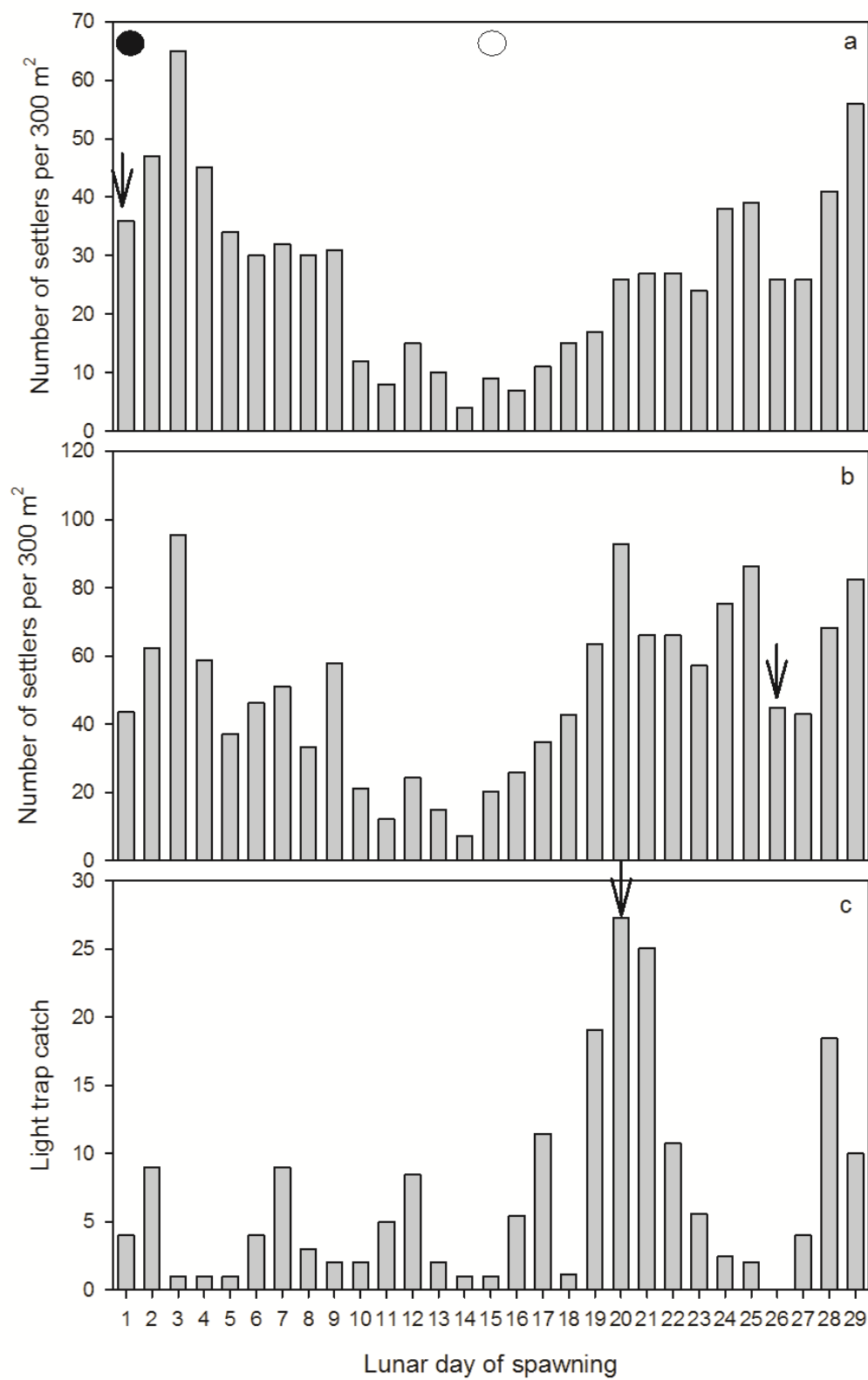
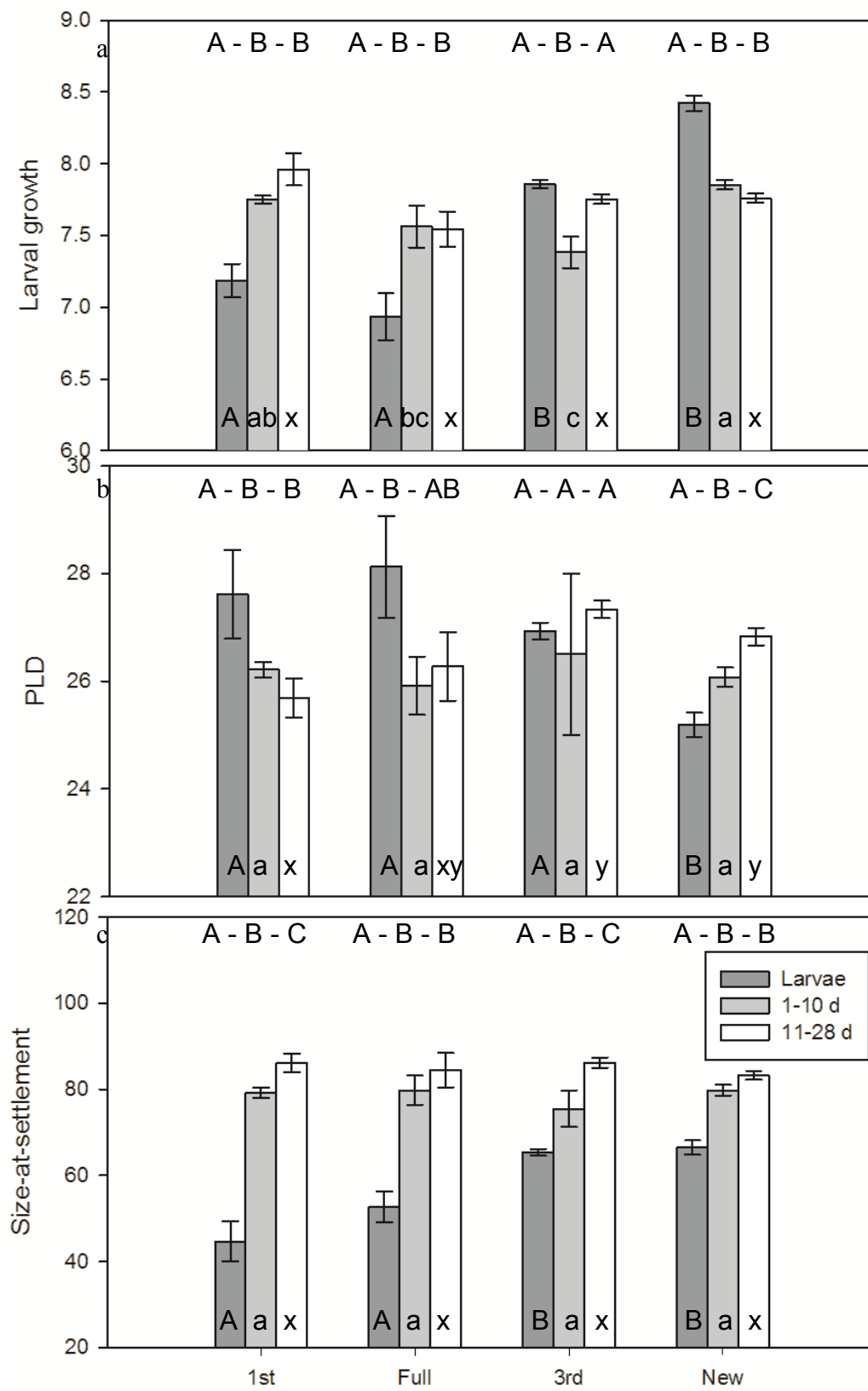


Figure 4.8. Mean otolith-derived (a) larval growth, (b) pelagic larval duration (PLD), and (c) size-at-settlement of *Stegastes partitus* settlement-stage larvae, recruits (1-10 d), and juveniles (11-28 d post-settlement) by lunar phase of settlement. Effect of temperature was minimized by including only 25 monthly cohorts collected from May 2003 to August 2008 with mean water temperatures of > 28 °C. Error bars represent SE. Letters above the bars indicate significant relationships among age groups, within lunar phases. Letters within the bars indicate significant relationships among lunar phases, within age groups (capital A, B denote differences among larvae, lowercase a, b denote differences among 1-10 d old recruits, lowercase x,y denote differences among 11-28 d old juveniles).



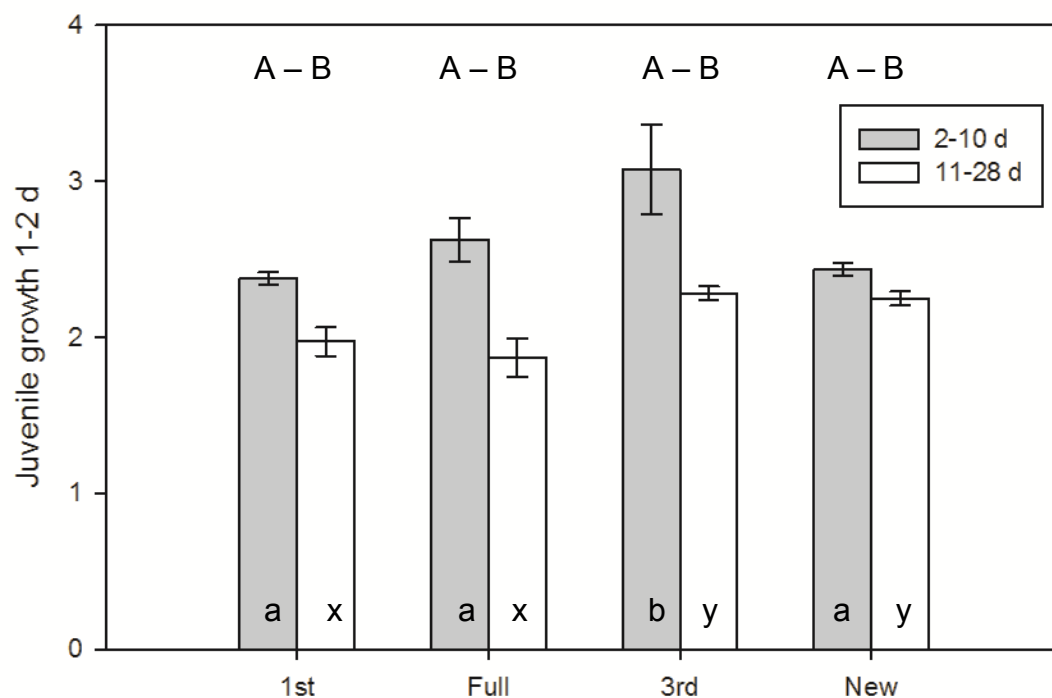


Figure 4.9. Mean otolith-derived juvenile growth over the first 2 d on the reef by lunar phase of settlement for *Stegastes partitus* divided into 2-10 d recruits and 11-28 d old juveniles. Effect of temperature was minimized by including only 25 monthly cohorts collected from May 2003 to August 2008 with mean water temperatures of > 28 °C. Error bars are SE. Letters above indicate significant relationships among age groups, within lunar phases. Letters within the bars indicate significant relationships among lunar phases, within age groups.

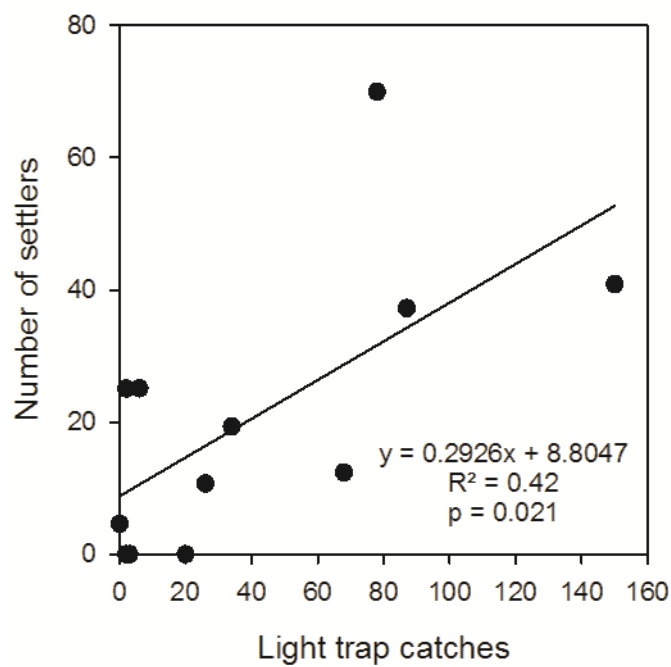


Figure 4.10. Relationship between number of *Stegastes partitus* settlers per 300 m² estimated from monthly recruitment densities and adjusted for post-settlement mortality, and light trap catches from May 2003 to January 2004.

