2012-07-31

Population Connectivity in a Dynamic Coastal System: Effects of Mesoscale Eddies on Distribution, Growth, Survival, and Transport of Larval Reef Fishes

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POPULATION CONNECTIVITY IN A DYNAMIC COASTAL SYSTEM: EFFECTS OF MESOSCALE EDDIES ON DISTRIBUTION, GROWTH, SURVIVAL, AND TRANSPORT OF LARVAL REEF FISHES

By

Kathryn Shulzitski

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

August 2012

UNIVERSITY OF MIAMI

A dissertation submitted in partial fulfillment of
the requirements for the degree of
Doctor of Philosophy

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SHULZITSKI, KATHRYN (Ph.D., Marine Biology and Fisheries)
Population Connectivity in a Dynamic Coastal System: Effects of Mesoscale Eddies on Distribution, Growth, Survival, and Transport of Larval Reef Fishes. (August 2012)

Abstract of a dissertation at the University of Miami.

Dissertation supervised by Professor Su Sponaugle.
No. of pages in text. (183)

Population connectivity (i.e., the exchange of individuals among geographically distinct subpopulations) is an issue of particular relevance in the marine environment, as the majority of benthic marine organisms have complex life cycles and dispersal events occurring in the early life stages are nearly impossible to track. As the magnitude and direction of larval dispersal are shaped ultimately by larval distributions, growth, mortality, and transport to adult habitat, this dissertation examined these processes for larval reef fishes in the Straits of Florida (SOF) to contribute to the understanding of patterns of population connectivity along a continental coastline. An analysis of spatially and temporally extensive ichthyoplankton collections and associated environmental data demonstrated that environmental variation through the vertical water column was most important in structuring larval assemblages in the SOF and that horizontal patterns in larval assemblages were only weakly related to oceanographic features (i.e., mesoscale eddies, ME, and the Florida Current). However, otolith analysis revealed that residence in MEs enhanced larval growth for four out of the five reef fish species examined, and this increased growth was consistent across three sampling periods and two years. These results indicate that MEs provide enhanced feeding environments for larval reef fishes. Additional otolith analysis of cohorts of two reef fishes tracked from the pelagic

environment to the reef (i.e., settlement-stage), demonstrated that for one species (*Cryptotomus roseus*) slow-growing larvae were selectively removed from the population just prior to settlement. In this same species, slow-growing larvae from offshore waters did not contribute to the surviving population of settlement-stage larvae, suggesting that for at least some species and settlement events, upstream Caribbean fish populations are not well-connected to populations in the SOF. Finally, several lines of evidence, including temporal changes in larval assemblages and patterns of larval abundance and age across water masses, are consistent with the existence of nearshore retention of locally-spawned larvae in the SOF and, thus, the potential for self-recruitment in reef fish populations of the Florida Keys.

ACKNOWLEDGEMENTS

The gratitude I feel towards so many people cannot fit onto mere pages, but I hope that this section at least begins to demonstrate my appreciation. Most importantly, the realization of this dissertation would not have been possible without the guidance, expertise, funding, and support of my advisor, Su Sponaugle. These past few months, when I was sure that there was no end in sight, Su kept me on track and somehow made all of this happen. In addition to this final push, over the past six years Su has been extremely patient with my extracurricular interests in outreach and education, and for allowing and actually encouraging such activities that diverted my attention away from research, I can't thank her enough. I admire the work ethic and professionalism that Su projects and imparts on her students, and feel lucky to have had an advisor that I can learn from, admire, and respect.

I have also been very lucky to have committee members who are both helpful and accommodating. Bob Cowen, Gary Hitchcock, Andy Bakun, and Sue Sogard have provided valuable feedback at committee meetings or impromptu office visits and Andy even rearranged lecture schedules so that I could enhance my knowledge of the physical dynamics of mesoscale eddies. I would like to extend a special thanks to Bob Cowen who contributed significant feedback on the data analysis of Chapter 2, always offered comforting and positive words, and provided me with invaluable experiences aboard the R/V McArthur II that I will not soon forget.

The field work, sample processing, and data collection that went into this dissertation was a massive effort involving so many people. Jenny Boulay, Lisa Havel, Kristen Walter, Evan D'Alessandro, Sean Bignami, Lindsay Jones, Tauna Rankin, Klaus

Huebert, and Tom Murphy were all involved with the shore-based sampling effort. In particular, I would not have made it through first field season without the initiative and hard work of Jenny. In addition, I want to thank Sean and Kristen for making the second field season relatively stress-free and surprisingly enjoyable. Bob Cowen, Cedric Guigand, Joel Llopiz, Martha Hauff, Adam Greer, Tom Murphy, Jonathan Kool, and the entire crew of the R/V Walton Smith carried out the offshore sampling during three long cruises. Tom Murphy, Laura Parsons, Jason Downing, Kathryn Doering, and Kat Ternus all helped to sort, measure, dissect, and organize countless samples. The reliability and efficiency of Laura Parsons was particularly helpful. The otolith reads for *T. bifasciatum*, *C. roseus*, and *S. barracuda* were provided by Kristen Walter, Martha Hauff, and Evan D'Alessandro, respectively. Finally, I want to convey extra special gratitude to Joel Llopiz; his expertise and patience is incredible, and he went above and beyond in teaching me how to identify fish larvae and answering countless questions about data processing and analysis.

All of this work was funded by a National Science Foundation Grant, no. OCE-0550732, to S. Sponaugle, R.K. Cowen, C. Paris, and V. Kourafalou. The University of Miami Fellowship and the Science Made Sensible (SMS) Fellowship provided a monthly stipend. In addition, through the SMS program I not only gained invaluable teaching experience and traveled to South Africa, I also discovered a passion for education that I didn't know I had.

All of the Sponaugle and Cowen lab members (past and present) have been a pleasure to work with and I feel extremely lucky to be part of such a fantastic lab. I especially want to acknowledge: Kristen Walter for listening to many complaints and

helping me with statistics, Sean Bignami for being a wonderful, tolerant, and laid-back officemate, and Esther Goldstein for providing the best company imaginable during long stints of otolith-reading.

Finally, I want to thank my family and friends for their support over the past six years. The hard work of my parents, Leo and Sue Shulzitski, got me here and served as a model throughout this experience. My sisters, Jenny and Meredith, provided me with endless encouragement and love. Jen Aquia not only listened to hours upon hours of stories about larval fishes and eddies she also kept me sane and provided perspective when I needed it most. I could never thank her enough for her friendship and support. Tina Cantu provided me with much needed balance over the years; her fiery attitude and amazing creativity entertained while her kind heart and limitless intelligence inspired. While arriving late on the scene, “the neighbors” were huge in helping me cross the finish line. The thanks I owe to Todd Greaux - for all of the coffee, meals, and most importantly his unwavering support - are immeasurable; I couldn’t have done this without him. Finally, Margaret Shulzitski, my “gram”, was instrumental in the completion of this dissertation. Over the past six years, not a conversation went by without her asking when I would be done with school. I thank her for her motivational prodding, her interest in the research, and most of all her belief that I could do this.

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Chapter 1. Introduction

Population connectivity, the exchange of individuals among geographically distinct subpopulations, is an issue of particular relevance in the marine environment as the majority of organisms exhibit a complex life cycle (Thorson 1950, Leis 1991). Relatively sedentary benthic adults produce larvae that spend days to months in the pelagic environment before transitioning into benthic juveniles. The small sizes and patchy distributions of larvae as well as the vast size of the pelagic environment make it difficult to directly track dispersal events that occur in the early part of this life cycle. Therefore, basic knowledge of the dynamics of exchange among marine populations is lacking. Multiple processes acting on the early life stages (i.e., growth, transport, and mortality) will collectively determine the magnitude and direction of larval dispersal, and ultimately, patterns of population connectivity. Thus, to gain a more mechanistic understanding of population connectivity, a greater knowledge of these processes is essential.

For decades, populations of benthic marine organisms that exhibited a planktonic larval phase were thought to be well-connected. This paradigm was based largely on the relatively long pelagic larval durations of numerous taxa, the collection of such stages far from adult habitats (Scheltema 1986), and the existence of widespread genetic homogeneity among geographically-distant populations (Shulman and Birmingham 1995). Yet the maintenance of endemic island populations (Robertson 2001) or populations in upstream locations (e.g., Barbados) simultaneously suggest the existence of mechanisms sustaining substantial levels of self-recruitment, where larvae return to natal populations after their time in the plankton. In addition to such observations, recent

studies utilizing novel mark-recapture techniques, high-resolution molecular markers, and more realistic bio-physical models, collectively provide evidence for high levels of self-recruitment in populations of benthic marine organisms (Jones et al. 1999, Swearer et al. 1999, Cowen et al. 2000, Planes 2002, Jones et al. 2005, Almany et al. 2007). However, much of this work supporting the importance of self-recruitment to population replenishment has been conducted for small island populations and the degree to which these results apply to contiguous continental coastlines is largely unknown.

Along continental coastlines complex flow associated with coastal topography, winds, tides, and mesoscale eddies (MEs) may form nearshore retention zones (Lee et al. 1994, Gawarkiewicz et al. 2007), while MEs and submesoscale eddies (Sponaugle et al. 2005, D'Alessandro et al. 2007), internal tidal waves and bores (Shanks 1983, Pineda 1991, Leichter et al. 1996), and upwelling fronts (Shanks et al. 2000) could serve as cross-shelf delivery mechanisms returning larvae to suitable habitats. In addition, larvae can exhibit significant behavioral control over movements in the pelagic environment through vertical migration, a relatively simple capacity found in both invertebrates and fishes. The vertical distributions of larvae are often non-random and small adjustments in position in the water column can lead to large variations in transport (Cowen et al. 1993, Cowen and Castro 1994, Cowen 2002, Paris and Cowen 2004, Hare and Govoni 2005, Muhling and Beckley 2007, Huebert et al. 2011). Horizontal swimming capabilities of late-stage fish larvae have also been demonstrated in both laboratory and field experiments and reveal the potential for enhanced control over transport at least in the late larval stages (Leis 2006). Thus biophysical transport, that is, the interaction of larvae with the physical environment is likely the dominant mode by which dispersal trajectories

are determined (Sponaugle et al. 2002). Yet, the effects of various biophysical interactions on retention and transport are not well understood. Are larvae retained in nearshore environments due to complex flow regimes? How does residence time in a mesoscale eddy affect larval dispersal trajectories? What proportion of larvae entrained in offshore waters successfully move onshore to suitable settlement habitat?

Growth-related processes also determine larval dispersal patterns as individuals must feed and develop in order to survive and transition out of the larval phase. Temperature is an important determinant of larval growth in temperate systems (Houde 1989) and recent work has demonstrated its significance in the subtropics as well (Meekan et al. 2003, Sponaugle et al. 2006). Alternatively, variation in growth can result from differences in food availability (Sponaugle et al. 2009). Starvation may be a significant factor in warm, oligotrophic waters since increased metabolic rates necessitate increased food intake (Houde 1989). However, recent work in a subtropical system shows that food-limitation may not be common as most fish larvae sampled had full guts and species-specific dietary preferences (Llopiz and Cowen 2009). Regardless of the ultimate cause, variation in growth will interact with predation and cannibalism to shape mortality occurring throughout the larval phase. This mortality can be random, or alternatively, result in selective loss of individuals with particular early life history traits (ELHTs; Sogard 1997). While we know that larval mortality rates are high and quite variable (Houde 1989), and that small changes in mortality can cause large fluctuations in recruitment and determine the structure of adult populations (Houde 1987, Doherty et al. 2004), empirical estimates of mortality rates are rare. A more explicit description of patterns of mortality experienced by early life stages is critical information for

determining connectivity as well as obtaining a mechanistic understanding of the processes shaping connectivity.

Both transport- and growth-related processes will be highly influenced by the water mass in which larvae reside. As the majority of coral reef fishes spawn on or near the reef, reproductive propagules will be released into nearshore (i.e., near-reef) waters. As larvae develop they may remain largely in a single water mass or, alternatively, transition from one water mass to another throughout the larval stage (e.g., nearshore to offshore or into an eddy). Environmental variables such as temperature, current speed, prey abundance, and predator field will vary by water mass, as will their collective impact on larval transport, growth, and survival. Thus, a mechanistic understanding of population connectivity requires an examination of this relationship between larvae and their environments, as well as the spatial and temporal variability associated with it.

Objectives

The overall goal of this study was to contribute to our understanding of the processes shaping patterns of population connectivity in a dynamic coastal system by addressing three broad questions: 1) what variables structure larval fish distributions in the Straits of Florida (SOF) and do these distributions have implications for retention of locally-spawned larvae, 2) how does the oceanographic environment including particular oceanographic features influence larval growth, and 3) how do ELHTs vary among oceanographic environments and which traits promote survival throughout the larval phase to settlement? To address these questions we undertook a large-scale sampling effort that encompassed three 16-d oceanographic cruises conducted over two summers which entailed the collection of ichthyoplankton and concurrent environmental data

throughout the SOF from inshore habitats and extending offshore into a major western boundary current. In addition, to track cohorts of reef fish larvae onto the reef, we synchronized collections of settlement-stage larvae over the reef tract with the collections conducted on offshore cruises. This sampling strategy allowed us to examine variability in the oceanographic environment and associated patterns of larval distribution, growth, and mortality across water masses in the SOF (e.g., FC versus MEs) and along the inshore-offshore axis. In addition, ichthyoplankton samples were collected from discrete 20 m depth bins enabling the examination of patterns of environmental parameters and larval distributions over the water column. Thus, our sampling effort provided us with a three-dimensional representation of larval habitats and associated larval demographics with extensive spatial coverage and replication over three sampling periods conducted during two summers.