Figure 4.11. Mean otolith-derived (a) larval growth, (b) pelagic larval duration (PLD), and (c) size-at-settlement of *Stegastes partitus* settlement-stage larvae by size of light trap pulse. Effect of temperature was minimized by including only 25 monthly cohorts collected from May 2003 to August 2008 that encountered mean water temperatures of > 28 °C. Error bars are SE. Asterisks (*) indicate significant differences with a $p < 0.05$.

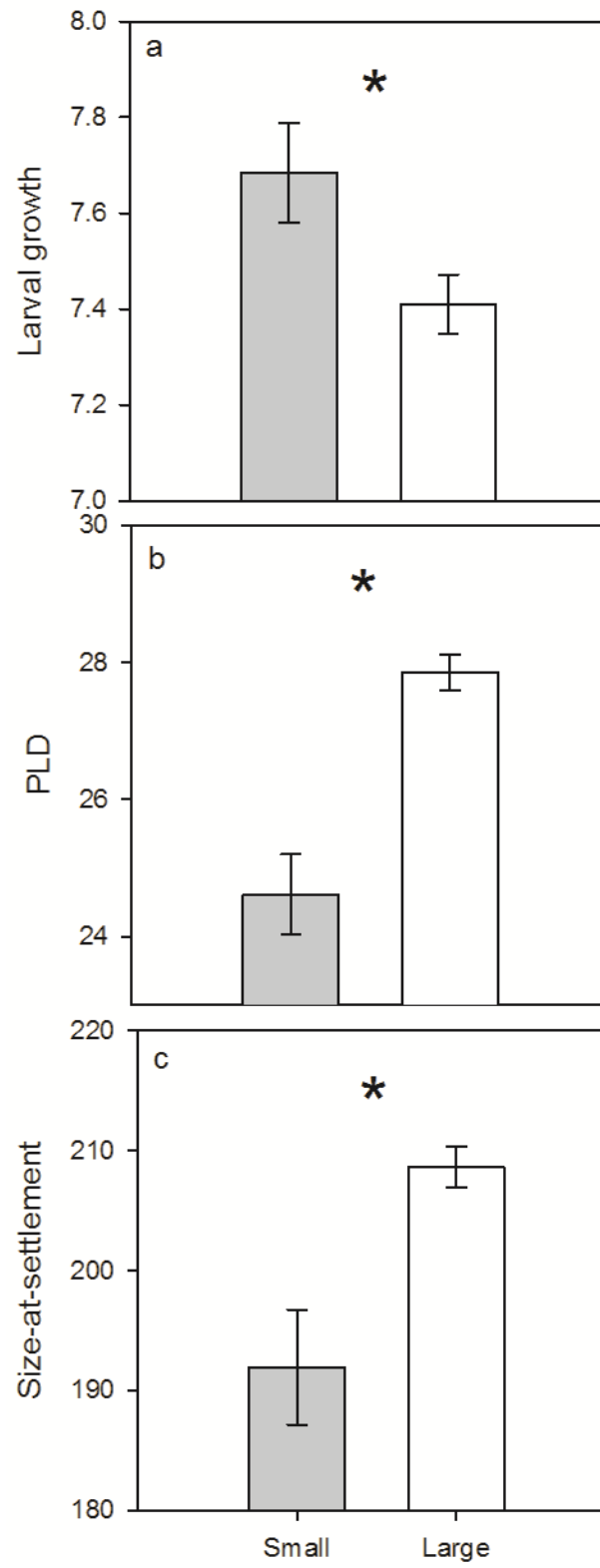
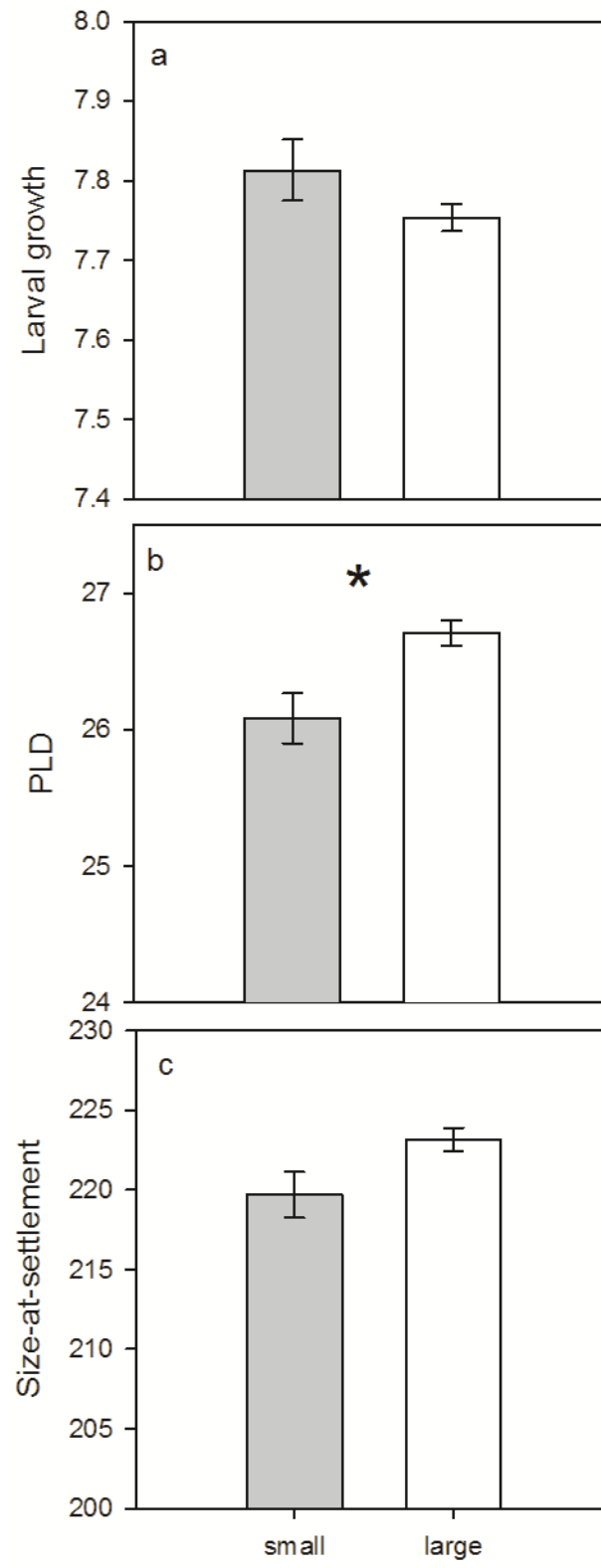


Figure 4.12. Mean otolith-derived (a) larval growth, (b) pelagic larval duration (PLD), and (c) size-at-settlement of *Stegastes partitus* 1-10 d old recruits by size of settlement event. Effect of temperature was minimized by including only larvae collected from May 2003 to August 2008 with mean water temperatures of > 28 °C. Error bars are SE. Asterisks (*) indicate significant differences with a $p < 0.05$.



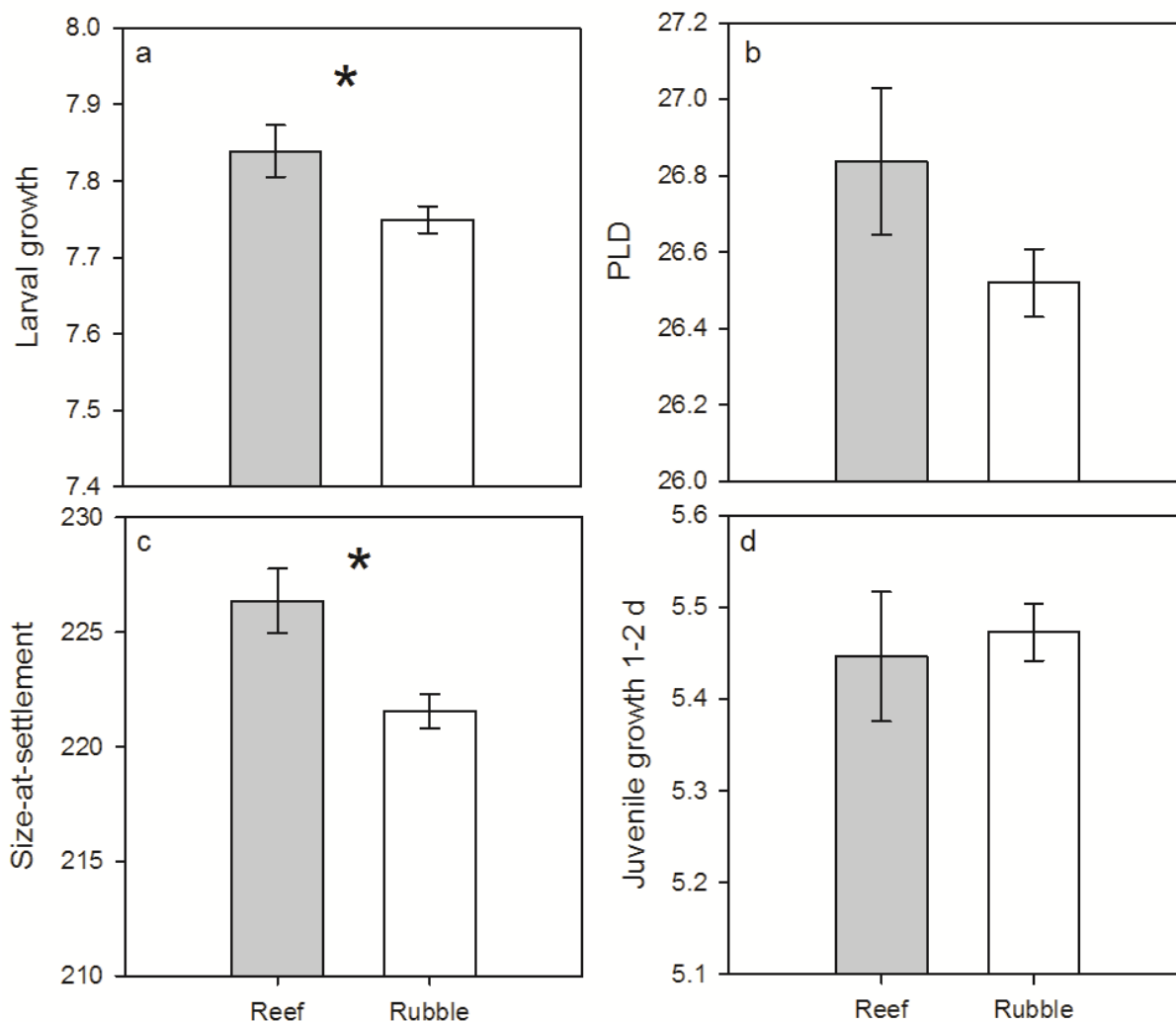


Figure 4.13. Mean otolith-derived (a) larval growth, (b) pelagic larval duration (PLD), (c) size-at-settlement, and (d) early juvenile growth of *Stegastes partitus* recruits (1-28 d post-settlement) by habitat type (i.e. reef crest and rubble). Effect of temperature was minimized by including only 25 monthly cohorts collected from May 2003 to August 2008 that encountered mean water temperatures of $> 28^{\circ}\text{C}$. Error bars are SE. Asterisks (*) indicate significant differences with a $p < 0.05$.