In Chapter 2, environmental data and ichthyoplankton collections were compiled to address our first question: what are the variables that structure larval distributions in the Straits of Florida (SOF) and what are the implications for retention of locally-spawned larvae? First we identified water masses in the SOF using a combination of satellite imagery, model outputs, and hydrographic data. Patterns of variability in the environment were also examined using traditional parametric methods and compared to our *a posteriori* classifications of water mass. We then examined larval assemblages and abundances in relation to both horizontal and vertical variation in the environment. Finally, we compared larval abundance and age distributions of larval reef fishes across water masses to assess the potential for retention of larval reef fishes in MEs in the western SOF.

In Chapter 3, we focused on the eddy water mass in the western SOF to address the second question: how does the oceanographic environment impact growth-related processes? Specifically, recent growth of larval reef fishes collected inside of MEs was compared to growth of larvae sampled outside of eddies. We conducted such comparisons for a range of diverse species across all three sampling periods so that we could identify temporal variability in and species-specific growth responses to the oceanographic environment.

Finally, in Chapter 4, larvae collected during the second of three cruises and settlement-stage larvae collected in light traps were used to address our third question: how do ELHTs vary among oceanographic environments and which traits promote survival throughout the larval phase to the settlement-stage? We compared ELHTs among water masses for two species of reef fish, and then examined those ELHTs in the population as larvae progressed through the larval stage and transitioned onshore to settle to determine whether larvae were subjected to selective mortality processes.

In summary, this dissertation is the first comprehensive effort to examine the processes by which reef fish larvae are dispersed and retained within the SOF, grow under variable oceanographic conditions, and survive to settle to reef populations. Results of these studies will contribute to our overall knowledge of the early life history and population connectivity of coral reef fishes.

Chapter 2. Larval fish assemblages in the Florida Keys and Loop Current with implications for larval transport and retention

Background

A wealth of ichthyoplankton studies conducted in diverse locations has demonstrated that larval fish distributions are both patchy and non-random. The elucidation of factors structuring these distributions has been a major focus of research since mortality during the larval stage has been linked to recruitment variability and patterns in adult population dynamics (Hjort 1914). Distributions of larval fishes and their existence in specific assemblages are determined ultimately by adult spawning strategies (Leis 1993, Grothues and Cowen 1999, Muhling et al. 2008), the interaction of larvae with physical processes (Olivar 1990, Hare et al. 2001, Franco et al. 2006, Muhling and Beckley 2007), and predator-prey fields (Yoklavich et al. 1996, Diekmann et al. 2006, Olivar et al. 2010, Granata et al. 2011).

Adult spawning in association with nearshore habitats contributes to a common pattern whereby concentrations of larvae produced by reef- or shelf-dwelling adults decrease with increasing distances from shore (Young et al. 1986, Leis 1993, Mullaney et al. 2011). Similarly, there is evidence that a dichotomy in spawning strategies (i.e., the production of benthic versus pelagic eggs), can drive patterns of larval concentration, with larvae hatched from benthic eggs exhibiting peaks in concentration closer to shore than those hatched from pelagic eggs (Leis and Miller 1976, Leis 1993). In addition, for species that form spawning aggregations that are temporally and spatially discrete, larval concentrations can be similarly discrete (Sponaugle et al. 2003, D'Alessandro et al. 2010). Although oceanographic environments are temporally and spatially variable, evidence suggests that spawning locations and times of some species may serve to place

larvae in conditions favorable for survival, retention, or delivery to suitable habitat (Parrish et al. 1981).

The effects of prevailing currents and mesoscale oceanographic features on larval distributions and compositions are mediated by taxon-specific larval behaviors (Gray and Miskiewicz 2000, Muhling and Beckley 2007). In recent decades, fish larvae, once considered to act as passive particles, have been found to interact with the physical environment through a range of behaviors, such as vertical migration and active swimming (reviewed in Leis 2006). Ontogenetic vertical migrations have been observed for a variety of larval reef fishes, where the most common pattern was a shift to greater depths with increased development (Huebert et al. 2011). Additional work focused on larval transport suggests that larvae may exhibit relatively simple behaviors adapted to physical structures that are ubiquitous across systems, such as onshore flow at depth (Cowen et al. 1993, Cowen and Castro 1994, Paris and Cowen 2004). Even these simple larval behaviors may have significant impacts on dispersal pathways and larval supply to nearshore populations.

Finally, larval distributions may be influenced by predator-prey fields through a variety of mechanisms. The co-occurrence of peaks in larval fish concentrations with peaks in densities of their prey is consistent with the concept that larvae can alter their location in the water column to exploit favorable feeding conditions (Olivar et al. 2010, Granata et al. 2011). Alternatively, such patterns may result from mortality due to starvation leading to reductions in larval concentrations in areas of low prey availability. Predation has been invoked to explain patterns in larval distributions where low larval fish concentrations are associated with areas of increased predation pressure on larval

fishes (Yoklavich et al. 1996, Diekmann et al. 2006). However, direct observations of predation on fish larvae in the plankton are rare.

While it is logistically difficult to directly observe fish larvae in the plankton, studying patterns of larval distribution and composition helps reveal the processes affecting this vulnerable life stage. Specifically, an increased understanding of the factors structuring larval assemblages and driving abundance patterns can help elucidate transport processes as well as potential dispersal pathways (Grothues and Cowen 1999, Powell et al. 2000, Hare et al. 2001, Marancik et al. 2005, Peguero-Icaza et al. 2011). For coral reef fishes which have relatively sedentary benthic adults, such information is particularly important as the larval stage represents the primary vector of dispersal and at the end of the larval period larvae must locate suitable settlement habitat (e.g., coral reefs, seagrass beds) to settle and metamorphose into juveniles.

Recent evidence suggests that some populations of coral reef fish are sustained by substantial levels of self-recruitment whereby local adults are contributing significantly to population replenishment (Jones et al. 1999, Swearer et al. 1999, Jones et al. 2005, Almany et al. 2007). However, much of this work has been conducted for small island populations and the degree to which these results apply to contiguous continental coastlines is largely unknown. Complex flow associated with coastal topography, winds, tides, and mesoscale eddies can form nearshore retention zones (Gawarkiewicz et al. 2007, Andutta et al. 2012). Larval growth and development in these retention zones may be advantageous as nutrient concentrations tend to be higher nearshore (Sander and Steven 1973, Denman and Powell 1984)) and suitable habitat will be in close proximity for successful settlement. Since the majority of coral reef fish spawn in nearshore

environments we can expect to find very young larvae in such habitats. If these larvae are then retained by biophysical processes, larvae of all ages will be found in these retention zones. Alternatively, if larvae are advected offshore for growth and development before returning to nearshore habitats to settle, nearshore age distributions will be bimodal consisting of the youngest larvae not yet advected offshore and older pre-settlement larvae returning to shore at the end of the larval period. In addition, due to the coupling of adult spawning location with the potential for complex flow to entrain locally-spawned larvae, the highest larval concentrations will be found nearshore if larvae are indeed being retained. Thus, larval concentrations and age distributions can be used to indirectly infer nearshore retention of larvae.

This study was designed to examine population replenishment, including retention and the likelihood of self-recruitment, to a continental shelf influenced by a dynamic oceanographic environment dominated by a major western boundary current (i.e., the Florida Current). The objectives of this study were to 1) characterize larval assemblages throughout the Straits of Florida (SOF) as they relate to the oceanographic environment, 2) describe patterns in larval concentrations and age distributions, and 3) use these data to evaluate the potential for retention of locally-spawned larvae in the SOF.

Materials and Methods

Oceanography of the study area

The SOF is bordered by the Florida Keys to the north and west, Cuba to the south, and Bahamas Bank to the east. As the largest reef system in the continental United States, the Florida Keys reef tract stretches from Key Largo to the Dry Tortugas. The Florida Current (FC), a major western boundary current, flows offshore of the Florida Keys reef

tract at an average speed of 160 $cm \cdot s^{-1}$ (Richardson et al. 1969). The FC is fed by the Loop Current (LC), which flows into the FC in a direct path from the Yucatan Peninsula to the Dry Tortugas or after making a large meander into the Gulf of Mexico. The frontal boundary associated with both the LC and FC is dynamic and the formation of both mesoscale eddies (ME) and sub-mesoscale eddies in this region is well-documented (Lee 1975, Lee et al. 1994, Fratantoni et al. 1998, Sponaugle et al. 2005).

Cyclonic MEs, forming at and propagating along the front of the LC, enter the SOF where they are often referred to as Tortugas eddies. The presence of these cyclonic MEs, which are can be hundreds of kilometers in diameter, is indicated by the offshore deflection of the FC axis. As a ME moves through the SOF, it becomes elongated in the alongshore direction as it interacts with local bathymetry. The propagation speed of MEs is considerably slower in the western SOF than the eastern SOF (e.g., 5 $km \cdot d^{-1}$ versus 16 $km \cdot d^{-1}$, respectively, Fratantoni et al. 1998), with increased speed in the eastern SOF followed by the decay of MEs and the formation of remnant sub-mesoscale structures.

Oceanographic data

Oceanographic data were collected during three 16-day cruises aboard the R/V Walton Smith in the summers of 2007 (May 29 - June 13 and July 30 - August 13) and 2008 (June 17 - July 1). During each cruise, the water column was sampled using a ship-mounted 76.8 kHz RD Instruments Acoustic Doppler Current Profiler (ADCP). Sensors attached to the plankton sampling system (see *Ichthyoplankton sampling*) collected data on temperature, salinity, and fluorescence. Two Lagrangian drifters drogued at 15 m were deployed during each cruise to aid in the delineation of MEs (Technocean).

Ichthyoplankton sampling

Ichthyoplankton samples were collected concurrently with ship-based oceanographic data as described above. During each cruise, we sampled throughout the SOF along ten cross-shelf transects. Specifically, transects were positioned in the waters off of the upper (UK), middle (MK), and lower Keys (LK), the Marquesas (MQ), and in the Loop Current (LC) as it entered the SOF (Figure 2.1). Along each transect ten stations were sampled, with four stations inside or over the reef tract and six stations offshore of the reef, extending into the FC. For the LC transects, the first four stations (i.e., inside or over the reef tract) were omitted. At each station an ichthyoplankton tow was completed using one of two net types as determined by bottom depth. A modified Multiple Opening Closing Net and Environmental Sensing System (MOCNESS, Guigand et al. 2005) was used outside of the reef tract while an inshore frame net (i.e., modified neuston net) was employed at the shallower stations. The MOCNESS sampled from discrete 20 m depth bins down to 80 m using paired nets (4 m^2 and 1 m^2) fitted with 1-mm and 150-µm mesh, respectively. The inshore frame net fished approximately 1 m below the surface using paired nets (2 m^2 and 0.5 m^2) fitted with 1-mm and 150-µm mesh, respectively. Flowmeters were attached to both the MOCNESS and the inshore frame net to determine the volume sampled during each net tow. All ichthyoplankton tows were conducted during daylight hours, excluding dawn and dusk. Samples were preserved immediately in 95% ethanol and transferred to 70% ethanol upon return to the laboratory. All ichthyoplankton samples collected with the large-mesh nets (i.e., 1 mm) were processed by separating all fish larvae from other plankton, and identifying each specimen to the

lowest possible taxonomic grouping with reference to a regional ichthyoplankton guide (Richards 2006).

Classification of the oceanographic environment

We assigned each sampling station to one of five water mass classifications: inshore (IN), near-shore/no eddy (NN), eddy (ED), eddy edge (EE), or Florida and Loop Current (FC). All stations located within or over the reef tract were clearly distinct from all offshore stations in terms of their physical environment; station depths ranged from 5-17 m and currents were dominated by wind and tides. Thus, these stations were all designated as IN. Offshore stations (i.e., stations located at least 2 km from the reef tract) that were not included in the ED, EE, or FC water masses were designated NN.

We classified the ED water mass using a suite of physical data. Eddies were first identified and their approximate location determined using a combination of satellite imagery, outputs from the FKeyS-HYCOM model (V. Kourafalou), and current fields. Station locations and drifter tracks were then overlaid onto plots of temperature-at-depth contours. The signal of upwelling at the core of each eddy was clearly visible in these plots as a low temperature isotherm at 50 m (June 2007) or 70 m (August 2007 and June 2008), which was consistent with eddy locations determined in the first step (e.g., satellite imagery). Stations falling within the 24°C isotherm (i.e., the cold eddy core) were classified as ED stations, and those falling between the 24°C and 25°C isotherms were designated EE. As it is challenging to delineate precise eddy boundaries, our classification of ED stations as those located in the core of each eddy is conservative and, thus, the ED water mass does not include stations located in the eddy periphery. Likewise, our EE group may contain stations that are located in the eddy, in the eddy

edge, or outside the eddy; thus, this group must be considered with caution as a likely mix of water masses. Finally, for each sampling period, we plotted average surface current speeds for all stations. Based on these bimodal plots (data not shown) we classified all stations with an average current speed exceeding 70.0 $cm \cdot s^{-1}$ as FC stations (i.e., those located in the FC or LC). Average current speeds are 160 $cm \cdot s^{-1}$ in the core of the FC with decreasing speeds as distance from the core increases (Richardson et al. 1969).

Plots of current speed determined from the first depth bin of ADCP data (i.e., 16-24 m) and temperature averaged across the water column (i.e., 2-80 m) were constructed to qualitatively examine the separation of sampling stations by water mass designations. In addition to the *a posteriori* classification of water masses based largely on temperature and current speed, we performed a principle components analysis (PCA) to collapse the variation across five environmental variables into two-dimensional space. We then examined the position of sampling stations, color-coded by *a posteriori* water mass designations, in this two-dimensional space. We used temperature, salinity, fluorescence, current speed, and distance from shore in the PCA as these variables are important in structuring the environment and therefore likely impact larval fish assemblages and concentrations. With the exception of distance from shore, all variables were averaged across 20 m depth bins so that stations were represented by depth-specific samples. These depth-specific samples were consistent with the analysis of larval assemblages by both depth bin and water mass. Salinity, fluorescence, current speed, and distance from shore were log-transformed so data approximated (multivariate) normality. All variables were then normalized (i.e., we subtracted the mean and divided by the standard deviation)

since environmental variables were measured on a range of scales (e.g., temperature versus salinity).