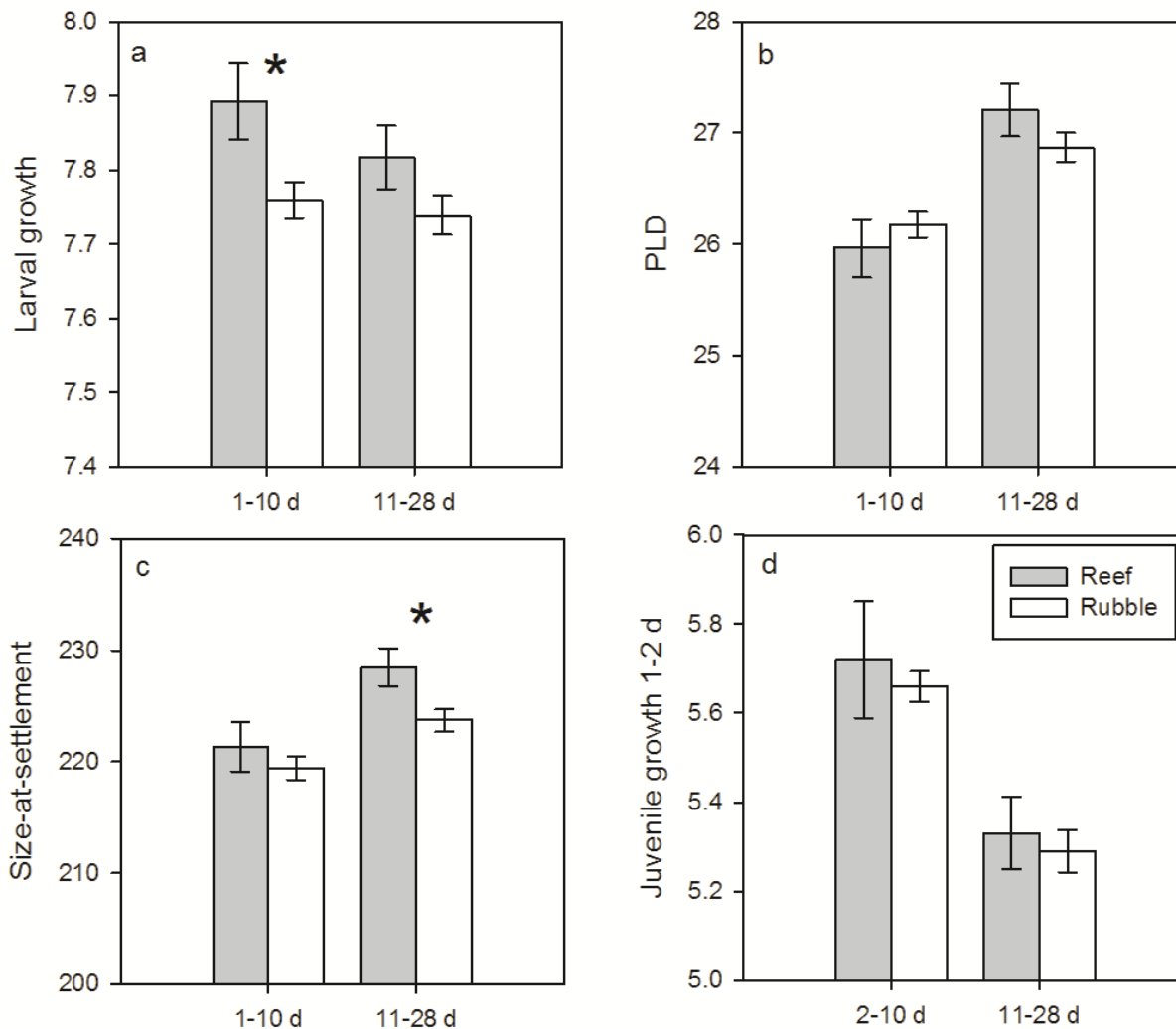


Figure 4.14. Mean otolith-derived (a) larval growth, (b) pelagic larval duration (PLD), (c) size-at-settlement, and (d) early juvenile growth for *Stegastes partitus* 1-10 d old and 11-28 d recruits by habitat type (i.e. reef crest and rubble). Effect of temperature was minimized by including only 25 monthly cohorts collected from May 2003 to August 2008 that encountered mean water temperatures of > 28 °C. Error bars are SE. Asterisks (*) indicate significant differences with a $p < 0.05$.

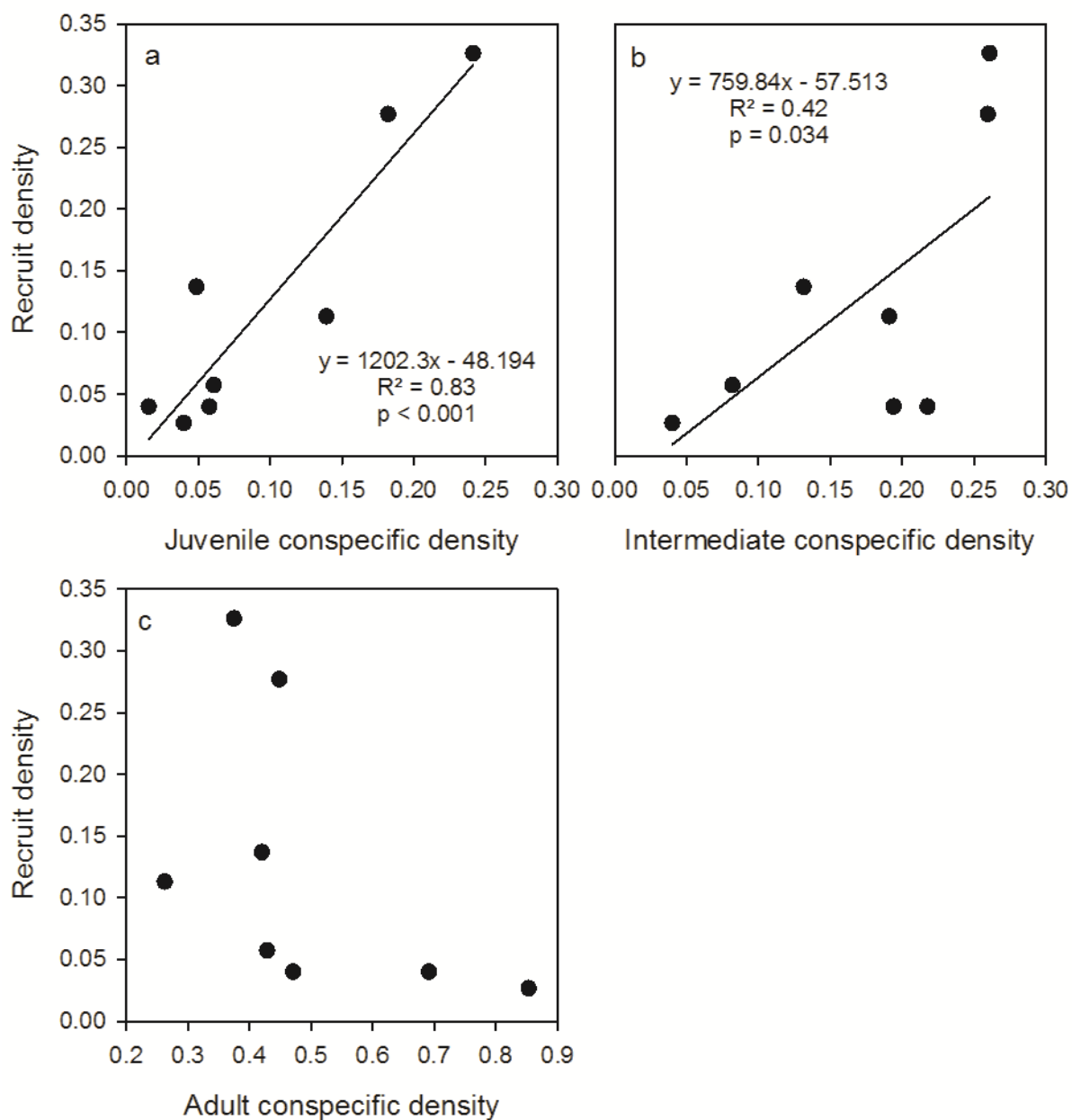


Figure 4.15. Relationship between monthly *Stegastes partitus* recruit density and densities of (a) > 1 mo. old juvenile (2-3 cm SL), (b) intermediate (3-5 cm SL), and (c) adult (> 5 cm) conspecifics from June 2007 to August 2008.

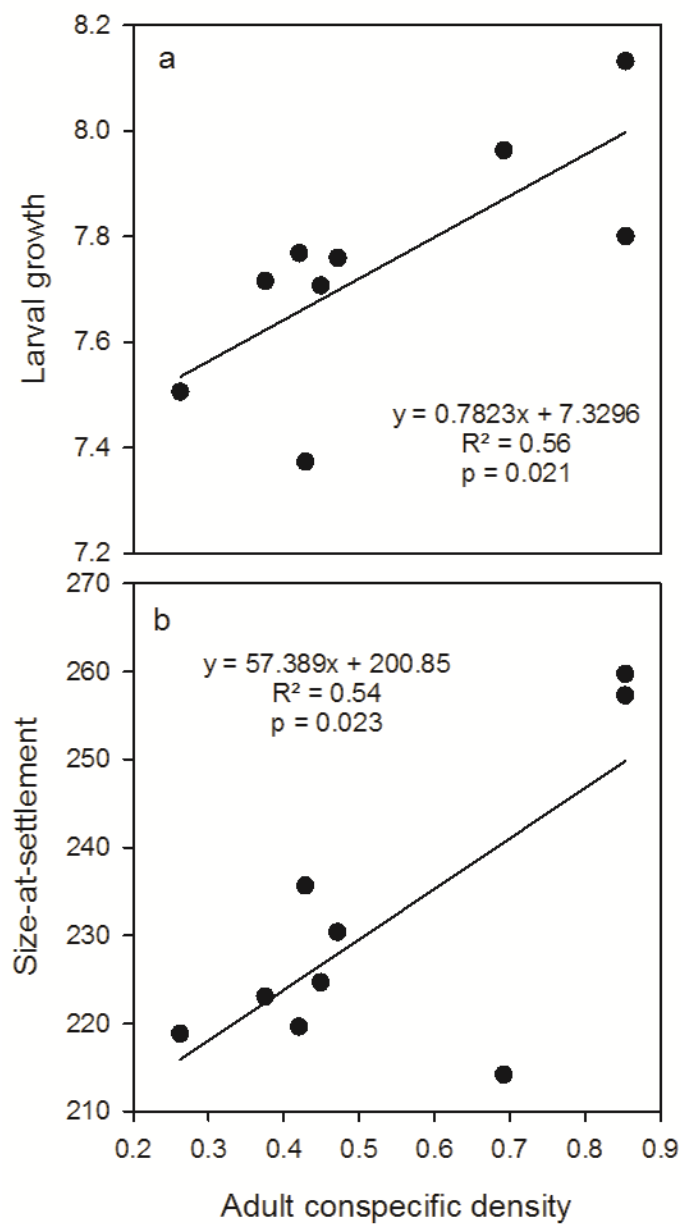


Figure 4.16. Relationship between mean otolith-derived (a) larval growth and (b) size-at-settlement of *Stegastes partitus* recruits and adult conspecific density from June 2007 to August 2008.

Chapter 5: Examination temporal patterns in genetic structure within and among cohorts of settlement-stage larvae and new recruits of a coral reef fish.

Background

Population connectivity is the exchange of individuals among two or more distinct sub-populations (Cowen et al. 2007). The degree to which marine populations are connected to each other over demographic timescales is important to their management and the understanding of population dynamics. For demersal species, such as coral reef fishes, population connectivity is mostly determined during the early life stages through a combination of larval dispersal and post-settlement survival (Pineda et al. 2007, Cowen and Sponaugle 2009).