Data analysis: Larval assemblages and abundances

Larval counts were standardized to the volume of water sampled by each net and resulting concentrations were $\log_{(x+1)}$ transformed to reduce the influence of the most common taxa on the interpretation of data. We used non-parametric multivariate techniques to examine the structure of larval assemblages in relation to both depth and water mass. As many ecological datasets do not conform to the assumptions of classic multivariate statistics (e.g., MANOVA), this non-parametric strategy has been developed as a robust alternative (Field et al. 1982, Clarke 1993) and its implementation has become common practice in studies of larval assemblages (e.g., Gray and Miskiewicz 2000, Hare et al. 2001, Muhling and Beckley 2007, Keane and Neira 2008, Muhling et al. 2008, Mullaney et al. 2011, Syahailatua et al. 2011). Analyses were first performed using all larval fish taxa that contributed to at least 5% of any one sample and, second, for all reef fish families (see Table 2.1) that contributed to at least 5% of any one sample. We treated each net (i.e., each 20 m depth bin) as a sample in the following analysis of larval assemblages.

Larval assemblages were examined by performing a two-way ANOSIM analysis for each sampling period in which both depth bin and water mass were included as factors (Primer v6, Clarke and Gorley 2006). A two-way ANOSIM is analogous to a two-way ANOVA in that it examines the effects of two categorical variables (e.g., water mass and depth bin) on a continuous dependent variable (e.g., larval assemblage). This is accomplished using a Bray-Curtis similarity matrix calculated for all sample pairs and

non-parametric permutation tests, thus, assumptions of normality and homoscedasticity are not required (Clarke 1993). In the two-way ANOSIM procedure, differences *among* depth bins were determined *within* a water mass by calculating a separate R statistic for each water mass grouping and then averaging them together to get R_{avg}. Depth bin labels were then reshuffled for samples *within* water mass to generate a permutation distribution of R values under the null hypothesis of no difference among depth bins. Finally, R_{avg} was compared to the permuted distribution of R values to determine the statistical significance for differences among depth bins. To examine differences *among* water masses, R statistics were calculated separately for each depth bin and averaged together. Then the permutation procedure described above was repeated with water mass labels reshuffled *among* samples *within* depth bins to determine the statistical significance for differences among water masses.

The R statistic generally ranges in value from 0 to 1, where 1 signifies that all samples within a group are more similar to each other than they are to any sample from another group. Conversely, an R statistic of 0 indicates that similarities between samples within a group are the same as similarities between samples from different groups. As the results of a permutation test are influenced by sample size, it is important to examine both the p-value and R statistic generated from each ANOSIM to determine if all statistically significant results are, in fact, biologically significant. In cases where we recognized biologically significant differences (criteria: $p < 0.01$ and $R > 0.1$), ANOSIM was followed up by the SIMPER procedure which uses the Bray-Curtis similarity matrix to determine percent contributions from each taxon to the similarity within groups. The IN water mass stations were not included in the two-way ANOSIM because they only

consisted of one depth bin that did not coincide with depth bins of the other water masses, thus they could not be included in a fully-crossed design. However, one-way ANOSIM tests were completed 1) among water masses with all depth bins combined and 2) among depth bins (i.e., surface, 0-20, 20-40, 40-60, and 60-80 m) with all water masses combined. Non-metric multidimensional scaling (MDS) plots were used to visualize the structure of larval assemblages in two-dimensional space, color-coded by either depth bin or water mass.

The BEST procedure was used to determine which environmental variables were important in driving the structure in larval assemblages (Primer v6, Clarke and Gorley 2006). This procedure compares the ranks of samples in the biological data matrix of Bray-Curtis dissimilarity to ranks of samples in the environmental data matrix of Euclidian distance using the Spearman coefficient. The combination of environmental variables resulting in the highest correlation was determined by calculating the coefficient for all possible combinations of environmental variables. As the use of standard statistical tables of Spearman's rank correlation is invalid in this particular use of the coefficient due to the interdependence of the dissimilarity values, a permutation test, in which all labels were randomly reshuffled, was used to assess statistical significance. We used temperature, salinity, fluorescence, current speed, and distance from shore as the environmental variables in the BEST procedure; each variable was transformed and normalized as described above for PCA analysis.

Larval concentrations were calculated for each sample (i.e., each net tow) for all fish taxa together and separately for only reef fish families. For each sampling period, concentrations were first compared among depth bins. For comparisons among water

masses, larval concentrations were converted to abundances by multiplying concentrations by the depth of the water column that was sampled; measures of abundance are often considered more appropriate than larval concentration when depths of sampling stations are variable (Lyczkowski-Schultz and Steen 1991, Leis 1993). Larval abundances were then compared among water masses using non-parametric Kruskal-Wallis tests since data did not conform to assumptions of normality and homoscedasticity.

Otolith analysis: Age distributions

We used otolith analysis to obtain ages for a subset of fish from both ED and FC water mass stations. We focused on these two water masses to use age distributions to test the long-standing hypothesis that MEs in the SOF retain locally-spawned reef fish larvae (e.g., Lee et al. 1992, Lee et al. 1994, Lee and Williams 1999). We limited our analysis spatially to samples collected along transects in the LK, MQ, and LC, because MEs form more coherent structures and have longer residence times in the western SOF and, thus, have greater potential for retention in this region. Based on sample sizes, the ability to identify individuals to the species level, and the utility of the otolith data in collaborative studies, five species of reef fish were chosen for otolith analysis: *Xyrichtys novacula* (pearly razorfish), *Thalassoma bifasciatum* (bluehead wrasse), *Cryptotomus roseus* (bluelip parrotfish), *Sphyraena barracuda* (great barracuda), and *Stegastes partitus* (bicolor damselfish). The concentration and size distribution of the fish used for otolith analysis was roughly proportional to that of the larvae in each sample. Standard length (SL) or notochord length (NL) was measured to the nearest 0.01 mm for each fish

using a Leica MZ12 dissecting microscope, a Cool Snap-Pro monochrome digital camera, and Image-Pro Plus 7.0 image analysis software (Media Cybernetics).

Sagittal (*X. novacula*, *T. bifasciatum*, and *C. roseus*) or lapillar (*S. partitus*) otoliths were dissected from each sample and stored in immersion oil for ~ 7-14 d to facilitate reading. The lapillar otoliths of *S. barracuda* were dissected and sectioned to facilitate reading. Specifically, one otolith from each larva was mounted in crystal-bond thermoplastic glue on a glass microscope slide and polished down to the primordium (core; using P2000 silicon-carbide abrasive paper, Nihonkenshi; D'Alessandro et al. 2010). All otoliths from a given species were analyzed by a single reader. Otoliths were read along the longest axis at 400X magnification (with the exception of *S. barracuda* lapilli which were read at 1000X magnification) through a Leica DMLB microscope and with the aid of the digital camera and Image-Pro Plus software. All otoliths were read at least twice, and if the reads differed by ≤ 5%, one read was randomly chosen for analysis. If reads differed by > 5%, a third read was conducted. This third read was then compared to the first two reads. If either comparison differed by ≤ 5%, one read from that comparison was randomly chosen for analysis; otoliths where all reads differed by > 5%, were removed from any further analysis (Sponaugle 2009). Mean ages were compared between ED and FC water masses for all possible species/sampling period combinations using one-way ANOVAs (SYSTAT 11).

Results

Water mass classification

We sampled approximately 100 stations during each cruise (Figure 2.1). In June 2007, 29 stations were designated IN, 11 NN, 11 ED, 13 EE, and 21 FC (Table 2.2). Due

to the large size of a ME off of the LK and MQ in August 2007, there were 29 ED stations and only 5 EE stations, but similar to June 2007, we classified 32 IN, 7 NN, and 21 FC stations. The water mass designations in June 2008 were similar to those in June 2007, but with more ED stations: 31 IN, 2 NN, 21 ED, 15 EE, and 19 FC. Based on current speed and temperature, the NN, ED, and FC stations were relatively distinct for all three sampling periods with some overlap among water masses (Figure 2.2). Current speeds in the FC water mass ranged from 46.2 to 179.19 $cm \cdot s^{-1}$, with overall faster current speeds occurring later in the summer. The average temperatures in the ED water mass were lower than those of the FC and NN due to the upwelling of cool water at ED stations. In addition, ED current speeds were generally slower than those in the FC, but comparable to the NN water mass. The NN water mass had warmer temperatures than the ED water mass and slower current speeds than FC waters. The EE stations overlapped with stations from all other water mass groupings with the exception of FC stations in August 2007 (Figure 2.2). As the EE stations may constitute a mix of NN, ED, and FC water masses, the overlap is not surprising.

The PCA analysis was largely consistent with our *a posteriori* water mass classifications; in addition, after overlaying depth-specific samples on the plots, environmental variation across depth bins was apparent (Figure 2.3). The first two principal component axes explained 74.9%, 78.1%, and 68.2% of the environmental variation among samples in June 2007, August 2007, and June 2008, respectively. In June 2007, eigenvectors indicated that variation in temperature and salinity were driving the distribution of samples along PC1 while distance from shore structured samples along PC2 (Table 2.3). In August 2007, a combination of temperature, salinity, and

fluorescence determined sample position along PC1 and contributions from current speed and distance from shore ordered samples along PC2. Finally, in June 2008, salinity and current speed drove variation along PC1 while fluorescence largely determined the arrangement of samples along PC2.

Ichthyoplankton collections

In total, 103,314 fish larvae were collected during all three cruises in the summers of 2007 and 2008, with 25,894 fish collected in June 2007, 43,488 in August 2007, and 33,932 in June 2008 (Table 2.1). Of this total, 32.81% constituted reef fish families. A total of 7,128 reef fish larvae were collected in June 2007, 15,563 in August 2007, and 11,202 in June 2008. Only 0.73% of all larvae could not be identified, and this was due most often to damage incurred upon collection in the net. Our collections represented 114 families and nine higher order groupings (e.g., suborder and superfamily), though nearly 50% of our collections consisted of larvae of Myctophidae, Scombridae, Paralichthyidae, Gobiidae, and Carangidae.

Vertical structure of larval assemblages

Larval assemblages consisting of all taxa were highly depth-structured during each sampling period (global R statistics: June 2007 = 0.493, August 2007 = 0.569, June 2008 = 0.378; Table 2.4; Figure 2.4). Not unexpectedly, larval assemblages of adjacent depth bins were more similar than larval assemblages of non-adjacent depth bins. In particular, comparisons of assemblages between 0-20 m and 60-80 m consistently exhibited high R statistics (June 2007 = 0.821, August 2007 = 0.911, June 2008 = 0.793). These high R statistics indicate that samples within a depth bin, but separated horizontally by 10s to 100s of km were more similar to each other than they were to

samples from depth bins separated vertically by only 40 m. In addition, all IN assemblages, made up of samples which were collected approximately 1 m below the surface, were significantly different from all other depth-specific assemblages (Table 2.5). Figure 2.4 illustrates that IN samples (labeled as 'surface') were not only very different from samples collected from all other depths but they also differed substantially from one another.

The SIMPER procedure was used to identify taxa contributing to these similarities within each depth-specific assemblage. We found that for assemblages of all taxa, the top 3-5 families contributing to each assemblage were similar across sampling periods indicating that vertical patterns were temporally consistent during the summer season (Table 2.6). Several families were important contributors to more than one depth-specific assemblage. These families tended to be very abundant overall and their contribution varied by depth. The surface depth bin which consisted only of stations in the IN water mass was comprised of families that tend to be more abundant in nearshore habitats; specifically, larvae from Clupeoidei, Monacanthidae, Atherinidae, and Gerreidae were among the five largest contributors to this larval assemblage for two of three sampling periods. Larvae from Scombridae, one of the most abundant families overall, were important contributors to the 0-20 m and 20-40 m larval assemblages; this reflects the decreasing occurrence and concentration of this family with increasing depth. Gonostomatidae larvae were also important contributors to the upper two depth bins while Carangidae was abundant in the 0-20 m assemblage. Larvae from Myctophidae, the most abundant family overall, were key contributors to larval assemblages from all depths (except the surface), with their percent contribution increasing with increasing

depth, consistent with the tendency of this family to be found deeper in the water column. Flatfish larvae from Bothidae and Paralichthyidae were key members of the larval assemblages in intermediate and deep depth bins, respectively. During August 2007 and June 2008, larvae of Gobiidae were also important contributors to several depth specific-assemblages.

Larval assemblages of reef fish families were less-structured for all sampling periods than assemblages which included all taxa (global R statistics for reef fishes: June 2007 = 0.278, August 2007 = 0.395, June 2008 = 0.216; Table 2.4; Figure 2.4). Again, comparisons of non-adjacent depth bins exhibited higher R statistics than comparisons of adjacent depth bins. However, in comparisons of adjacent depth bins, the 0-20 m and 20-40 m assemblages were the most distinct for all sampling periods. Similar to results from comparisons including all taxa, reef fish assemblages of the IN water mass were distinct from all other assemblages (Table 2.5). The R statistics (Table 2.4) and MDS plots (Figure 2.4) both show that reef fish assemblages were most structured by depth in August 2007 compared with June 2007 and 2008.