To assess the level of exchange of individuals among populations or subpopulations, both direct and indirect methods have been employed. Oceanographic data and life history and behavior of larvae have been modeled to estimate dispersal kernels (Mullon et al. 2003, Paris and Cowen 2004, Cowen et al. 2006, Fiksen et al. 2007) in addition to some efforts to measure dispersal directly through physical tagging (Jones et al. 1999, Jones et al. 2005, Almany et al. 2007). Due to the small and diffuse nature of fish larvae and the high mortality rates that they suffer, direct methods of larval tracking from spawning to settlement have had limited success, except within simple and/or isolated systems such as island populations (Jones et al. 1999, Jones et al. 2005, Almany et al. 2007). Indirect methods of inferring dispersal include the use of natural markers, such as the growth history and trace elements captured in hard parts (Swearer et al. 1999, Becker et al. 2007, Hamilton et al. 2008) and genetics (Shulman and Bermingham 1995, Baums et al. 2005, Purcell et al. 2006). There has been some success

in detecting larval retention to natal reefs using trace element analysis (Swearer et al. 1999), but this technique has been most useful for species that utilize nearshore spawning habitats that differ markedly from each other and the open ocean (Forrester and Swearer 2002, Swearer et al. 2003, Gillanders 2005), and increasing evidence indicates that such signatures are frequently temporally unstable (Swearer et al. 2003). Genetic approaches utilize neutral or nearly neutral markers (proteins or DNA fragments) to estimate the balance between gene flow (effective dispersal) and genetic drift that creates spatial or temporal patterns in population structure (Bohonak 1999). While the other methods of assessing population connectivity provide evidence for the amount of dispersal or retention that can occur over short timescales (i.e. length of pelagic larval durations), genetic tools can measure effective dispersal that results in individuals that contribute to the population (i.e. successfully breed; Palumbi 2003).

Several different molecular markers are commonly used to estimate levels of population connectivity, including allozymes (Planes et al. 1998, Planes and Fauvelot 2002), mitochondrial DNA (mtDNA; Shulman and Bermingham 1995, Taylor and Hellberg 2003), and microsatellites (Knutsen et al. 2003, Purcell et al. 2006, Gerlach et al. 2007). Allozymes are proteins and therefore reflect variation in coding DNA. As a result, they are often conserved and exhibit low variability among individuals and populations. Microsatellites are tandem repeats of noncoding nuclear DNA. Because they are not usually under selection, they generally experience mutation rates higher than other markers and are thus extremely variable. Mitochondrial DNA is usually uniparentally (maternally) inherited, which means that it represents a smaller effective population size, whereby alleles can become fixed more quickly in a population.

However, they are thought to mutate more slowly than microsatellites and therefore may reveal genetic structure that was created over evolutionary (tens or hundreds of thousands of generations) rather than ecological (hundreds or thousands of generations) time scales.

Many studies have examined the spatial genetic population structure of marine organisms. Despite the potential for long-distance dispersal, significant genetic structure has been detected for some species (Taylor and Hellberg 2003, Baums et al. 2005, Purcell et al. 2006, Gerlach et al. 2007), although generally over large spatial scales, on the order of 100s to 1000s of km. Furthermore, estimates of dispersal and connectivity vary widely among published findings (Shulman and Bermingham 1995, De Innocentiis et al. 2001, Purcell et al. 2006). This may be due, in part, to the different scales (ecological vs. evolutionary) over which various markers estimate genetic structure (microsatellites vs. mtDNA or allozymes). Differences in dispersal estimates may also reflect variation in factors influencing dispersal (e.g., ocean currents, stochastic physical oceanographic features, storms, larval production, larval life history and development). Temporal variation in monthly recruitment is common among coral reef fishes (Doherty and Williams 1988, Robertson et al. 1988, Robertson 1992, Milicich and Doherty 1994, Sponaugle and Cowen 1996a, Wilson 2001, Sponaugle and Pinkard 2004b) and includes both consistent monthly and seasonal patterns as well as stochastic fluctuations in recruitment strength. Variation in settlement and recruitment can correspond to variation in the composition of new recruits (Sponaugle and Pinkard 2004b, Sponaugle et al. 2006). For instance, growth-related early life history traits, such as larval growth, have been shown to vary with recruitment magnitude (Bergenius et al. 2002, Wilson and Meekan 2002, Bergenius et al. 2005, Chapter 4).

Studies utilizing genetic markers have also examined temporal variability among young cohorts (Li and Hedgecock 1998, Lenfant and Planes 2002, Hepburn et al. 2009) and within cohorts tracked through time (Planes and Romans 2004, Jones and Barber 2005, Vigliola et al. 2007). Variability among monthly cohorts of settling larvae could be the result of stochastic events that randomly affect larval dispersal and survival (e.g., storms) or the chance reproductive success of a few adults (i.e. sweepstakes effect; Hedgecock 1994). If larvae that successfully settle to the reef are from a unrepresentatively small group of adults, then the larvae would be less diverse than the adult population and they would be more closely related to each other than expected (Hedgecock 1994, Ruzzante et al. 1996, Selkoe et al. 2006). Additionally, genetic variation can change within cohorts through time as a consequence of selective mortality of particular individuals, or the loss of genetic variation by chance (i.e. genetic drift). Previous results have revealed a selective loss of *Stegastes partitus* recruits with particular growth-related early life history traits (i.e. smaller sizes at settlement, slower early juvenile growth; ELHTs) on reefs in the upper Florida Keys (Chapter 2). Although ELHTs vary significantly with temperature (Chapter 2), the degree to which variation in those traits is due to differences in genetic makeup or other influences is unknown. Other studies have demonstrated a concurrent loss in growth-related traits and genetic alleles (Planes and Lenfant 2002, Jones and Barber 2005, Vigliola et al. 2007).

The purpose of this study was to track and sample multiple monthly cohorts of settling larvae and surviving juveniles. The genetic composition of different stages was compared (as well as to concurrently collected adults) to determine (1) if the genetic composition of larvae is temporally variable due to stochastic dispersal processes and/or

differential spawning success (i.e. sweepstakes effect), and (2) if the genetic composition of cohorts changes through time as a result of selective mortality during the transition from the larval to juvenile stage or genetic drift. I used two different molecular markers, microsatellites and a section of the mtDNA control region I, with different mutation rates to capture genetic structure over different scales. To my knowledge, this is the first attempt to examine temporal genetic variability in recruitment across multiple scales (interrannual, monthly, across life history stages) using two different molecular markers (mtDNA, microsatellites).

Materials and Methods

Study species and site

Stegastes partitus is a common coral reef fish distributed from Brazil to the Florida Keys (FK; Emery 1973, Lieske and Myers 1996). Throughout the year, adults spawn demersal eggs on a monthly basis, peaking during summer months and near the third quarter moon within each month (Schmale 1981, Robertson et al. 1988, Dorsey 1999). Larvae spend approximately 30 d in the plankton (Sponaugle and Cowen 1996a), which is sufficient time for potentially long-distance dispersal. The timing of settlement appears to be synchronized with lunar phase and peaks occur during the third quarter and/or new moon (Robertson et al. 1988, Sponaugle and Cowen 1996a, Dorsey 1999, D'Alessandro et al. 2007). Seasonal peaks in settlement to the FK typically occur during summer months (D'Alessandro et al. 2007).

The FK reef tract is a barrier reef on the southeast U.S. continental shelf, bordered by the Florida Current (FC), a major western boundary current. The FC is fed by two main sources: the Loop Current (LC) and the Antilles Current. The LC connects the

Yucatan Current to the FC, which once it exits the Straits of Florida (SOF), becomes the Gulf Stream. The velocity of the FC through the SOF is considerable, with mean speeds of 1.6 m s^{-1} (Richardson et al. 1969), varying seasonally with wind and tidal cycles.

Cyclonic frontal eddies that form along the boundaries of the LC and FC are the dominant mesoscale features in the southern SOF (Fratantoni et al. 1998) and larval replenishment to the reefs has been hypothesized to be influenced by the formation and shedding of mesoscale eddies at the frontal boundary (Lee et al. 1994).

Field sampling

To capture settlement-stage *S. partitus* larvae as they settled to the reef, light traps were deployed on a monthly basis periodically from August 2004 until April 2007, coinciding with the third quarter moon, a known peak time in larval supply to this area (D'Alessandro et al. 2007). Six traps were deployed at French Reef (FR; $25^{\circ}02.06' \text{ N}$, $80^{\circ}21.00' \text{ W}$) located within the Florida Keys National Marine Sanctuary. FR was chosen because it consistently receives a greater supply of larvae than some surrounding reefs (D'Alessandro et al. 2007). Larvae were removed from the traps between 0700-0800 h and measured to the nearest 0.5 mm standard length (SL). Each larva was sacrificed with the anterior half stored in 95% ethanol to preserve the otoliths and the posterior half stored in urea prior to DNA extraction. If *S. partitus* larvae were collected during the first night of trap deployment, sampling continued for up to three consecutive nights or until 100 larvae were collected. If ≥ 40 larvae were collected, newly settled recruits were sampled a week later by divers using hand nets and the anesthetic Quinaldine. However, because FR is a sanctuary protected area where benthic sampling is not permitted, 50 recruits were collected from each of two neighboring reefs: Sand Island Reef (SI;

25°01.09' N, 80°22.08' W) and Pickles Reef (PI; 24°59.23' N, 80°24.88' W). Recruits were measured and preserved via similar methods applied to the larvae. Once a year, 100 adult *S. partitus* were collected (50 each from SI and PI). The SL of each fish was measured to the nearest mm on the research vessel and a fin clip was taken and stored in urea for DNA extraction. Afterwards, the adults were released live back onto the reef. Over the three years of sampling, I accrued five monthly cohorts with sufficient sample sizes of larvae and juveniles (≥ 40) to do genetic analyses. Three cohorts (August 2004, May 2005, April 2007) were selected for genetic analyses to encompass as many different years as possible. Adults collected each year were also included in the analyses, with the exception of 2007. Instead, adults collected late in 2006 (November) were compared with the larvae and juveniles collected in 2007, but for simplicity, from this point on the entire cohort will be referred to as '2007'.

Genetic analysis

DNA was extracted from fin and muscle tissue using standard extraction techniques (modified from Bruford and Saccheri 1998), then dissolved in 10 mM of Tris-HCL and stored at 4 °C. Six microsatellite loci were amplified for one cohort of 96 ea. of larvae, juveniles, and adults collected in 2004, using primer pairs developed by Williams et al. (2003): SpAAC33, SpAAC42, SpAAC47, SpAAT40, SpGATA16, SpGATA40. One primer from each pair was 5'-labelled with FAM, NED, PET, or VIC. Polymerase chain reactions (PCRs) were performed in a total volume of 10.0 μ L with the following components: 50-100 ng genomic DNA, 0.5 μ M each primer, 0.20 mM dNTPs, PCR buffer (500 mM Tris-HCL, 160 mM $(\text{NH}_4)_2\text{SO}_4$, 1.5 mM MgCl_2 , 1% Tween), 0.5 U *Taq* and dH_2O . PCR was carried out on a ThermoHybaid PxE Thermal Cycler. Annealing

temperature was 55 °C (except for SpAAC42, which was 60 °C). Fragments were separated on the Applied Biosystems 3730 XL DNA Analyzer and scored with Applied Biosystems Prism Gene Mapper v. 3.0 software.

Because the extremely high number of polymorphisms found in the microsatellites precluded my ability to detect any temporal or stage patterns, the same individuals were also amplified at a 400 base pair section of the mitochondrial control region I using the primers (L15995 and H16498) and PCR protocol developed by Bay et al. (2004). PCR products were neutralized of primers and dNTPs through incubation with exonuclease I (0.1 units) and shrimp alkaline phosphatase (1 unit) and sequenced in the forward direction with primer L15995. BigDye labeled sequencing products were cleaned using magnetic beads, 70% ethanol, and tetraethylene glycol (TEG) reagents and visualized on an ABI 3730 XL (Applied Biosystems). Sequences were trimmed and edited with Sequencher v. 4.8 then aligned in Bioedit v7.0.9 software (Hall 1999). An additional 32 ea. larvae, juveniles, and adults collected during 2005 and 2007 were also sequenced for a total of 160 larvae, 160 juveniles, and 160 adults across 3 years.

Statistical and population genetic analyses

Genepop, Ver. 3.3 was used to calculate number of alleles, allelic richness, expected and observed heterozygosities, and pairwise and global F_{ST} values, to test for genotypic differentiation and linkage disequilibrium for the six microsatellites. For the individuals sequenced at the control region I of the mtDNA, the number of haplotypes and haplotype diversity were calculated for each stage and year using GenAIEx v6.1 (Peakall and Smouse 2006). A neighbor-joining tree was created using all pair-wise Kimura two-parameter genetic distances (Kimura 1980) between all unique haplotypes using MEGA

v. 4.0 (Tamura et al. 2007). Reliability of branch points was tested with 1000 bootstraps. To test whether genetic variability was partitioned within collection years or life stages (larvae, juvenile, adults) I used an analysis of molecular variance (AMOVA) in GenAlEx 6.1. Pairwise genetic distances (phiPT) were used in a principle coordinates analysis (PCA) to determine if age groups or years clustered together. To resolve the level of genetic differentiation among stages and years, non-biased genetic distances (D; Nei 1972) were calculated for all pairwise comparisons.

Results

Microsatellites

The microsatellite loci were highly variable with loci containing 15 – 52 alleles and observed heterozygosity ranging from 0.62 – 0.91. The number of different alleles per locus across all life stages ranged from 23 to 69, with a mean of 40.83 ± 8.87 .

The observed heterozygosities were consistently lower than expected based on Hardy Weinberg equilibrium across all loci and age groups with the exception of SpAAC47 in larvae (0.90 and 0.90 respectively) and SpAAT40 in adults (0.98 and 0.92 respectively; Table 5.1). The mean observed heterozygosities across loci ranged from 0.62 ± 0.06 to 0.91 ± 0.04 . The mean expected heterozygosities across loci ranged from 0.89 ± 0.01 to 0.97 ± 0.00 . All of the mean observed heterozygosities across loci were lower than the mean expected heterozygosities (Table 5.2).

The test for genotypic disequilibrium yielded one significant value ($P < 0.05$) within juveniles between the loci SpAAC47 and SpAAT40. After Bonferroni correction, however, none of the combinations remained significant, suggesting that the loci utilized in this study were undergoing random recombination.

Neither pairwise nor global F_{ST} values were significantly different among age or year classes (Table 5.3). Furthermore, there were no significant genotypic frequency differences among groups (G-test: $p > 0.05$).

Mitochondrial DNA

The mtDNA locus in *Stegastes partitus* individuals was also highly variable with 99 haplotypes and haplotype diversities ranging from 0.65 – 0.85 across age and year classes. Of the 99 different haplotypes observed, 77 were unique to one individual (Fig. 5.1). Neighbor joining of haplotypes resulted in a star pattern with little differentiation among haplotypes (Fig. 5.2). Only branch points with $> 50\%$ bootstrap support are depicted in Fig. 5.2, although, even these were only weakly supported with $< 65\%$ support in all cases. Furthermore, the genetic diversity (h) was fairly similar across years and stages of life (ranging from 0.658 to 0.850; Table 5.4). Results of an AMOVA revealed that only $\sim 1\%$ of the total variation among individuals was partitioned among stages and years (Table 5.5; the remaining 99% was within stages and years). There were no overall significant differences among year/stages ($\Phi = 0.005$, $p = 0.216$). Moreover, there were no significant pairwise differences in Φ among years or stages (Table 5.6). Small values of pairwise Nei's unbiased genetic distance (D) among years/stages further reinforce the general lack of differences among these groups (Table 5.7).

Several genetic patterns emerged by year. Principle coordinates analysis (PCA) of the pairwise Φ values for the different stages and years revealed a cluster of the three different stages (adults, larvae, and juveniles) collected during 2007 (Fig. 5.3). Therefore, all stages collected in 2007 were more similar to each other than to any of the collections made during other years. However, none of the other years clustered together.

Additionally, juveniles and adults collected in 2005 exhibited a greater proportion of private (unique) haplotypes than those collected in other years (Fig. 5.4).

Discussion

Temporal analysis of genetic structure using both microsatellites and mtDNA indicates that there was very high genetic diversity in *Stegastes partitus* populations in the upper FK. Furthermore, almost none of this genetic variation was partitioned among stages of life or years of collection. The most parsimonious explanation is that *S. partitus* has a very large effective population size. Indeed, *S. partitus* is one of the most abundant reef fish species in the Caribbean, with estimated census sizes in the tens of millions within the upper Florida Keys (unpublished data). Coupled with the fact that *S. partitus* has a consistent pattern of spawning and settlement throughout the year (Robertson et al. 1988, Dorsey 1999, Chapter 4) and is highly fecund, spawning up to 5,000 eggs per clutch several times a month (Knapp 1993), the life history of this species is concordant with large effective population sizes.

Heterozygote deficits were evident in all six microsatellite loci, resulting in deviations from Hardy-Weinberg equilibrium (HWE). One typical cause of this phenomenon is inbreeding, but because of the high allelic diversity and large population size of *S. partitus* in the upper FK, inbreeding is unlikely to be responsible. Another potential explanation is that more than one population was sampled (Wahlund effect; Wahlund 1928). This is also unlikely given the very low genetic divergence among the age groups and across populations in the Caribbean (Purcell et al. 2009). The most probable cause of the departures from HWE is the presence of null alleles. This may be a common phenomenon in marine fishes which generally have large effective population

sizes (DeWoody and Avise 2000, O'Reilly et al. 2004). Large populations can harbor high nucleotide variation in the regions flanking the microsatellite locus and so it is more likely that primer – DNA nucleotide mismatches will occur and result in the non-amplification of some alleles. Similar heterozygote deficits have been observed for *S. partitus* throughout the Caribbean, using these same microsatellite markers (Purcell et al. 2006, Ospina-Guerrero et al. 2008, Hepburn et al. 2009). Null alleles can upwardly bias F-statistics (Chapuis and Estoup 2007). Correcting for null alleles almost invariably results in lower genetic divergence between groups (Chapuis and Estoup 2007), which in this study would simply reinforce the lack of differences among age and year classes.

Because there was so much within-cohort variation, differences among stages or years could not be detected. Therefore, it is unlikely that the larval and juvenile *S. partitus* collected in the upper FK are the offspring of a few adults. The loss of genetic variation in a population due to chance reproductive success is argued to be a common condition of many marine populations because they are usually characterized by high fecundity, have extremely high mortality rates during early life stages, and encounter variable environmental conditions that may result in disproportionate success of larval cohorts (i.e. sweepstakes effect; Hedgecock 1994). Evidence for sweepstakes effects has been presented for various species, including *S. partitus* (Ruzzante et al. 1996, Li and Hedgecock 1998, Planes and Lenfant 2002, Selkoe et al. 2006, Hepburn et al. 2009). Hepburn et al. (2009) detected a temporally variable pattern of genetic structure among neighboring populations of *S. partitus* juveniles along the Mesoamerican Barrier Reef System using eight microsatellite markers. They attributed the temporal instability of these patterns to stochastic effects on dispersal. However, they did not detect significant

patterns of genetic structure over larger spatial scales (among atolls). Furthermore, they did not have adult collections to compare to the juveniles. Lacson et al. (1989) observed similar temporal variation in the heterogeneity of protein loci of adult *S. partitus* populations in the FK and they speculated that it was due to environmental perturbations followed by the effects of genetic drift. Based on the two different neutral markers that I used, my results suggest that *S. partitus* in the upper FK are not under the effects of genetic drift or sweepstakes effect.

Pairwise genetic distances suggested that larvae, juveniles, and adults from 2007 were more similar to each other than to any of the other cohorts collected in different years. Interestingly, samples from none of the other years clustered together. One possible explanation for why cohorts collected during 2007 were more similar to each is that there was a higher proportion of self-recruitment that month (April 2007). However, this does not explain why there were such large differences between the larval and juvenile stages during 2004 and 2005. It is possible that the populations of newly recruiting *S. partitus* are so large that I was not able to randomly sample all the available variation.

In addition, I did not detect differences between the larval and juvenile stages that would be consistent with selective mortality or genetic drift. The effects of genetic drift are most profound in small populations where alleles can reach fixation or extinction in a short period of time. All evidence suggests that the effective population size of *S. partitus* in the upper FK is extremely large and therefore would not experience a noticeable effect of drift. It is also not surprising that I did not observe a selective loss of certain alleles within the juveniles, as the genetic markers that I chose are putatively neutral and

therefore not assumed to be under selection. Evidence of genetic selection has been observed through the loss of an allozyme allele associated with slower growth in white sea bream recruits off the coast of southwestern France (Planes and Romans 2004). In that case, the expressed protein may have influenced growth in some manner. Temporal genetic shifts with age have also been detected in the common damselfish *Neopomacentrus filamentosus* using a fragment of the mitochondrial control region (Vigliola et al. 2007) and microsatellites (Jones and Barber 2005). The microsatellites and mitochondrial locus used in these two studies appear to be linked to expressed genes that influence survival in *N. filamentosus*. For contrast, the loci I used do not seem to be linked to genes under selection in *S. partitus*.

The main conclusion that can be gleaned from the present study is that *S. partitus* has a very large effective population size in the upper Florida Keys. Populations elsewhere in the Caribbean are likely to be large as well, and this may explain why there is no strong pattern of genetic structure over large spatial scales for this species throughout the Caribbean (Ospina-Guerrero et al. 2008, Hepburn et al. 2009, Purcell et al. 2009). I utilized two different molecular markers that are thought to measure genetic differentiation over different temporal scales, and yet I observed similarly large amounts of variation and a lack of differentiation among the age groups. A potential problem of using hypervariable molecular markers is that homoplasy, the convergent evolution of similar alleles or traits, can occur. Size homoplasy is particularly common in microsatellites where products of the same size can arise from independent mutation events. Such homoplasy can be particularly problematic for species with large population sizes and loci with high mutation rates and strong allele size restraints (Estoup et al.

2002). The degree to which homoplasy has occurred within the six microsatellite and one mtDNA loci that I used is unknown. What is clear is that the level of variation within each cohort of larval, juvenile, and adult *S. partitus* precludes the ability to detect fine scale differences among age groups and years. These issues highlight the need to match the temporal scale of ecological questions with molecular markers with the proper level of variability.

Table 5.1. Sample sizes (N), number of alleles (A), allelic richness (A_R), and observed and expected heterozygosity (H_O and H_E) at six microsatellite loci for *Stegastes partitus* adults, settlement-stage larvae, and juveniles collected in the upper Florida Keys in 2004. All refers to the mean values across all three age groups.

Locus		Adults	Larvae	Juveniles	All
SpAAC33	N	93	83	82	258
	A	19	20	17	18.67
	A_R	17.45	18.58	15.78	17.27
	H_O	0.66	0.51	0.70	0.62
	H_E	0.90	0.89	0.88	0.89
SpAAC42	N	89	65	71	225
	A	25	23	26	24.67
	A_R	23.68	22.75	25.16	23.86
	H_O	0.79	0.85	0.85	0.83
	H_E	0.94	0.93	0.93	0.93
SpAAC47	N	92	83	85	260
	A	19	20	15	18
	A_R	17.91	18.55	14.48	16.98
	H_O	0.88	0.90	0.88	0.89
	H_E	0.91	0.90	0.89	0.90
SpAAT40	N	94	77	86	257
	A	29	28	27	28
	A_R	26.22	26.67	25.19	26.03
	H_O	0.98	0.84	0.90	0.91
	H_E	0.92	0.92	0.94	0.92
SpGATA16	N	94	83	86	263
	A	49	49	45	47.67
	A_R	43.22	43.04	40.72	42.33
	H_O	0.80	0.84	0.84	0.83
	H_E	0.97	0.96	0.97	0.97
SpGATA40	N	90	63	66	219
	A	52	48	36	45.33
	A_R	44.45	48.00	35.58	42.68
	H_O	0.77	0.87	0.79	0.81
	H_E	0.97	0.97	0.96	0.97

Table 5.2. Sample sizes (N), mean number of alleles (A), mean allelic richness (A_R), and mean observed and expected heterozygosity (H_O and H_E) across six microsatellite loci for *Stegastes partitus* adults, settlement-stage larvae, and juveniles collected in the upper Florida Keys in 2004. Sample sizes were determined by the lowest sample size across the loci.