Horizontal structure of larval assemblages

In contrast to the strong depth-structure we observed for larval assemblages consisting of all taxa, overall differences among assemblages grouped by water mass were comparatively weak (global R statistics: June 2007 = 0.137, August 2007 = 0.170, June 2008 = 0.245; Table 2.7; Figure 2.5). However, pairwise comparisons of water mass assemblages indicated that FC and ED assemblages were significantly different for all sampling periods. Additionally, there was a significant difference between FC and EE assemblages in August 2007 and June 2008, between FC and NN assemblages in June

2008, and between ED and EE assemblages in June 2008. All but one comparison involving the IN water mass were significant with high R statistics (Table 2.5). MDS plots (Figure 2.5) show that despite a high variability within the water mass, the IN water mass assemblage was unique from all other water masses. Finally, the strongest structuring of assemblages of all larval fishes by water mass occurred in June 2008.

Larvae of Myctophidae, the most abundant family collected in our samples, were particularly important in delineating FC and ED assemblages (Table 2.8). Larvae of Scombridae and Carangidae were important in defining NN assemblages, while larvae of Paralichthyidae were important contributors to both EE and ED assemblages.

Similar to results including all taxa, reef fish larval assemblages were only weakly structured by water mass (global R statistics: June 2007 = 0.122, August 2007 = 0.100, June 2008 = 0.184; Table 2.7; Figure 2.5). However, in pairwise comparisons, FC and ED assemblages were significantly different for all sampling periods and ED and EE assemblages were significantly different in June 2008. Despite the consistent differences between FC and ED larval assemblages, there was a great deal of overlap among these stations in MDS plots. With one exception, the larval assemblages of the IN water mass were distinct from all other assemblages (Table 2.5).

Linking larval assemblages to environmental variables

The combination of environmental variables providing the highest correlation with the biological data matrix for all taxa was different for each sampling period. In June 2007, structure in larval assemblages was most correlated with temperature alone (Table 2.9). Later in the summer, August 2007, a combination of four out of five possible variables accounted for more than half of the variation between biological and

environmental data matrices. Finally, in June 2008, temperature and salinity resulted in the highest correlation coefficient.

In comparisons of reef fish assemblages to environmental variables, the correlations between data matrices were lower overall (Table 2.9). However, the same environmental variables exhibited the highest correlations for all taxa and reef fish assemblages, with the exception that both temperature and distance from shore were correlated with the reef fish assemblages in June 2007.

Larval abundances

Larval concentrations of all taxa were rather uniform across depth bins, indicating that larval fishes were present in roughly similar concentrations throughout the water column in all water masses (Figure 2.6). When examining only reef fish families, depth distributions tended to be skewed with higher larval concentrations in shallow depth bins (i.e., 0-20 and 20-40 m; Figure 2.7). Only in the ED water mass in August 2007 and the FC water mass in August 2007 and June 2008 were reef fish larvae uniformly distributed throughout the water column.

Larval abundances of all taxa combined differed across water masses; specifically, abundances were consistently low in the IN water mass (Figure 2.8). Larvae were most abundant in the NN water mass in June 2007 and 2008, although only in June 2007 was the difference between NN and all other water masses significant. In the examination of reef fishes, abundances in the IN water mass were still very low in all sampling periods, and overall differences among water masses tended to be greater than those observed for all taxa (Figure 2.9). In June 2007, reef fishes were significantly more abundant in NN than in IN, ED, and FC water masses. In August 2007, the EE water

mass contained significantly more larvae than IN, ED, and FC water masses, and abundances were greater in NN waters than they were in the FC water mass. Finally, in June 2008, larvae were significantly more abundant in the NN water mass compared to all other water masses.

Larval age distributions

Larval age distributions in ED versus FC water masses were species-specific and temporally variable. In June 2007, age distributions were similar in ED and FC water masses for *X. novacula* and *T. bifasciatum*, although the mean age of *X. novacula* was significantly older in the ED compared to the FC water mass (Table 2.10, Figure 2.10). During the August 2007 sampling period, age distributions for *X. novacula*, *T. bifasciatum*, and *C. roseus* differed between ED and FC water masses. The age range of larvae in the ED water mass was broad and skewed towards young ages, while in the FC water mass young ages were largely absent (Figure 2.11). This difference in age distributions between ED and FC water masses was particularly apparent for *T. bifasciatum* and *C. roseus* as the mean age of ED fish was significantly younger than the age of FC fish for both species (Table 2.9). During this same sampling period, the age distributions in ED versus FC water masses were similar for *S. barracuda* and *S. partitus* (Figure 2.11). In addition, age ranges of *S. barracuda* and *S. partitus* larvae tended to be narrower than those observed for *X. novacula*, *T. bifasciatum*, and *C. roseus*. Finally, in June 2008, *C. roseus* exhibited an age distribution similar to the pattern observed in August 2007 (Figure 2.12). Specifically, larvae in the ED water mass displayed a broad age range skewed towards younger fish while the larval age distribution in the FC was

lacking young fish. Consequently, the mean age of ED larvae was significantly younger than that for larvae from the FC water mass (Table 2.9).

Discussion

Our examination of ichthyoplankton assemblages in the SOF over two summers highlights distinct vertical structure in larval fish assemblages in the face of weak horizontal patterns corresponding to water mass. Specifically, larval assemblages were more similar over horizontal distances of 10s to 100s of km than they were across vertical distances of 10s of m. In contrast, larval abundances generally exhibited stronger distributional patterns among water masses than depth bins. Variation in the physical environment and taxon-specific responses to this variation likely account for these distribution patterns of larval fishes. Combined evidence of such patterns and species-specific age distributions suggest that the dynamic oceanographic environment in the SOF provides opportunities for retention of locally-spawned larvae which can contribute to subsequent larval supply and population replenishment.

Water masses in the Straits of Florida

Although the oceanographic environment of the SOF is dynamic, using a combination oceanographic data, we could identify relatively distinct water masses. The inshore (IN) water mass included all stations inside and over the reef tract. Here currents are highly influenced by winds and tides, nutrient inputs are high, and bottom depths are shallow. Stations in the NN water mass were ~ 2-20 km offshore of the reef tract, on the shoreward side of the FC front, and not immediately impacted by the passage of a ME; NN waters were characterized by warm temperatures and slow current speeds. High current speeds were observed at stations in the FC water mass. Stations in the ED water

mass were defined by temperature profiles (after the location of MEs were determined using a variety of physical oceanographic data). The FC and ED water masses correspond to the major oceanographic features identified in previous studies conducted in the SOF (Lee et al. 1992, Sponaugle et al. 2005). The EE water mass consisted of stations that could not be conclusively assigned to ED, NN, or FC groupings and thus likely represents of a mix of water masses. Locating precise boundaries between water masses can be difficult as these boundaries are dynamic with heterogeneous hydrographic characteristics; however, the exclusion of questionable stations from NN, ED, and FC groupings ensured a conservative classification approach. Water mass designations allowed us to examine variation in larval assemblages and abundances in a cross-shelf orientation (i.e., IN, NN, and FC) and along-shelf in association with MEs which are a dominant oceanographic feature in the SOF.

Environmental variation among samples collapsed adequately into two-dimensional space through PCA and corresponded well with *a posteriori* classifications of water mass. Temperature was negatively correlated with salinity and fluorescence, particularly during the summer of 2007. This is consistent with expectations of an upwelling scenario, in which cool, upwelled waters tend to be more saline and exhibit higher productivity. In addition, distance from shore was highly correlated with current speed due to the offshore location of the Florida and Loop Currents. Differences between the PCA plot for June 2008 and those for 2007 indicate the occurrence of temporal variations in the oceanographic environment. Specifically, in June 2008, fluorescence was positively correlated with distance from shore while temperature was likewise correlated with current speed. This may have resulted in part from differences in the

warming of nearshore waters and processes driving primary production. In addition to among-water mass variability, the environment was highly structured by depth. Temperatures were considerably warmer in shallow samples while salinity and fluorescence increased with depth. This observation of warm water overlaid upon cool, salty water with a deep chlorophyll maximum is consistent with hydrographic expectations. Thus, the environmental variability in the SOF, a complex oceanographic system, can be characterized based on major features such as the FC and MEs, as well as a highly structured water column.

Ichthyoplankton collections

In terms of familial diversity, our collections were similar to other regional studies of larval distributions. Ichthyoplankton tows conducted in the 1980's offshore of the Florida Keys (from UK to LK) sampled a total of 84 families (excluding leptocephali; Limouzy-Paris et al. 1994); during this same cruise, 65 families were represented in night-tows conducted at offshore stations (Cha et al. 1994). In comparison, samples collected across the LC boundary in the Gulf of Mexico contained 100 families (Richards et al. 1993). In the present study, we identified fish larvae from 123 families, with the increase in diversity likely due to increased temporal coverage as we collected ichthyoplankton during three two-week cruises over two summers. Larvae of Myctophidae were highly abundant in all collections referenced above and, similarly, constituted ~15% of our samples. In addition, larvae of Gonostomatidae, Paralichthyidae, Scombridae, Gobiidae, and Serranidae were abundant in all regional studies considered here (Richards et al. 1993, Cha et al. 1994, Limouzy-Paris et al. 1994). While our study

was representative of previous ichthyoplankton work it further increases the inventory of larval diversity in the region.

Vertical structure of larval assemblages

Our finding of distinct and temporally-stable vertical structure in larval assemblages is consistent with results for other temperate and tropical reef systems. Gray and Miskiewicz (2000) describe strong vertical structure in larval assemblages along the inner continental shelf of southeastern Australia. Similarly, larval assemblages from the Great Barrier Reef and from coral reef lagoons in French Polynesia were more distinct among depths than they were across horizontal distances separated by hundreds of kilometers (Leis 1993).

The families contributing to similarities within depth-specific assemblages were temporally consistent. Our results can be placed in a regional context by comparisons to a previous study of vertical distributions of fish larvae offshore of the Florida Keys (Cha et al. 1994: one cruise, 8 stations). Although differences in sampling methods (i.e., time of sampling and depth bin range) prevent quantitative comparisons, patterns of relative abundance across depth bins sampled in 1989 can be qualitatively compared to the results of our SIMPER analyses. Specifically, high relative abundances of Scombridae at 0-25 m and Gonostomatidae at 0-50 m are consistent with our finding that larvae from these families contributed substantially to within-assemblage similarities in the upper 20 m of the water column and that contributions decreased with increasing depth. In addition, our finding that larvae of Paralichthyidae were important in delineating deeper larval assemblages (i.e., 40-80 m) corresponds to the high relative abundance of this family in the 50-75 m stratum sampled by Cha et al. (1994). Thus, regional patterns in taxon-

specific vertical distributions were similar across studies conducted ~ 20 yrs apart. In addition, our study significantly extends the temporal and spatial coverage of ichthyoplankton collections in the SOF by sampling from the UK to the LC during three cruises conducted over two summers. Our results based on this extensive sampling effort suggest that the taxonomic stability we observed in depth-specific larval assemblages is driven by temporally- and spatially-consistent patterns of vertical distributions.

Although the existence of such vertical patterns in larval distributions has been reported in the literature (Leis 1991, Cowen 2002), less is known about the mechanisms shaping them. Physical parameters (e.g., temperature, salinity, visible and UV light, pressure and turbulence) and biological parameters (e.g., prey abundance and predator field) often vary with depth and likely affect larval growth and survival in complex ways. If fish larvae can orient vertically to high prey abundance, growth will likely increase; alternatively, survival may be enhanced if larvae adjust their position in the water column to avoid predators. Increased light levels may be advantageous for larvae as they are visual predators, despite the fact that they may become more vulnerable to predation themselves. We found that temperature variation was significantly correlated with the structure of larval assemblages in the SOF (for all taxa and reef fishes alone). Temperatures were generally warmer in the upper 40 m of the water column where the majority of reef fish larvae reside (Cowen 2002), and temperature increases should enhance growth (Houde 1989). Yet, results from PCA analyses indicated that temperature was correlated to a suite of variables, including salinity, fluorescence, depth, and in June 2008, current speed. While temperature was the environmental variable ‘explaining’ the greatest amount of variation in larval assemblages, this does not imply causation.

Temperature varied by depth and, thus, with hydrostatic pressure; this latter variable has been shown to be important in influencing larval reef fish distributions in the SOF (Huebert 2008, Huebert et al. 2010). Thus, the mechanisms responsible for observed depth-specific patterns in larval assemblages cannot be determined at this point. However, our finding that larval assemblages are more similar across horizontal distances of 10s to 100s of km than they are over vertical distances of 10s of m has implications for transport processes.

Vertical larval distributions can substantially influence dispersal trajectories because current speed and direction vary across depth (Cowen 2002). At Barbados, high abundances of reef fish larvae occurred at depths corresponding to onshore flow (Cowen and Castro 1994, Paris and Cowen 2004). Off the coast of southwestern Australia, larval fish with neustonic distributions were dispersed farther offshore by Ekman transport compared to larvae that avoided surface waters (Muhling and Beckley 2007). In the SOF, Huebert et al. (2011) reported 15-75% reduction in northward transport for larvae distributed at depths nearing 100 m in the FC water column. Thus, the effect of vertical larval distributions on horizontal transport can be significant, although the specifics of this transport vary by the water mass in which larvae are entrained (e.g., coastal zone versus boundary current).

Horizontal structure of larval assemblages

Larval assemblages in the SOF exhibited weak horizontal structure with respect to water mass. The exception was a significant difference between ED and FC assemblages during all sampling periods. Similarly, larval assemblages in MEs in the Gulf of Alaska differed from assemblages in basin waters and over the continental shelf (Atwood et al.