Stages	N	A	Mean		
			A_R	H_O	H_E
Adults	89	32.17	28.82	0.81	0.93
Larvae	63	31.33	26.15	0.80	0.93
Juveniles	66	27.67	29.60	0.82	0.93

Table 5.3. Pair-wise F_{ST} values between stages of *Stegastes partitus* collected in 2004 in the upper Florida Keys. None of the comparisons yielded significant values.

	Adults	Larvae
Adults		
Larvae	-0.0010	
Juveniles	-0.0004	0.0010

Table 5.4. Sample size (N), number of haplotypes (Na), and haplotype diversity (h) by population for *Stegastes partitus* adults, settlement-stage larvae, and juveniles collected in the upper Florida Keys from 2004-2007.

Year	Stage	N	Na	h
2004	Adults	86	34	0.782
	Larvae	81	28	0.845
	Juveniles	77	21	0.733
2005	Adults	16	10	0.844
	Larvae	26	10	0.740
	Juveniles	27	15	0.850
2007	Adults	29	11	0.673
	Larvae	28	12	0.689
	Juveniles	28	13	0.658

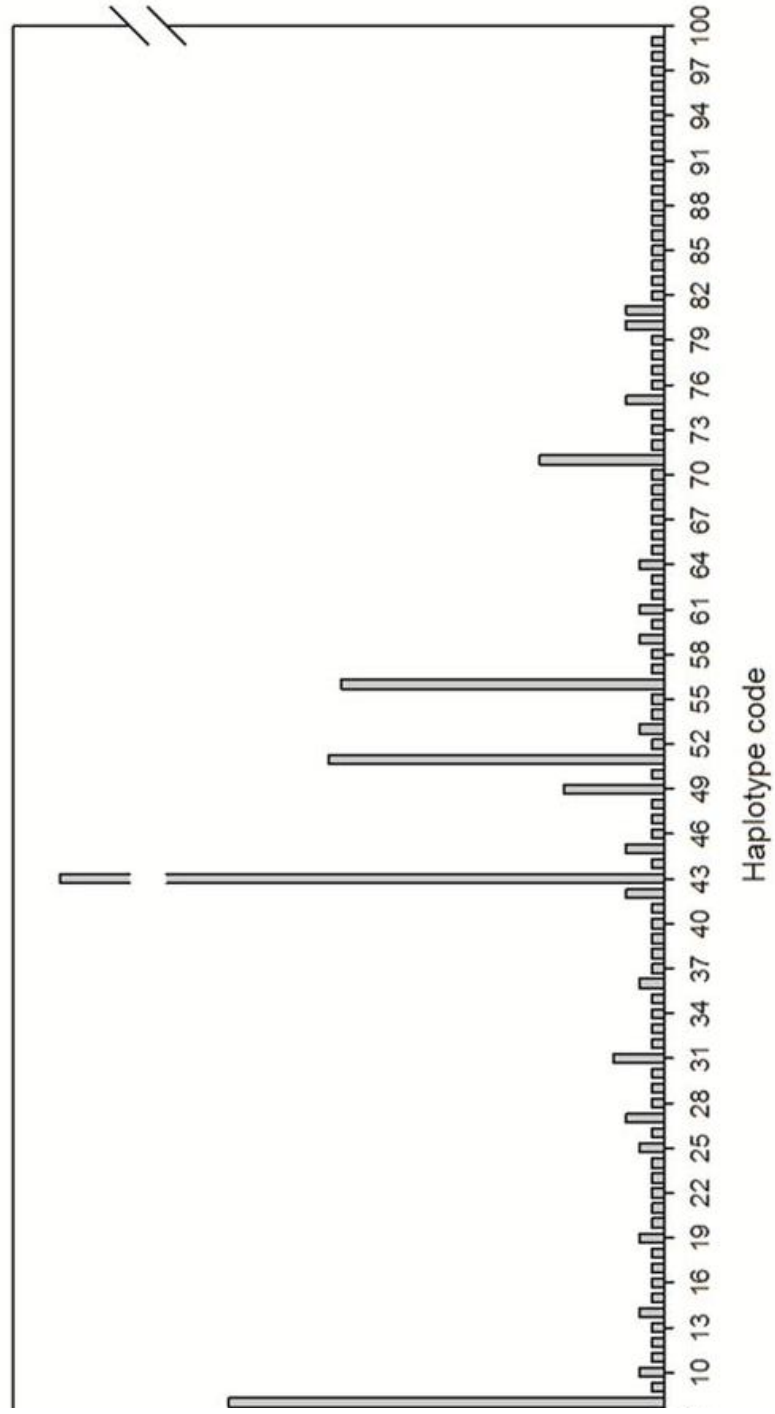
Table 5.5. Results of analysis of molecular variance (AMOVA) of different years and life stages (larvae, juveniles, adults) of *Stegastes partitus* collected in the upper Florida Keys during 2004-2007. The amount of variation partitioned among stages and years was not significant ($\Phi = 0.005$, $p = 0.216$).

Source of variation	<i>df</i>	SS	MS	Variance Components	% of Variation
Among stages & years	8	3.86	0.48	0.002	1
Within stages & years	389	152.51	0.39	0.392	99
Total	397	156.37		0.394	100

Table 5.6. Results of pairwise comparisons of genetic distances (Φ) among stages (A, adults; L, larvae; J, juveniles) and years (2004-2007) of *Stegastes partitus* collections. ϕ iPT (Φ) values are below the diagonal and probability values based on 999 permutations are shown above the diagonal.

	A2004	J2004	L2004	A2005	J2005	L2005	A2007	L2007	J2007
A2004	0	0.083	0.108	0.362	0.228	0.360	0.407	0.340	0.267
J2004	0.009	0	0.145	0.120	0.038	0.381	0.329	0.358	0.322
L2004	0.007	0.006	0	0.392	0.216	0.383	0.059	0.143	0.040
A2005	0.000	0.024	0.000	0	0.366	0.387	0.136	0.271	0.080
J2005	0.005	0.031	0.006	0.000	0	0.298	0.084	0.156	0.053
L2005	0.000	0.000	0.000	0.000	0.005	0	0.382	0.355	0.334
A2007	0.000	0.001	0.019	0.024	0.026	0.000	0	0.363	0.366
L2007	0.000	0.000	0.012	0.010	0.015	0.000	0.000	0	0.332
J2007	0.003	0.002	0.024	0.034	0.030	0.000	0.000	0.000	0

Figure 5.1. Frequency distribution of haplotypes of a 400 bp section of the mitochondrial control region I in *Stegastes partitus* larvae, juveniles, and adults collected from 2004-2007 in the upper Florida Keys.



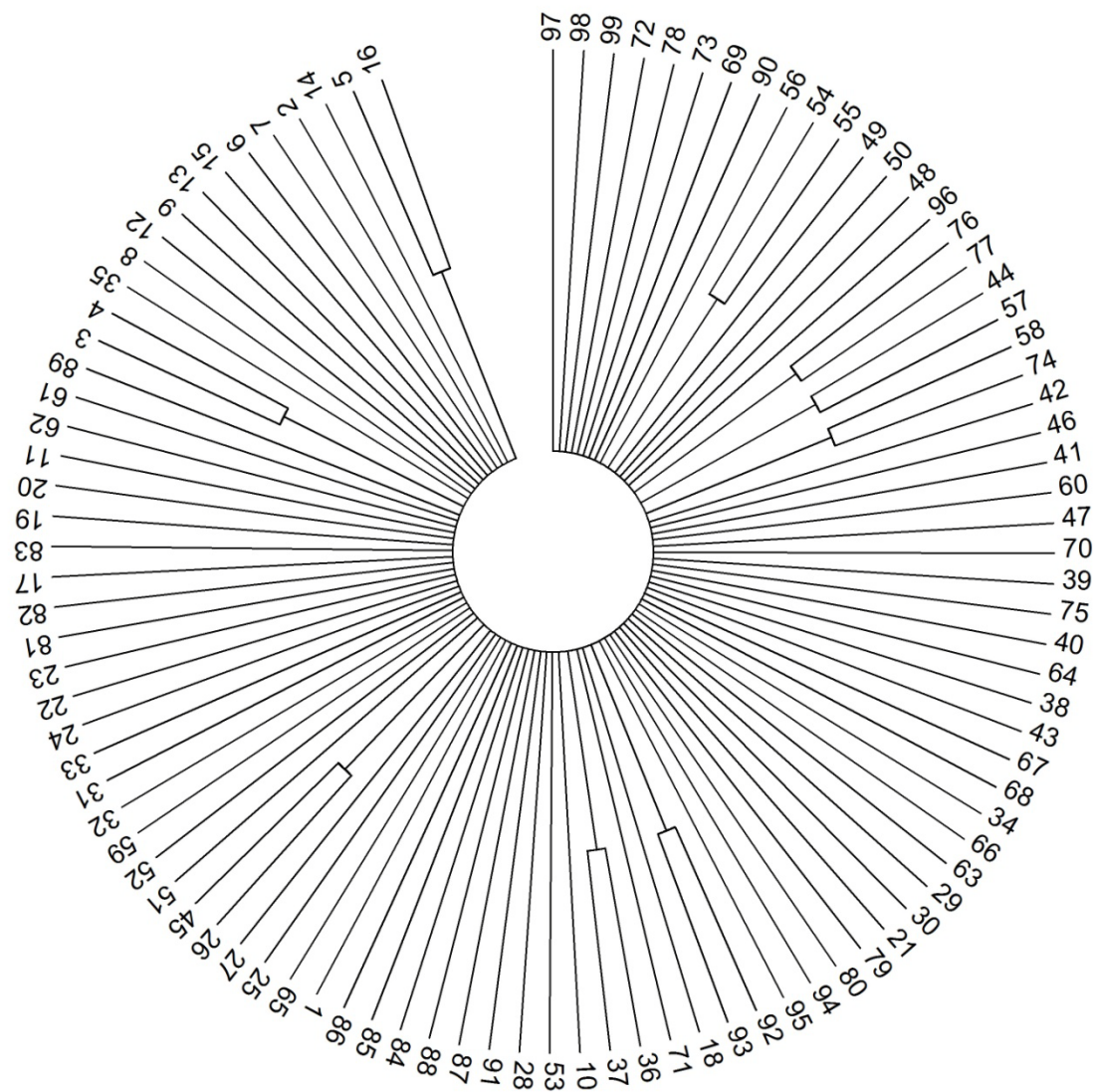


Figure 5.2. Neighbor-joining haplotype tree depicting genetic distance relationships based on Kimura two-parameter genetic distances (Kimura 1980) among all cohorts of *Stegastes partitus* collected from 2004-2007 in the upper Florida Keys.