2010). Based on relative contributions of abundant families, eddy assemblages identified off southwestern Australia were a mix of oceanic and coastal taxa, and therefore differed from assemblages originating from either ocean or coastal water masses (Holliday et al. 2011). Eddy assemblages are determined by the fish larvae present during eddy formation, in addition to the chance encounter of a ME with another water mass containing fish larvae or the entrainment of larvae spawned within or near an eddy. Eddy assemblages may be altered from those in neighboring water masses due to the dynamic trophic environment driven by the new production occurring as a result of eddy-induced upwelling (see Chapter 3). Specifically, fish larvae in eddies may experience reduced starvation as prey fields are enhanced by nutrient enrichment and the concentration of prey in areas of convergence (Bakun 2006). Alternatively, it has been shown that a variety of marine predators target MEs for feeding (e.g., Cotte et al. 2007, Sabarros et al. 2009, Kai and Marsac 2010); consequently, fish larvae unable to escape these potentially high rates of predation may be removed from the ED assemblage. Regardless of the underlying mechanisms, our findings are consistent with the idea that larval assemblages in MEs are different from assemblages in surrounding waters and are thus likely modified in some way by the unique physical and biological environment of MEs.

In addition to distinct differences between ED and FC larval assemblages, we found evidence of an inshore-offshore gradient in larval distributions of all taxa. Larvae of Clupeoidei, Monacanthidae, Gerreidae, and Atherinidae were abundant in the IN water mass while larvae of Scombridae, Myctophidae, and Bothidae dominated waters farther offshore (i.e., NN and FC). Similarly, ichthyoplankton tows conducted over the FK reef tract (corresponding spatially with the IN water mass) collected large numbers of larvae

of Atherinidae, Clupeidae, and Engraulidae, and relatively few larvae of Scombridae, Myctophidae, and Bothidae (Sponaugle et al. 2003). These differences in the taxonomic composition of larval assemblages correspond to adult spawning locations which contribute substantially to changes in larval assemblages along other inshore-offshore axes (Leis 1993). The large differences we observed between the IN and offshore assemblages has been identified elsewhere (Gray and Miskiewicz 2000, Muhling et al. 2008, Granata et al. 2011) and, specifically, in studies near coral reefs (Leis 1978, Young et al. 1986). The distinct shift we observed in larval assemblages along the inshore-offshore axis and its occurrence over a relatively short distance (~ 2 km) suggests that adult habitat (rather than water mass) may be a better indicator of larval distributions in the SOF.

Larval abundances

In contrast to our finding of distinct vertical structure in the face of weak horizontal patterns, larval abundances of all taxa combined were similar throughout the water column yet exhibited significant differences among water masses. As vertical distributions are typically taxon-specific (Leis 1986, Cha et al. 1994) and often ontogenetically-mediated (Huebert et al. 2011), it is likely that the combination of all taxa abundances masked any taxon-specific depth preferences, resulting in a relatively uniform distribution. This is illustrated on a coarse level by the finding that larval depth distributions of only reef fishes were skewed toward the shallowest depth bins. Reef fish larvae are known to be concentrated in the upper 50 m of the water column (Cha et al. 1994, Cowen 2002, Huebert et al. 2011), although this vertical structure is thought to break down at night as larvae undergo diel vertical migrations. Our study did not address

such migrations with our sampling design; however, Huebert et al. (2011) found evidence of diel vertical migrations for several reef fish families in the SOF (i.e., Pomacentridae, Scorpaenidae, and two species of Serranidae). Therefore, the patterns we observed in larval reef fish depth distributions may be maintained primarily during daylight hours.

In comparing larval abundances of all taxa across water masses, we found that IN stations consistently exhibited extremely low larval abundances compared to stations from all other water masses. Although larvae were quite abundant at NN stations, differences between NN and all other water masses were only significant in one of three sampling periods. When examining abundances of larval reef fishes only, differences among water mass became more pronounced. Larval abundances at IN stations were still very low, while abundances in the NN water mass were now significantly higher than those in ED and FC water masses during all sampling periods. The extremely low abundances observed in the IN water mass may result from high predation rates in these shallow habitats consisting of seagrass beds and coral reefs (Deikmann et al. 2006). However, D'Alessandro and Sponaugle (2011) observed greater predation on settlement stage larvae offshore of the FK reef tract corresponding roughly to the NN water mass where consistently high larval abundances occurred.

After peaking in the NN water mass (~2-10 km offshore), larval abundances tended to decrease with increasing distance from shore. This distributional pattern along the inshore-offshore axis is similar to that found by Young et al. (1986) across the northwest continental shelf of Western Australia, though their peak in larval concentration was located 40-50 km offshore. Another study conducted off the eastern coast of Australia found that larval concentrations decreased with increasing distance

from shore in the Tasman Front region, although this pattern in concentration was not consistently maintained off of northern New South Wales (Mullaney et al. 2011). The high abundances of larval reef fishes that we observed in nearshore waters may be due in part to adult spawning in proximity to reef habitat located ~ 2 km inshore of the nearest NN station. Subsequent to any spawning event, propagules may be entrained in complex current patterns and retained in nearshore waters contributing to the high larval abundances in the NN water mass in the face of potentially high predation rates (D'Alessandro and Sponaugle 2011, Andutta et al. 2012).

Larval age distributions

Patterns in larval age distributions between ED and FC water masses were species-specific and varied temporally. However, for three of the five species examined during the August 2007 sampling period (i.e., *X. novacula*, *T. bifasciatum*, and *C. roseus*) and for *C. roseus* in June 2008, the wide age distribution in the ED water mass and lack of younger ages in the FC is consistent with the hypothesis that MEs in the SOF serve to retain locally-spawned larvae (Lee et al. 1992, Lee et al. 1994, Lee and Williams 1999). The presence of young fish in the eddy indicates that when spawning occurs in concert with the passage of a ME, larvae can be entrained within that water mass. But perhaps more importantly, the simultaneous presence of both young and older larvae in the eddy suggests that larvae can survive there for the duration of the larval stage. However, during this same sampling period, *S. barracuda* and *S. partitus* age distributions provide no evidence for retention, suggesting that the interaction of larvae with MEs is species-specific. In contrast to August 2007, age distributions during the June 2007 sampling period were similar between ED and FC water masses for *X. novacula* and *T.*

bifasciatum, suggesting that retention may also be temporally variable within a species perhaps in concert with the age, formation, and decay of the eddy. The lack of young larvae in the ED water mass sampled in June 2007 may be due to the mismatch between spawning and the formation or passage of eddies during this time. *Thalassoma bifasciatum* spawns daily year-round with larvae present in the SOF in all months but especially June to November (Sponaugle et al. 2009). Therefore, spawning likely occurred during the passage of eddies in June 2007, but spawning output may have been relatively low compared to that occurring in August 2007 when water temperatures were warmer. In summary, the impact of MEs on larval retention and transport appears to be species-specific and changes temporally as spawning differentially overlaps with eddy formation and propagation.

Implications for transport and retention in the SOF

Reef fish populations in the Florida Keys are likely maintained by inputs of both locally-spawned larvae and larvae transported from distant sources (e.g., the Yucatan). Understanding the magnitude of both contributions, and how they change with time and oceanographic conditions is crucial to the development of proper policies for management and conservation. A growing body of evidence supports the concept that locally-spawned larvae of marine fishes are disproportionately contributing to population replenishment through high levels of self-recruitment (Swearer et al. 2002, Jones et al. 2005, Almany et al. 2007). Regional evidence suggests that larval dispersal throughout the Caribbean and SOF is restricted for some species (Purcell et al. 2006) and that local populations supply the majority of settlers to the Florida Keys reef tract (Sponaugle et al. 2012). However, for self-recruitment to occur, larvae must be retained in the SOF so that

they can successfully settle at the end of the larval stage. As individuals entrained in the FC will likely be rapidly transported downstream, retention mechanisms (i.e., keeping larvae out of the FC) must be strong enough to counteract advective processes.

Results of our study are consistent with the idea that locally-spawned larvae are retained in the SOF. The finding of high abundances of larval reef fishes in the NN water mass is indicative of larval retention in nearshore waters, although the mechanism in this case is unknown. Complex flow associated with coastal topography can form nearshore retention zones (Gawarkiewicz et al. 2007); additionally, slow current speeds observed in the NN water mass may allow reef fish larvae with relatively strong swimming capabilities, to maintain a position close to shore. In addition to retention of larvae in the NN water mass, high rates of larval delivery to these waters by sub-mesoscale eddies (Sponaugle et al. 2005, D'Alessandro et al. 2007), remnant mesoscale eddies, or internal tidal bores (Leichter et al. 1996), may further contribute to observed patterns in abundance. Larval age distributions suggest that MEs forming and propagating in the western SOF provide a possible mechanism for retention. MEs have also been implicated in the retention of fish larvae in Hawaiian waters (Sale 1970). Likewise, distributions of anchovy eggs and larvae in an eddy associated with the Kuroshio Current provide evidence for entrainment of early life stages off the coast of Japan (Nakata et al. 2000).

In conclusion, our results highlight strong vertical structure in larval assemblages and consistent horizontal patterns in larval abundances. Taxon-specific responses to variation in the physical environment likely account for these distributional patterns. In addition, larval abundances and species-specific age distributions together suggest that the dynamic oceanographic environment in the SOF provides opportunities for retention

of locally-spawned larvae which can contribute to subsequent larval supply and population replenishment.

Table 2.1. Mean larval abundances (·1000 m^{-3}) for all fishes collected across three sampling periods in 2007 and 2008.

Family Name		June 2007	August 2007	June 2008	Total
Acanthuridae	Acanthurus spp.	247.24	117.65	132.50	497.40
Achiridae	Spp.	4.34	13.07	5.26	22.67
Acropomatidae	Spp.	167.69	96.15	80.40	344.24
Alepisaruidae	Spp.	6.78	4.21	2.11	13.10
Antennariidae	Spp.	149.33	452.52	19.78	621.63
Apogonidae	Spp.	560.25	899.31	788.90	2248.47
Ariommatidae	Spp.	271.63	290.69	79.59	641.91
Atherinidae	Spp.		548.18	554.36	1102.54
Aulopidae	Aulopus nanae	16.40	6.25	2.49	25.14
Aulostomidae	Aulostomus maculatus	3.68	2.89	2.13	8.70
Balistidae	Spp.	230.49	44.20	53.54	328.23
Barbourisiidae	Barbourisia rufa	0.77			0.77
Bathysauridae	Bathysaurus spp.	1.14			1.14
Beloniidae	Spp.	9.00	5.47	53.39	67.86
Berycidae	Beryx spp.	2.27	6.49	1.90	10.66
Suborder: Blennioidei	Spp.	168.99	40.63	124.94	334.56
Blenniidae	Spp.	32.41		9.39	41.81
Bramidae	Spp.	127.71	22.14	24.81	174.65
Bregmacerotidae	Spp.	723.17	491.01	781.09	1995.28
Bythitidae	Spp.	1.35			1.35
Callionymidae	Spp.	230.77	951.72	342.55	1525.04
Caproidae	Antigonia spp.	212.34	159.08	420.76	792.18
Carangidae	Spp.	2846.77	3887.90	1005.63	7740.30
Carapidae	Spp.	117.03	81.99	99.88	298.90
Suborder: Ceratioidei	Spp.	74.79	13.45	15.45	103.69
Chaenopsidae	Spp.			1.09	1.09
Chaetodontidae	Chaetodon spp.	61.13	43.30	23.79	128.22
Chiasmodontidae	Spp.	25.22	17.80	12.42	55.44
Chlorophthalmidae	Spp.	219.62	269.78	155.44	644.84
Cirrhitidae	Amblycirrhitus spp.	11.48	8.28	1.57	21.33
Suborder: Clupeoidei	Spp.	1002.50	546.79	241.99	1791.27
Coryphaenidae	Coryphanea spp.	582.60	42.79	174.88	800.27
Cynoglossidae	Symphurus spp.	111.67	190.55	232.20	534.42
Dactylopteridae	Dactylopterus volitans	15.75	14.70	11.76	42.22
Diodontidae	Spp.	19.54	7.88	3.43	30.85
Diretmidae	Spp.	0.67	2.52		3.19
Echeneidae	Spp.	25.68	20.10	45.15	90.93
Superorder: Elopomorpha	Spp.	576.36	741.46	690.02	2007.84

Table 2.1. (*continued*)

Family Name		June 2007	August 2007	June 2008	Total
Epigonidae	Spp.		1.03		1.03
Evermannellidae	Spp.	27.36	37.76	20.95	86.08
Exocoetidae	Spp.	75.89	47.74	129.93	253.56
Fistulariidae	Fistularia spp.	6.84	10.57	0.94	18.34
Gempylidae	Spp.	1300.35	261.94	454.62	2016.91
Gerreidae	Spp.	171.51	788.67	471.07	1431.24
Gibberrichthyidae	Gibberichthys pumihus	1.74			1.74
Giganturidae	Gigantura spp.	3.47	2.46	7.74	13.67
Gobiidae	Spp.	795.01	4217.29	2949.62	7961.92
Gobiosocidae	Spp.	4.98		4.68	9.66
Gonostomatidae	Spp.	1250.50	2781.55	1536.77	5568.82
Haemulidae	Spp.	70.24	99.92	65.12	235.28
Hemiramphidae	Spp.	40.83	126.69	79.35	246.87
Holocentridae	Spp.	305.23	580.92	57.00	943.14
Howellidae	Spp.	144.43	66.27	54.15	264.85
Idiacanthidae	Spp.	4.01			4.01
Ipnopidae	Spp.	2.19			2.19
Istiophoridae	Spp.	58.62	112.09	84.51	255.21
	Istiophorus platypterus	0.77			0.77
Kyphosidae	Kyphosus spp.	3.52	3.76		7.29
Labridae	Bodianus spp.		0.84		0.84
	Clepticus parrae	34.36	26.39	5.73	66.48
	Decodon puellaris	12.09	92.14	12.06	116.29
	Doratonotus megalepis	33.32	21.37	21.39	76.07
	Halichoeres spp.	54.99	84.32	33.71	173.02
	Lachnolaimus maximus	0.95			0.95
	Thalassoma bifasciatum	761.67	215.99	111.30	1088.95
	Xyrichtys spp.	728.78	1695.06	656.06	3079.91
	Spp.	3.71	7.52	5.39	16.61
Order: Lampridiformes	Spp.	35.05	7.38	6.22	48.65
Lampridae	Lampris guttata	2.22		1.06	3.29
Lobotidae	Lobotes surinamensis	2.84	2.51		5.35
Lophiidae	Spp.	2.14	10.22	0.99	13.36
Lutjanidae	Spp.	379.42	1775.39	1379.11	3533.93
Luvaridae	Luvarus imperialis	3.19			3.19
Malacanthidae	Spp.	24.38	140.59	73.66	238.63
Melamphaidae	Spp.	56.31	19.98	17.39	93.68
Microdesmidae	Spp.	37.68	65.84	44.76	148.29