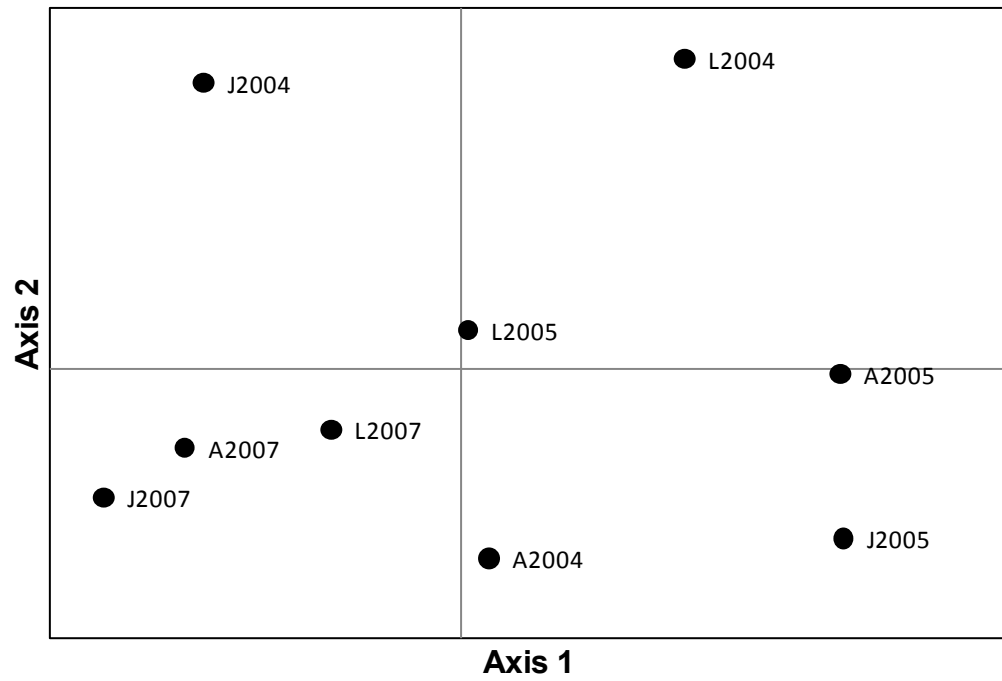


Figure 5.3. Principle coordinate analysis ordination of pairwise PhiPT (Φ) values for different stages (A, adults; L, larvae; J, juveniles) and years of *Stegastes partitus* collected from the upper Florida Keys during 2004-2007.

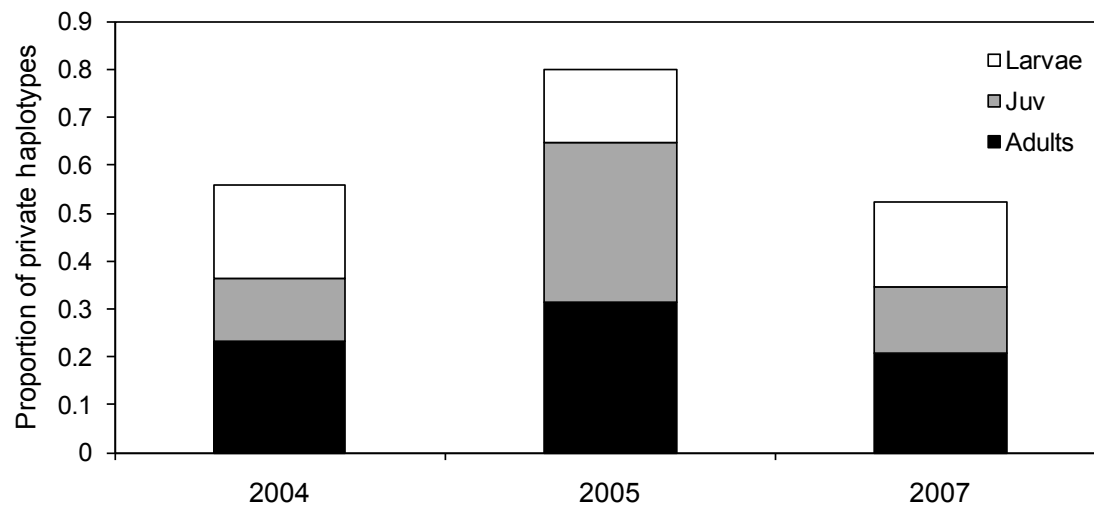


Figure 5.4. Proportion of private (unique) alleles for different years/stages of *Stegastes partitus* collected in the upper Florida Keys during 2004-2007.

Chapter 6: Summary and Conclusions

Temporal and spatial patterns of recruitment

For marine organisms with relatively sedentary adult stages, population replenishment is largely determined by larval supply and post-settlement survival. Results of nearly six years of monthly recruit surveys revealed interannual, seasonal, and monthly patterns of recruitment, and lunar patterns of settlement for a common coral reef fish, the bicolor damselfish *Stegastes partitus* (Chapter 4). Monthly recruitment consistently peaked during the summer (July and August). Back-calculated settlement peaked near the new moon, even after adjusting for estimated post-settlement mortality. Seasonal variation in recruitment magnitude is likely driven largely by patterns in production (Robertson et al. 1988, Dorsey 1999). While seasonal fluctuations in reproduction have been shown to influence patterns of settlement and recruitment (Robertson et al. 1988, Meekan et al. 1993, Green 2008), often variation in settlement is decoupled from spawning output (Robertson et al. 1993, McIlwain 2002). Recent evidence suggests that the pelagic environment plays a greater role than natal source in shaping the quality of larval supply (Shima and Swearer 2009) and growth-related early life history traits (ELHTs) have been correlated with recruitment magnitude (Bergenius et al. 2002, Wilson and Meekan 2002, Bergenius et al. 2005).

Recruitment also varied spatially with higher densities of recruits on dead coral rubble piles, on offshore bank reefs. This seem to be primarily due to the higher prevalence of optimal habitat containing more suitable shelters and higher zooplankton prey abundance (Nemeth 1997, 1998).

Sources of variation in early life history traits

Larval history and successful recruitment are often influenced by variability in the pelagic environment (Blaxter 1991, Green and Fisher 2004, Sponaugle and Pinkard 2004b, Bergenius et al. 2005, Valles et al. 2009). For 16 cohorts of *S. partitus* settlers and recruits collected across seasons and years, ELHTs were significantly correlated with mean water temperature over the length of the larval period (Chapter 2). Individuals that developed and settled during warmer water temperatures grew more quickly during the beginning of their planktonic larval and early benthic juvenile phases, had shorter pelagic larval durations (PLDs), and as a result, settled at smaller sizes.

ELHTs of *S. partitus* also vary with the magnitude, timing, and location of settlement and/or recruitment, and this variation can influence the intensity and direction of selective mortality. For instance, there were significant relationships between several ELHTs and size of settlement events (Chapter 4). Some of these relationships were driven by seasonal variation in ELHTs, as both ELHTs and recruitment magnitude are significantly correlated with water temperature (Chapter 2). Examination of all recruitment, without controlling for the influence of seasonal water temperature, revealed that larvae settling in larger pulses exhibited faster larval growth, shorter PLDs, and larger sizes-at-settlement than those settling during smaller events (Chapter 4). These patterns generally agree with previous studies examining this and other species (Rutherford and Houde 1995, Bergenius et al. 2002, Wilson and Meekan 2002). However, when the effects of seasonal temperature were minimized by comparing large and small settlement events occurring only within the warmest months, the relationship between larval growth and settlement magnitude reversed and individuals that arrived in

larger pulses tended to exhibit slower mean larval growth. The mechanism underlying this relationship between larval growth and size of settlement events is unknown, but could be related to patterns of larval prey abundance. Interestingly, this pattern did not remain significant for recruits (1-10 d post-settlement; below).

ELHT composition of settlers also appears to be related to lunar timing of settlement. In general, *S. partitus* larvae settling during the darker portion of the lunar cycle, the third quarter and new moons, grew faster, spent less time in the plankton, and settled at larger sizes (Chapter 4). This relationship could be the result of differences in maternal/parental contribution with lunar phase, as successful spawning and settlement both peak near the new moon (Robertson et al. 1988, Robertson 1992, Chapter 4). Given that ELHTs are influenced by the pelagic environment, an equally plausible explanation is that lunar phase is an important settlement cue for this species and individuals with less optimal traits (i.e. slower larval growth, smaller sizes at settlement) are unable to settle at the best time (i.e. third quarter and new moons), so they remain in the plankton eventually becoming less discriminatory and settling during less optimal phases (i.e. first quarter and full moons). Evidence for this has been observed in invertebrate taxa with non-feeding larval stages or specific diet requirements, whereby delay of settlement can result in striking declines in larval condition (Marshall and Keough 2003, Botello and Krug 2006). Although *S. partitus* are feeding during their larval stage, they have a relatively invariant PLD, which suggests that there may be less flexibility in settlement timing and deviations from the optimum result in sacrifices to larval quality.

Difference in genetic make-up is another important source of variation in traits. However, despite variation in growth-related ELHTs with timing of settlement, there

were no differences in genetic composition on six microsatellite loci and part of the control I region of the mitochondrial genome among monthly cohorts of settling *S. partitus* larvae and new recruits (Chapter 5). Due to the extremely high level of genetic variation within the monthly cohorts, the results are somewhat inconclusive, but suggest that *S. partitus* has a very large effective population size and the observed variation in the growth-related ELHTs (Chapters 2 & 4) was not likely the result of successful spawning of a disproportionately small group of adults. These findings echo the lack of clear spatial patterns in genetic differentiation demonstrated for populations of this species throughout the Caribbean (Purcell et al. 2006, Ospina-Guerrero et al. 2008, Hepburn et al. 2009).

Habitat selection at the time of settlement can create spatial patterns of recruit abundances (Tupper and Boutilier 1995, Tolimieri 1998) and growth-related ELHTs (Tupper and Boutilier 1995, Caley and Munday 2003). For *S. partitus* in the upper Florida Keys, recruitment was higher on the offshore bank reefs than on the inshore patch reefs (Chapter 4). Within the offshore reefs, more recruits were found in dead coral rubble piles around the base of the reef than on the reef crest. Additionally, ELHTs of recruits varied by reef microhabitat, with more individuals that grew faster as larvae and settled at larger sizes observed and collected on the reef crest compared to the surrounding rubble (Chapter 4). These differences in larval growth between individuals on the reef crest or rubble habitat were exhibited by the younger recruits (1-10 d post-settlement), but disappeared in the older juveniles (11-28 d post-settlement). These initial patterns in larval quality could be the result of either differences in habitat selection at the time of settlement or early selective mortality processes acting before the recruits were

surveyed and collected (see below). In either case, selective mortality over time obscured initial patterns.

Patterns in selective mortality

Natural variability in ELHTs coupled with particularly high mortality rates during the early stages of life establish conditions on which selective mortality processes can act (Sogard 1997). As such, selective mortality commonly operates on growth-related ELHTs and larval experience can carry over to influence juvenile survival (i.e. carry-over effects; Meekan and Fortier 1996, Searcy and Sponaugle 2001, McCormick and Hoey 2004, Raventos and Macpherson 2005a). Generally, larger size-at-hatching (Meekan and Fortier 1996, Vigliola and Meekan 2002, Raventos and Macpherson 2005a), faster larval growth rate (Meekan and Fortier 1996, Searcy and Sponaugle 2001, Shima and Findlay 2002, Raventos and Macpherson 2005a), shorter pelagic larval duration (PLD; Meekan and Fortier 1996, Shima and Findlay 2002), larger size-at-settlement (McCormick and Hoey 2004), higher condition at metamorphosis (Searcy and Sponaugle 2001, Grorud-Colvert 2006, Sponaugle and Grorud-Colvert 2006, Hamilton et al. 2008), and faster early juvenile growth (Searcy and Sponaugle 2001, Grorud-Colvert 2006, Sponaugle and Grorud-Colvert 2006) enhance survival of juvenile fishes and is consistent with the growth-mortality hypothesis (Anderson 1988). Similar selective mortality pressures influence the distribution of ELHTs in *S. partitus* recruits. Examination of 13 cohorts of *S. partitus* larvae and recruits tracked through time revealed that larger sizes-at-settlement and slower juvenile growth over the first 6 d post-settlement consistently conveyed preferential survival to *S. partitus* juveniles, regardless of seasonal water temperature (Chapter 2).

While enhanced survival of individuals with larger sizes-at-settlement is consistent with the growth mortality hypothesis, higher survivorship of individuals with reduced early juvenile growth is not. There are several physiological and behavioral trade-offs that could explain why accelerated growth is not always optimal. Physiologically, rapid growth may compromise development, tissue maintenance and repair, and, for fish, swimming capabilities (Arendt 1997, Sogard and Olla 2002), resulting in reduced ability to escape predation. Potential behavioral trade-offs of faster growth are increased foraging activity or selection of foraging habitats which may expose individuals to greater risk of predation (Damsgard and Dill 1998, Hurst et al. 2005). An alternative explanation for the decoupling of size-at-settlement and juvenile growth in *S. partitus* is that larger settlers are less vulnerable to gape-limited predation (Miller et al. 1988, Leggett and Deblois 1994, Chapter 2), and may be able to quickly begin defending benthic territories. While larger settlers experience higher survival, they may also attract more chasing and other agonistic behavior from conspecifics, resulting in increased allocation of energy to territory defense and reduced juvenile growth, relative to smaller settlers. The physiological costs of agonistic behavior include build-up of lactic acid, production and release of stress hormones (Wilson et al. 1990, Briffa and Sneddon 2007), injury, and energy expenditure (Neat et al. 1998).