Table 2.1. (*continued*)

Family Name		June 2007	August 2007	June 2008	Total
Mirapinnidae	Spp.	3.11	4.32	3.75	11.18
Molidae	Spp.			0.76	0.76
Monacanthidae	Spp.	260.69	506.21	749.24	1516.14
Moridae	Spp.	13.38	8.81	13.81	36.01
Mugilidae	Spp.	42.58	2.03	1.44	46.05
Mullidae	Spp.	129.81	15.55	34.25	179.60
Myctophidae	Spp.	9614.20	5318.01	4524.10	19456.32
Neoscopelidae	Spp.	0.79	5.04	6.99	12.82
Nomeidae	Spp.	608.79	361.32	525.65	1495.76
Notosudidae	Spp.	1.09	5.02		6.11
Ogcocephalidae	Spp.	60.79	352.22	213.29	626.30
Ophidiidae	Spp.	399.52	405.34	398.63	1203.49
Opistognathidae	Spp.	77.81	4.40	93.86	176.07
Ostraciidae	Spp.	13.19	6.22	22.03	41.44
Paralepididae	Spp.	531.25	416.82	341.20	1289.27
Pempheridídae	Spp.		1.09		1.09
Percophidae	Spp.	14.57	0.87		15.44
Peristediidae	Spp.	15.59	1.80	0.79	18.17
Phosichthyidae	Spp.	371.84	408.30	503.06	1283.20
Order: Pleuronectiformes	Spp.		0.63	3.61	4.24
Bothidae	Spp.	1633.28	3172.93	1688.51	6494.71
Paralichtyidae	Spp.	1652.92	7114.16	4428.27	13195.34
Polymixiidae	Spp.	6.67	22.39	4.54	33.61
Pomacanthidae	Spp.	85.59	164.23	45.67	295.49
Pomacentridae	Abudefduf spp.	4.51	11.61	47.84	63.96
	Stegastes partitus	108.13	251.68	76.91	436.72
	Spp.	250.55	92.95	116.56	460.07
Priacanthidae	Spp.	216.07	789.57	373.68	1379.32
Rachycentridae	Rachycentron canadum	1.82			1.82
Scaridae	Cryptotomus roseus	103.43	945.00	157.88	1206.31
	Scarus spp.	20.59	176.44	80.67	277.70
	Sparisoma spp.	337.82	1167.62	238.99	1744.43
	Spp.	11.33	30.82	7.18	49.32
Sciaenidae	Spp.	35.92			35.92
Scombridae	Acanthocybium solandri	35.14	31.34	33.42	99.90
	Spp.	3618.62	6416.37	3735.16	13770.15
Scombrolabracidae	Scombrolabrax heterolepis	0.78	0.99		1.77
Scopelarchidae	Spp.	3.59	2.50	1.59	7.68

Table 2.1. (*continued*)

Family Name		June 2007	August 2007	June 2008	Total
Scorpaenidae	Spp.	463.70	1259.32	827.83	2550.85
Serranidae	Subfamily: Anthiinae	1774.29	678.12	350.78	2803.19
	Subfamily: Epinephelinae	29.11	13.83	5.59	48.53
	Tribe: Grammistini	100.60	267.70	118.63	486.93
	Tribe: Liopropomini	319.69	205.04	100.57	625.30
	Subfamily: Serraninae	796.55	748.14	346.69	1891.38
	Spp.	1.48	0.84		2.32
Sparidae	Spp.		3.92		3.92
Sphyraenidae	Sphyraena spp.	247.77	706.54	344.93	1299.24
Sternoptychidae	Spp.	7.47		55.12	62.59
Superfamily: Stomioidea	Spp.	118.44	191.05	83.97	393.46
Symphysanodontidae	Spp.	7.52	21.60	2.43	31.55
Syngnathidae	Spp.	58.68	44.00	70.19	172.88
Synodontidae	Spp.	75.03	188.57	69.26	332.86
Tetraodontidae	Spp.	304.71	470.27	457.33	1232.31
Trachichthyidae	Spp.	0.90			0.90
Triacanthodidae	Spp.	2.56	1.29	1.03	4.89
Trichiuridae	Spp.	113.60	2.96	4.24	120.80
Triglidae	Spp.	117.60	125.98	151.94	395.52
Uranoscopidae	Spp.	0.88			0.88
Xiphiidae	Xiphias gladius	20.22	5.53	6.65	32.40
Order: Zeiformes	Spp.	1.82			1.82
Unknown	Spp.	475.73	393.47	172.16	1041.36

Table 2.2. Water mass designation at all stations for each of three sampling periods. Stations were sampled along two transects at each alongshore location. IN = inshore, NN = no eddy/nearshore, FC = Florida or Loop Currents, ED = eddy, and EE = eddy edge. Empty cells denote stations that were not sampled.

June 2007

		Cross-shelf									
Alongshore	Upper Keys	IN	IN	IN	IN	NN	NN	FC	FC	FC	FC
		IN	IN	IN	IN	NN	NN	NN	FC	FC	FC
	Middle Keys	IN	IN	IN	IN	NN	NN	NN	FC	FC	
		IN	IN	IN	IN	NN	NN	NN	EE	FC	
	Lower Keys	IN	IN	IN	IN	EE	ED	ED	ED	ED	ED
		IN	IN	IN	IN		ED	ED	ED	EE	EE
	Marquesas	IN	IN	IN	IN	EE		EE	FC	FC	FC
		IN	IN	IN	IN	EE	EE	EE	EE	EE	FC
	Loop Current					ED	EE	FC	FC	FC	FC
						EE	ED	ED	FC	FC	FC

August 2007

		Cross-shelf									
Alongshore	Upper Keys	IN	IN	IN	IN	FC	FC	FC	FC	FC	FC
		IN	IN	IN	IN	NN	NN	NN	NN	FC	FC
	Middle Keys	IN	IN	IN	IN	NN	NN	NN	FC	FC	FC
		IN	IN	IN	IN	EE	EE	EE	FC	FC	FC
	Lower Keys	IN	IN	IN	IN	ED	ED	ED	ED	ED	ED
		IN	IN	IN	IN	ED	ED	ED	ED	ED	ED
	Marquesas	IN	IN	IN	IN	EE	ED	ED	ED	ED	ED
		IN	IN	IN	IN	EE	ED	ED	ED	ED	ED
	Loop Current				ED	ED	FC	FC	FC	FC	FC
					ED	ED	ED	ED	ED	FC	FC

June 2008

		Cross-shelf									
Alongshore	Upper Keys	IN	IN	IN	IN	NN	FC	FC	FC		FC
		IN	IN	IN	IN	NN	FC	FC	FC	FC	FC
	Middle Keys	IN	IN	IN	IN	EE	EE	EE	FC	FC	FC
		IN	IN	IN	IN	EE	EE	EE	FC	FC	FC
	Lower Keys	IN	IN	IN	IN	ED	ED	ED	EE	EE	EE
		IN	IN	IN	IN	ED	ED	ED	ED	EE	EE
	Marquesas	IN	IN	IN	IN	ED	ED	ED	ED		ED
		IN	IN	IN	IN	ED	ED	ED	ED	ED	ED
	Loop Current					ED	ED	ED	EE	EE	
						FC	FC	FC	EE	EE	FC

Table 2.3. Eigenvectors from principle components analysis conducted for each of three sampling periods. Values > 0.500 in bold. Percent variation indicates the amount of variability in the data explained by a given axis.

	June 2007				
Environmental variable	PC1	PC2	PC3	PC4	PC5
Temperature	**0.541**	-0.301	0.304	-0.089	-0.719
Salinity	**-0.538**	0.307	-0.286	0.254	-0.686
Fluorescence	-0.392	0.182	0.902	-0.006	0.010
Current speed	0.450	0.474	0.104	0.744	0.092
Distance from shore	0.249	**0.747**	-0.046	-0.611	-0.068
% Variation	49.6	25.3	14.2	7.4	3.5
	August 2007				
Environmental variable	PC1	PC2	PC3	PC4	PC5
Temperature	**0.577**	-0.241	0.085	0.137	0.764
Salinity	**-0.551**	-0.131	0.236	0.760	0.212
Fluorescence	**-0.552**	0.238	-0.290	-0.437	0.603
Current speed	0.231	**0.643**	-0.572	0.453	0.011
Distance from shore	0.073	**0.674**	0.725	-0.081	0.091
% Variation	49.2	28.9	12.4	6.4	3
	June 2008				
Environmental variable	PC1	PC2	PC3	PC4	PC5
Temperature	0.407	-0.327	-0.758	0.386	-0.071
Salinity	**-0.598**	-0.167	-0.156	0.312	0.702
Fluorescence	-0.116	**0.729**	-0.031	0.638	-0.216
Current speed	**0.521**	-0.223	0.593	0.482	0.308
Distance from shore	0.438	0.533	-0.223	-0.337	0.600
% Variation	38.7	29.5	15.9	9.4	6.6

Table 2.4. Comparisons of larval assemblages between depth bins based on a two-way ANOSIM analysis with depth bin and water mass included as factors. Results are shown for all taxa larval assemblages (top) and reef fish assemblages (bottom). To correct for multiple pairwise comparisons, we used an adjusted alpha of 0.01. * $p < 0.01$, ** $p = 0.001$, ns = not significant.

All taxa	June 2007	August 2007	June 2008
Groups	R statistic	R statistic	R statistic
Global	0.493 **	0.569 **	0.378 **
0-20 vs 20-40	0.327 **	0.503 **	0.265 **
20-40 vs 40-60	0.283 **	0.306 **	0.216 **
40-60 vs 60-80	0.256 **	0.285 **	0.110 *
0-20 vs 40-60	0.618 **	0.718 **	0.568 **
0-20 vs 60-80	0.821 **	0.911 **	0.793 **
20-40 vs 60-80	0.711 **	0.771 **	0.589 **

Reef fishes	June 2007	August 2007	June 2008
Groups	R statistic	R statistic	R statistic
Global	0.278 **	0.395 **	0.216 **
0-20 vs 20-40	0.203 **	0.361 **	0.194 **
20-40 vs 40-60	0.101 *	0.160 **	0.126 **
40-60 vs 60-80	0.145 **	0.131 **	0.081 *
0-20 vs 40-60	0.381 **	0.524 **	0.400 **
0-20 vs 60-80	0.548 **	0.704 **	0.491 **
20-40 vs 60-80	0.388 **	0.516 **	0.330 **

Table 2.5. Comparisons of inshore (IN, labeled as 'surface') larval assemblages with assemblages from all other depth bins (top), and comparisons of IN larval assemblages with those from all other water masses (bottom). In comparisons among water masses, all depth bins were combined. Results of one-way ANOSIM analyses are shown for all taxa larval assemblages and reef fish assemblages. To correct for multiple pairwise comparisons, we used an adjusted alpha of 0.01. * $p < 0.01$, ** $p = 0.001$, ns = not significant.

Comparison among depth bins			
	June 2007	August 2007	June 2008
Groups	R statistic	R statistic	R statistic
All taxa			
Surface vs 0-20	0.769 **	0.911 **	0.803 **
Surface vs 20-40	0.846 **	0.924 **	0.896 **
Surface vs 40-60	0.874 **	0.927 **	0.918 **
Surface vs 60-80	0.920 **	0.957 **	0.943 **
Reef fish			
Surface vs 0-20	0.614 **	0.780 **	0.463 **
Surface vs 20-40	0.725 **	0.846 **	0.745 **
Surface vs 40-60	0.663 **	0.860 **	0.643 **
Surface vs 60-80	0.788 **	0.895 **	0.676 **
Comparison among water masses			
	June 2007	August 2007	June 2008
Groups	R statistic	R statistic	R statistic
All taxa			
IN vs NN	0.495 **	0.789 **	0.117 ns
IN vs FC	0.856 **	0.928 **	0.823 **
IN vs ED	0.803 **	0.896 **	0.752 **
IN vs EE	0.792 **	0.775 **	0.730 **
Reef fish			
IN vs NN	0.363 **	0.668 **	-0.084 ns
IN vs FC	0.711 **	0.838 **	0.403 **
IN vs ED	0.511 **	0.778 **	0.640 **
IN vs EE	0.604 **	0.625 **	0.494 **

Table 2.6. Results of SIMPER analyses for each of three sampling periods showing the five taxa contributing most to within-group similarities of depth-specific larval assemblages. Percent contributions are listed to the right of each taxon.