Similarly, there was consistent selective loss of individuals with smaller sizes-at-settlement and faster mean juvenile growth, regardless of lunar phase of settlement (Chapter 4). This is in contrast to the trends in selective mortality acting on larval growth and PLD which were opposite between individuals settling during the brighter phases of the moon (i.e. first quarter and full moon) and those settling on the new moon (see

below). Interestingly, the resulting changes in settlement size and juvenile growth were more dramatic for individuals that settled during the brighter phases of the moon, as they arrived to the reef with less optimal traits than those settling during the darker phases. It is worth noting that similar patterns of selective mortality were observed using two different techniques: the longitudinal sampling of individual cohorts (Chapter 2) and the cross-sectional division of cohorts into age groups (Chapter 4). The similarity in the results further substantiates the patterns of preferential survival for individuals with larger sizes-at-settlement and slower early juvenile growth and underscores the importance of these two traits.

Behavioral mediation of selective mortality

Results of behavioral observations of both experimentally manipulated and naturally settled *S. partitus* recruits indicate that the relationship between size-at-settlement, early juvenile growth, and survival may indeed be explained by differences in activity levels and energy allocation (Chapter 3). *Stegastes partitus* recruits that were larger at settlement typically experienced slower post-settlement growth. Larger settlers also spent less time within the protection of coral rubble shelters and traveled farther horizontally from those shelters. Furthermore, individuals that sheltered less often, traveled farther from shelters, and were in closer proximity to conspecifics exhibited slower juvenile growth. Additional observations of a subset of experimentally manipulated recruits revealed that individuals that were chased more often and exhibited faster escape swimming speeds also grew more slowly as juveniles. Collectively, these findings indicate that larger settlers tend to be more active, and at least initially, grow more slowly as juveniles.

The resulting reduction in juvenile growth of *S. partitus* appears to be related to greater activity, particularly agonistic exchanges with conspecifics, and more energy allocation to development or tissue maintenance which enhances escape swimming ability. Superior burst swimming speeds have obvious implications for survival, but proximity to conspecifics may also confer a survival advantage. The presence of adults of several species of damselfish has been shown to increase settlement (Sweatman 1983, Lecchini et al. 2007) and post-settlement survivorship of conspecifics (Almany 2003). Based on surveys of *S. partitus* conducted in 2007 and 2008, recruit densities were positively correlated with densities of juvenile (2-3 cm SL) and intermediate (3-5 cm SL) conspecifics (Chapter 4), suggesting that the presence of conspecifics does indeed enhance recruitment in *S. partitus*. However, there was no significant relationship between recruit densities and densities of adult conspecifics, and if anything, the trend appeared negative (Chapter 4). Furthermore, there were several significant relationships between the ELHTs of the recruits and the surrounding densities of adult conspecifics. Both mean larval growth and size-at-settlement of *S. partitus* recruits were positively correlated with adult conspecific density (Chapter 4), indicating that recruits living within high densities of adult conspecifics possess more optimal traits (i.e. faster larval growth, larger sizes-at-settlement; see below), possibly as a result of higher levels of selective mortality or emigration of recruits with less optimal traits. It seems likely that only the strongest recruits, with the most optimal traits (i.e. large settlement size and slow early juvenile growth; Chapters 3 & 4), can maintain territories in close proximity to adult conspecifics. Since I was unable to compare the distance to nearest conspecific of the recruits that did not survive the experimental trials (because the majority of them

disappeared within the first 24 h), I cannot elucidate the exact mechanism for the relationships between juvenile growth, proximity to conspecifics, and survival. However, high densities of *S. partitus* have been correlated with higher mortality rates of conspecific juveniles (Tupper and Hunte 1994, Johnson 2008). Therefore it is likely that close proximity to conspecifics increases competition, as evident by greater agonistic behavior, resulting in selective loss of individuals that do not possess advantageous traits.

Interaction among ELHTs, environment, and selective mortality

For other *S. partitus* ELHTs, such as larval growth and PLD, selective mortality processes are more complicated and appear to be mediated by water temperature (Chapter 2). During the winter and spring months, selective mortality acted to remove *S. partitus* recruits that had slower larval growth and longer PLDs. This is in accordance with predictions of the growth-mortality hypothesis and observations of other species (Meekan and Fortier 1996, Searcy and Sponaugle 2001, Shima and Findlay 2002). However, during the warmest, summer months, mortality with regard to larval growth was less selective, and if anything, became disruptive, removing individuals with intermediate levels of larval growth. Even more surprising, *S. partitus* recruits surviving up to three weeks after settlement during the summer months, exhibited longer PLDs, the reverse pattern exhibited during winter and spring months. There is other recent evidence that intensity of selective mortality on other species can vary with temperature (Moran and Emler 2001, Gagliano et al. 2007b, Durieux et al. 2009, Grorud-Colvert and Sponaugle unpublished data), however, this is the first demonstration that direction of selective mortality processes can reverse on a seasonal basis. These results point to the existence of

a stabilizing mechanism acting on PLDs over seasonal time scales and may explain, in part, why juveniles of this species exhibit relatively invariant PLDs.

Variation in selective loss of traits was also observed between large and small recruitment events in that larvae that settled during large events arrived with slower mean larval growth, longer PLDs, and larger sizes-at-settlement than those that settled during smaller events, but this disparity did not remain in the recruit population (Chapter 4). This shift in the distribution of larval growth in the recruits settling during larger events indicates that selective mortality processes acted to remove the individuals with the slowest larval growth. Likewise, the disparity between sizes-at-settlement of larvae settling in larger and smaller pulses disappeared in the recruits, as individuals with the smallest settlement sizes were quickly removed. The only significant difference in ELHTs traits that remained between recruits from small vs. large events, was PLD. Surviving recruits that settled in larger events maintained longer PLDs than those settling in small events. The fact that mean PLD did not shift much between the larval and early juvenile stage suggests that selective mortality processes did not act as strongly on PLD as on the other traits.

Differences in larval growth and PLD among individuals settling during distinct lunar phases, coupled with the variation in predation levels during different lunar phases, led to variable patterns of selective mortality (Chapter 4). For fish settling during the brighter phases of the lunar cycle (i.e. first quarter and full moons), there was a selective loss of individuals with slower larval growth and longer PLDs between the larval and juvenile stage. The reverse pattern (i.e. selection against fast larval growth and short PLDs) was exhibited in recruits that settled during the darkest periods, around the new

moon. The result was that older juveniles (11-28 d post-settlement) exhibited little variation in mean larval growth and PLD among lunar phases of settlement, with mean values intermediate between those of larvae arriving during light and dark phases (Chapter 4). These converging trends in selective mortality suggest that individuals with optimal traits have intermediate values of mean larval growth and PLD.

Selective mortality also differed by microhabitat. As discussed earlier, larval growth and size-at-settlement varied among individuals collected on the reef crest vs. the surrounding rubble. While differences in larval growth between the two habitats observed in the young recruits (1-10 d post-settlement) disappeared in the older juveniles (11-18 d post-settlement), the opposite trend was observed for size-at-settlement. Young recruits did not differ in settlement size between the two microhabitats, whereas older juveniles from reef habitats were larger at settlement. The shift to larger settlement sizes in the juveniles (11-18 d post-settlement) collected on the reef crest is consistent with differential post-settlement mortality based on habitat location or quality. Whether or not ELHTs traits influence habitat selection at settlement is unknown because I did not sample *S. partitus* immediately following settlement and some amount of post-settlement mortality likely occurred prior to collection. However, larval growth varied among early recruits in the two microhabitats, which may have carried over from differences at the time of settlement.

It is likely that some quality of predation varies between these two microhabitats, which may explain the differences in selective mortality. Higher densities of predators on the reef crest may result in greater selective mortality (Holbrook and Schmitt 2003), or predators may be more selective on the reef crest. Another equally plausible explanation

is that the suite of predators varies between habitats and subjects recruits to different levels of selectivity (Hoey and McCormick 2004, McCormick and Hoey 2004), as the predominant predators of small recruits appear to differ between the two microhabitats (pers. obs.).

In contrast, there was no evidence of selective mortality acting on the loci that were examined (Chapter 5). While other studies have demonstrated genetic selective loss of alleles between the larval and juvenile stage (Planes and Romans 2004, Jones and Barber 2005, Vigliola et al. 2007), the results of the present study are not surprising because the loci used were chosen based on the knowledge that they are likely neutral and not under selection. I would expect to detect differences in the distribution of alleles between the larval and the juvenile stages only if they are somehow linked to a coding gene that is under selection. Because there was no selective shift in the distribution of alleles from the larval to juvenile stage, and the loci are assumed to be neutral and not linked to any growth-related genes, I cannot determine if a portion of the observed variation in ELHTs is primarily due to genetic differences or environmental influences. However, a significant portion of the variation in ELHTs was related to mean water temperature over the larval period (Chapter 2).

Summary

Collectively, this dissertation emphasizes the importance of several temporal (e.g., seasonal, monthly, lunar) and spatial (e.g., microhabitat, conspecific density) mechanisms that influence both the composition and quality of young recruits and the strength and direction of selective mortality processes they experience. For some ELHTs (i.e. larval growth and PLD), patterns of selective mortality can be variable based on the

initial composition of traits and settlement conditions (i.e. pelagic environment, timing and location of settlement, density and composition of predators; Chapters 2 & 4). While these ELHTs are influenced by selective mortality processes, the optimal condition (e.g. shorter or longer PLD) can change depending on circumstances (e.g., lunar phase of settlement, microhabitat, seasonal temperature). The complex nature of different processes interacting to influence which individuals survive the vulnerable early post-settlement period may explain why studies carried out over shorter periods have sometimes yielded contradictory results. Results of this dissertation highlight the need for more ecological research that encompasses temporal and spatial variability at different scales.

For other ELHTs (i.e. size-at-settlement, early juvenile growth), selective mortality pressures consistently act to remove individuals with less optimal traits (i.e. smaller settlement sizes, faster juvenile growth; Chapters 2 & 4). Furthermore, the relationship between these growth-related ELHTs and the selective mortality processes acting on them are, at least in part, behaviorally mediated (Chapter 3) and influenced by the presence of conspecifics (Chapter 3 and 4). While some traits, such as size-at-settlement, are important to survival because they likely reduce susceptibility of predation, other traits, such as juvenile growth, may be linked through the behaviors of individuals of different sizes (i.e. larger individuals expend energy in territorial behavior). Size-at-metamorphosis has consistently emerged as an important trait to early juvenile survival. The importance of this trait is not species-specific, as theoretical and empirical evidence support its significance in a diversity of organisms (Alford and Harris 1988, Miller et al. 1988, Leggett and Deblois 1994, Marshall and Keough 2003, McCormick

and Hoey 2004). If individuals with these advantageous traits continue to preferentially survive over time, patterns of adult demography may reflect these processes occurring during early juvenile life.

Due to certain limitations of this study and the lack of genetic differentiation within and among monthly cohorts using neutral molecular markers, the relative importance of genetic-makeup, maternal contribution, and pelagic and post-settlement processes in shaping juvenile and adult demography remains unknown. What is clear from these results is that variation in ELHTs is introduced during the larval stage and several ELHTs carry-over to influence patterns of recruitment and juvenile survival. Some of the variation introduced by settling larvae is maintained through time, while some is obscured by post-settlement processes. Variation in the strength of larval supply is generally reflected in benthic population structure (Chapter 4), but post-settlement processes, especially selective mortality, further shape the distribution of ELHTs to influence juvenile demography (Chapters 2 & 4).

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