	June 2007		August 2007		June 2008	
	Taxon	%	Taxon	%	Taxon	%
Surface	Clupeoidei	22.71	Clupeoidei	18.33	Clupeoidei	14.23
	Monacanthidae	8.08	Monacanthidae	14.98	Monacanthidae	14.94
	Blennioidei	11.63	Atherinidae	21.82	Atherinidae	11.97
	Scombridae	8.25	Gerreidae	15.47	Gerreidae	10.51
	Syngnathidae	6.91	Hemiramphidae	7.95	Carangidae	7.33
0-20	Scombridae	10.28	Scombridae	14.18	Scombridae	16.31
	Myctophidae	13.63	Myctophidae	6.85	Myctophidae	12.66
	Gonostomatidae	8.37	Gonostomatidae	10.71	Gonostomatidae	10.14
	Carangidae	9.96	Carangidae	13.06	Carangidae	6.34
	Coryphaenidae	6.70	Lutjanidae	5.42	Scorpaenidae	5.16
20-40	Myctophidae	15.94	Myctophidae	8.24	Myctophidae	13.94
	Bothidae	9.96	Bothidae	11.33	Bothidae	10.38
	Scombridae	8.35	Scombridae	10.14	Scombridae	9.62
	Gonostomatidae	6.95	Gonostomatidae	8.13	Gonostomatidae	9.62
	Paralichtyidae	6.70	Paralichtyidae	8.79	Gobiidae	7.92
40-60	Myctophidae	26.17	Myctophidae	13.82	Myctophidae	20.71
	Paralichtyidae	7.64	Paralichtyidae	7.98	Paralichtyidae	8.82
	Bothidae	7.07	Bothidae	7.68	Bothidae	8.95
	Serranidae	6.92	Gobiidae	6.43	Gobiidae	6.35
	Gempylidae	6.51	Scombridae	6.24	Leptocephali	5.96
60-80	Myctophidae	30.76	Myctophidae	19.32	Myctophidae	25.49
	Paralichtyidae	6.31	Paralichtyidae	9.2	Paralichtyidae	12.99
	Bregmacerotidae	12.23	Bregmacerotidae	6.49	Bothidae	7.71
	Gempylidae	11.40	Gobiidae	5.61	Gobiidae	6.81
	Labridae	4.83	Callionymidae	7.63	Paralepididae	6.28

Table 2.7. Comparisons of larval assemblages between water masses based on a two-way ANOSIM analysis with depth bin and water mass included as factors. Results are shown for all taxa larval assemblages (top) and reef fish assemblages (bottom). To correct for multiple pairwise comparisons, we used an adjusted alpha of 0.01. * $p < 0.01$, ** $p = 0.001$, ns = not significant.

All taxa	June 2007	August 2007	June 2008
Groups	R statistic	R statistic	R statistic
Global	0.137 **	0.170 **	0.245 **
NN vs FC	0.125 ns	0.121 ns	0.604 **
NN vs EE	-0.008 ns	0.079 ns	0.017 ns
NN vs ED	0.159 ns	-0.034 ns	0.139 ns
FC vv EE	0.075 ns	0.418 **	0.106 *
FC vs ED	0.253 **	0.213 **	0.359 **
ED vs EE	0.077 ns	0.133 ns	0.199 **

Reef fishes	June 2007	August 2007	June 2008
Groups	R statistic	R statistic	R statistic
Global	0.122 **	0.100 **	0.184 **
NN vs FC	0.103 ns	0.005 ns	0.137 ns
NN vs EE	-0.030 ns	0.064 ns	-0.071 ns
NN vs ED	-0.084 ns	-0.053 ns	0.261 ns
FC vv EE	0.055 ns	0.171 ns	0.014 ns
FC vs ED	0.256 **	0.180 **	0.263 **
ED vs EE	0.067 ns	-0.077 ns	0.257 **

Table 2.8. Results of SIMPER analyses for each of three sampling periods showing the top five taxa contributing to within-group similarities of larval assemblages associated with each water mass. Percent contributions are listed to the right of each taxon. IN = inshore, NN = nearshore/no eddy, FC = Florida/Loop Current, EE = eddy edge, and ED = eddy.

	June 2007		August 2007		June 2008	
	Taxon	%	Taxon	%	Taxon	%
IN	Clupeoidei	22.71	Clupeoidei	18.33	Clupeoidei	12.7
	Monacanthidae	8.08	Monacanthidae	14.98	Monacanthidae	14.6
	Syngnathidae	6.91	Gerreidae	15.47	Gerreidae	10.78
	Blennioidei	11.63	Atherinidae	21.82	Atherinidae	9.12
	Scombridae	8.25	Hemiramphidae	7.95	Scombridae	8.08
NN	Scombridae	10.45	Scombridae	10.96	Scombridae	8.21
	Carangidae	7.32	Carangidae	7.77	Carangidae	7.8
	Myctophidae	12.09	Bothidae	6.21	Bothidae	7.66
	Gempylidae	7.25	Paralichtyidae	7.2	Gerreidae	7.75
	Serranidae	7.11	Scorpaenidae	5.82	Apogonidae	6.09
FC	Myctophidae	21.71	Myctophidae	13.27	Myctophidae	27.08
	Scombridae	6.18	Scombridae	8.87	Scombridae	10.31
	Bothidae	7.25	Bothidae	6.82	Bothidae	7.3
	Gempylidae	5.96	Gonostomatidae	8.65	Gonostomatidae	11.17
	Serranidae	5.87	Carangidae	7.72	Phosichthyidae	4.65
EE	Paralichtyidae	7.48	Paralichtyidae	12.61	Paralichtyidae	7.42
	Bothidae	6.34	Bothidae	6.46	Bothidae	9.15
	Myctophidae	23.34	Gobiidae	10.38	Myctophidae	16.79
	Gonostomatidae	6.44	Labridae	6.16	Gonostomatidae	5.98
	Gempylidae	6.31	Scorpaenidae	5.78	Scombridae	8.59
ED	Myctophidae	28.17	Myctophidae	13.65	Myctophidae	14.81
	Paralichtyidae	5.52	Paralichtyidae	11.4	Paralichtyidae	13.28
	Bothidae	7.41	Bothidae	7.9	Bothidae	6.72
	Gempylidae	7.95	Gobiidae	7.83	Gobiidae	13.36
	Bregmacerotidae	5.74	Scombridae	8.31	Scorpaenidae	5.82

Table 2.9. Environmental variables that explained the highest amount of variation in the biological data (i.e., larval assemblages) for each of three sampling periods. Tests were conducted with all taxa (top) and reef fishes (bottom). Correlation coefficients are shown with significant values determined by permutation tests. * $p < 0.05$, ** $p < 0.01$, *** $p = 0.001$, ns = not significant.

All taxa	June 2007	August 2007	June 2008
Rho	0.404 ***	0.560 ***	0.424 ***
Variable selection	Temperature	Temperature	Temperature
		Salinity	Salinity
		Fluorescence	
		Distance from shore	
Reef fishes	**June 2007**	**August 2007**	**June 2008**
Rho	0.266 ***	0.560 ***	0.211 ***
Variable selection	Temperature	Temperature	Temperature
	Distance from shore	Salinity	Salinity
		Fluorescence	
		Distance from shore	

Table 2.10. Comparisons of mean (± SE) ages and age ranges for reef fish species during three sampling periods. ED = eddy and FC = Florida/Loop Currents. P-values are based on one-way ANOVAs that compared mean age between water masses. Significant results are in bold with directionality of the difference given in parentheses.

		ED		FC		
Sampling period	Taxon	Mean (± SE) age (d)	Age range (d)	Mean (± SE) age (d)	Age range (d)	
June 2007	*Xyrichtys novacula*	25.00 (0.47)	15 - 35	21.42 (0.59)	16 - 31	**p < 0.001 (FC<ED)**
	Thalassoma bifasciatum	24.28 (0.41)	14 - 35	23.96 (0.64)	16 - 43	p = 0.675
August 2007	*Xyrichtys novacula*	24.58 (0.81)	13 - 40	25.15 (0.74)	16 - 33	p = 0.645
	Thalassoma bifasciatum	19.93 (1.24)	12 - 37	25.25 (0.67)	15 - 42	**p < 0.001 (ED<FC)**
	Cryptotomus roseus	22.21 (0.46)	15 - 40	27.11 (0.84)	14 - 35	**p < 0.001 (ED<FC)**
	Sphyraena barracuda	14.17 (0.32)	11 - 20	14.68 (0.38)	9 - 20	p = 0.308
	Stegastes partitus	12.68 (0.86)	8 - 21	12.05 (0.39)	9 - 23	p = 0.448
June 2008	*Cryptotomus roseus*	22.23 (0.97)	13 - 34	29.10 (1.07)	14 - 43	**p < 0.001 (ED<FC)**

Figure 2.1.Sampling station locations (black points) in the Straits of Florida shown for each of three sampling periods. Transects are labeled according to region: UK = upper Keys, MK = middle Keys, LK = lower Keys, MQ = Marquesas, and LC = Loop Current.

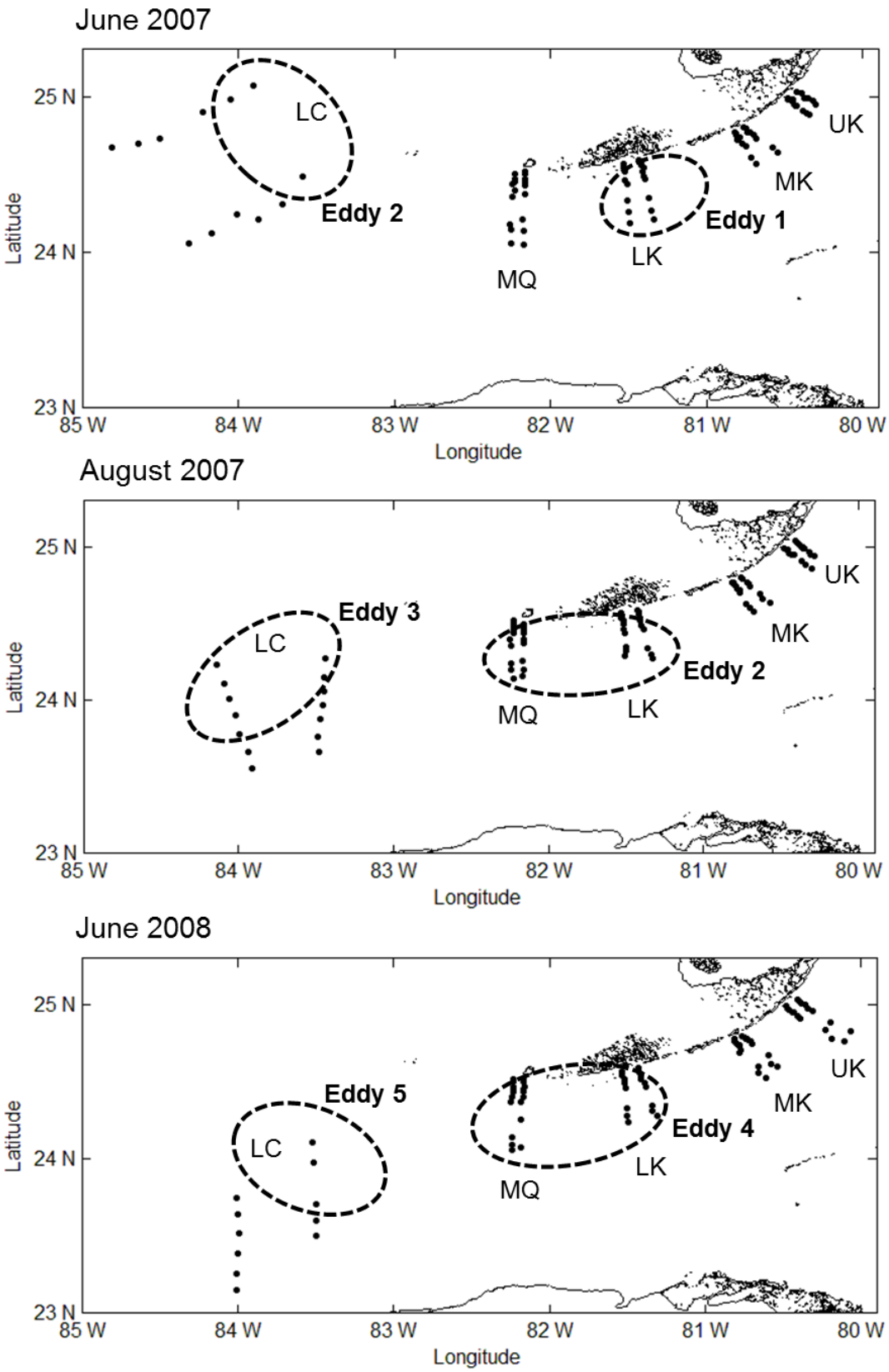
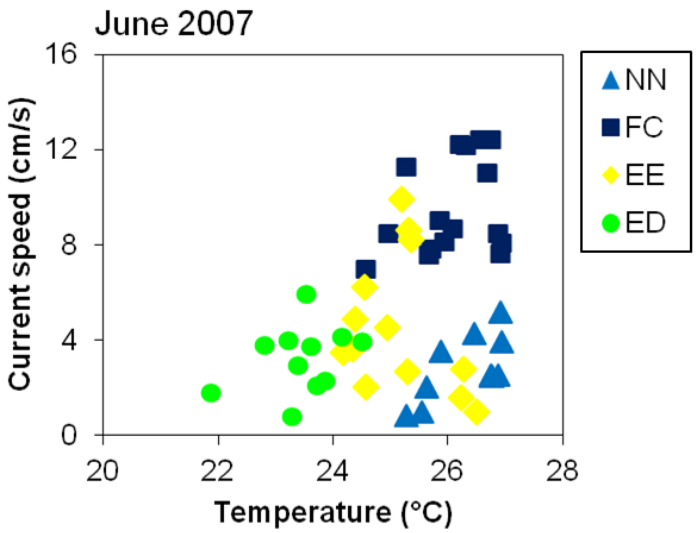
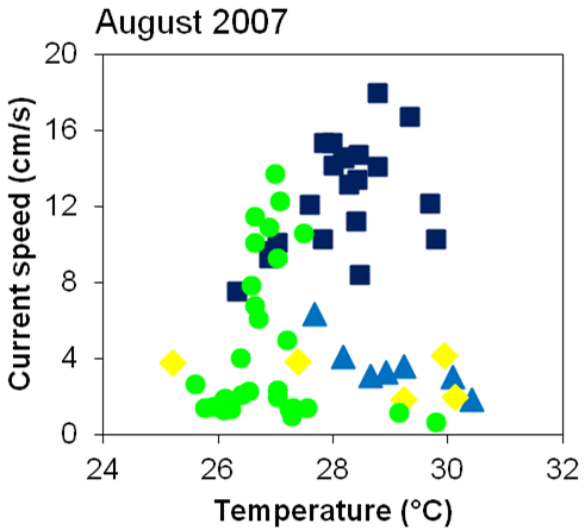

June 2007
LC
Eddy 2
Eddy 1
MQ
LK
MK
UK
25 N
24 N
23 N
Latitude
85 W
84 W
83 W
82 W
81 W
80 W
Longitude
August 2007
Eddy 3
LC
Eddy 2
MQ
LK
MK
UK
25 N
24 N
23 N
Latitude
85 W
84 W
83 W
82 W
81 W
80 W
Longitude
June 2008
Eddy 5
LC
Eddy 4
MQ
LK
MK
UK
25 N
24 N
23 N
Latitude
85 W
84 W
83 W
82 W
81 W
80 W
Longitude

Figure 2.2. Plots illustrating variations in current speed and temperature among sampling stations, coded by water mass designation for each of three sampling periods. NN = nearshore/no eddy, FC = Florida/Loop Current, EE = eddy edge, and ED = eddy. Temperatures at each station were averaged across the water column (2-80 m) and current speeds determined from the first depth bin of ADCP data (16-24 m).


June 2007
Current speed (cm/s)
Temperature (°C)
NN
FC
EE
ED


August 2007
Current speed (cm/s)
Temperature (°C)

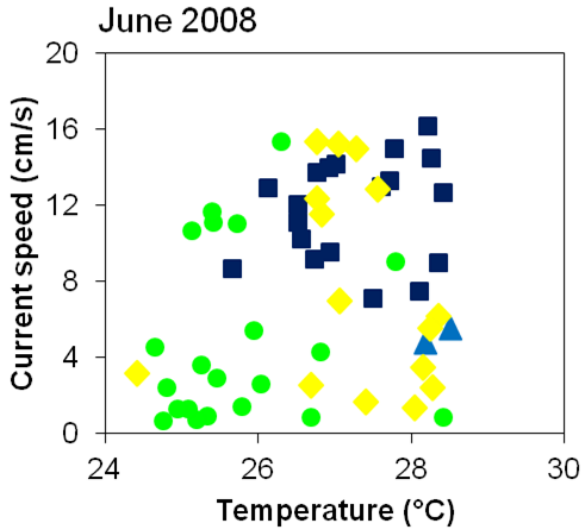
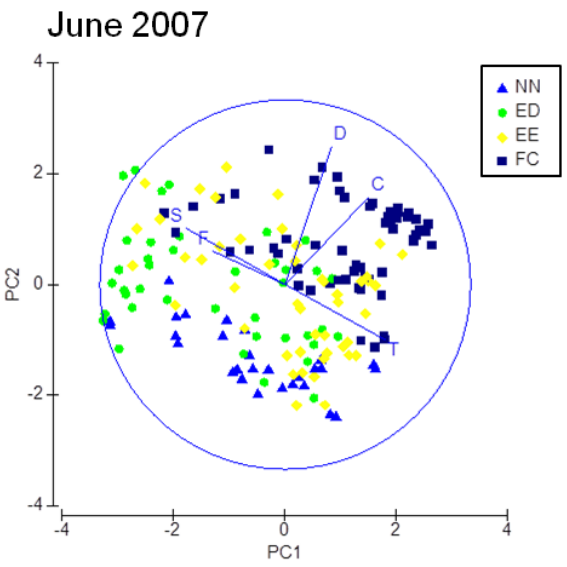
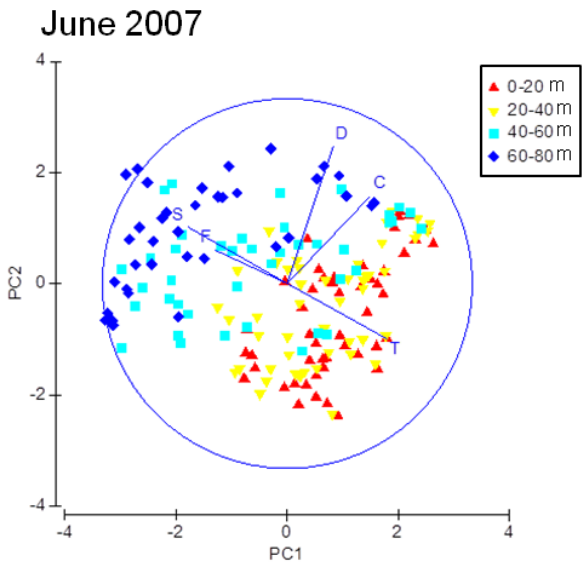
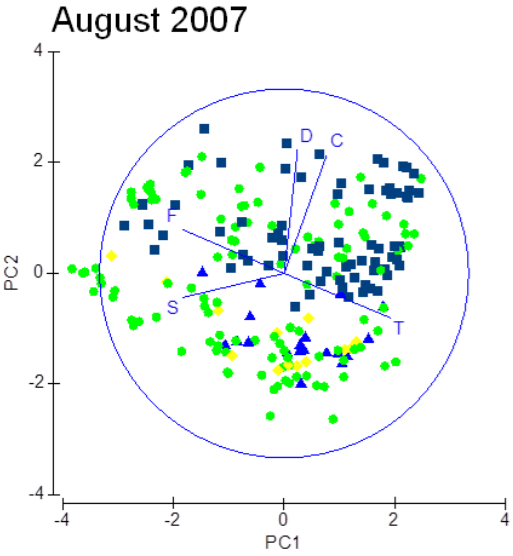
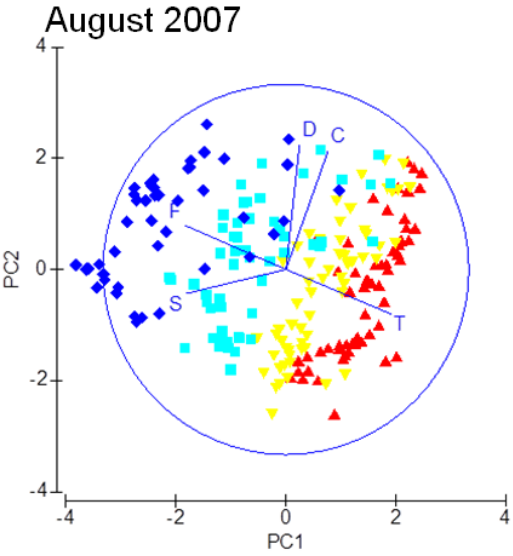

June 2008
Current speed (cm/s)
Temperature (°C)

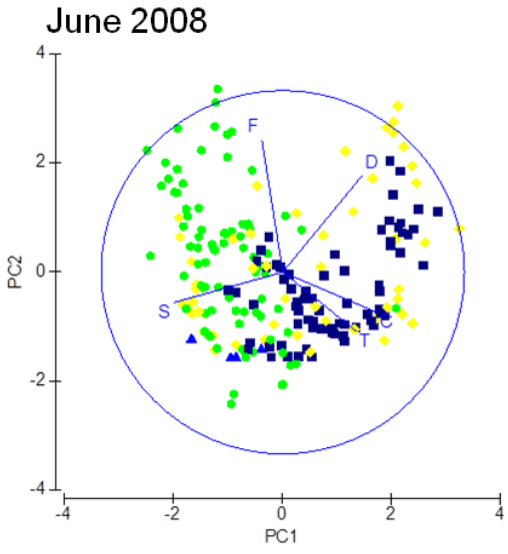
Figure 2.3. PCA ordinations for each of three sampling periods shown with eigenvectors superimposed for each environmental variable (T = temperature, S = salinity, F = fluorescence, C = current speed, and D = distance from shore). Samples, color-coded by water mass designation (left) or depth bin (right), are overlaid on each plot. NN = nearshore/no eddy, FC = Florida/Loop Current, EE = eddy edge, and ED = eddy.

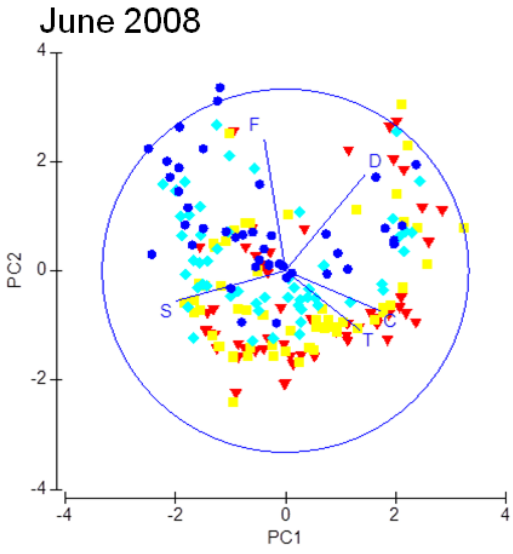

June 2007
NN
ED
EE
FC
D
C
S
F
T
PC1
PC2


June 2007
0-20 m
20-40 m
40-60 m
60-80 m
D
C
S
F
T
PC1
PC2


August 2007
D
C
F
S
T
PC1
PC2


August 2007
D
C
F
S
T
PC1
PC2


June 2008
F
D
S
T
C
PC1
PC2


June 2008
F
D
S
T
C
PC1
PC2

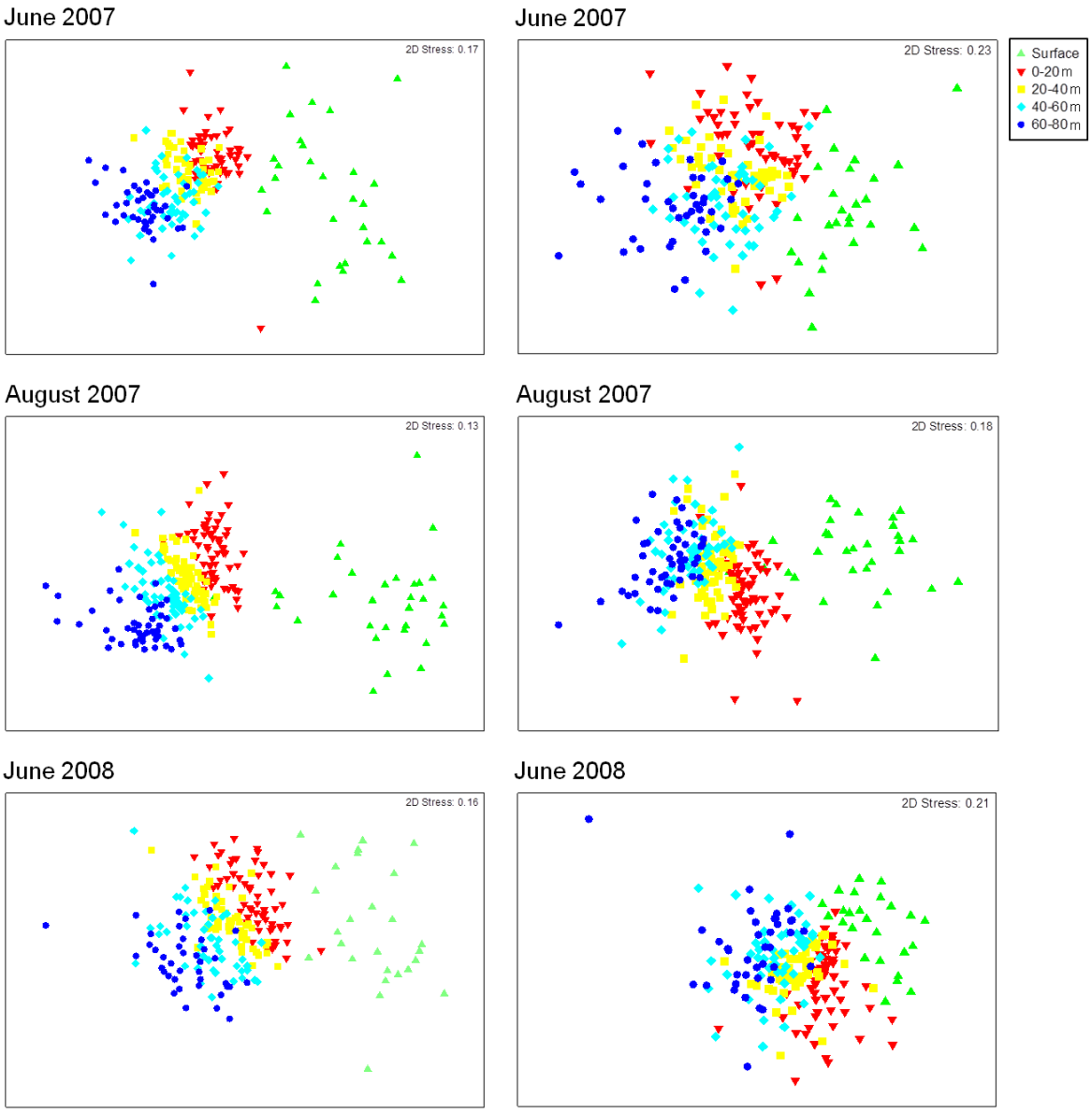


Figure 2.4. Non-metric multidimensional scaling plots illustrating vertical structure in larval assemblages consisting of all taxa (left) and of only reef fishes (right) across each of three sampling periods. Stress values are indicated in the upper-right corner of each plot. Samples color-coded by depth, but note that surface samples are exclusively IN stations.

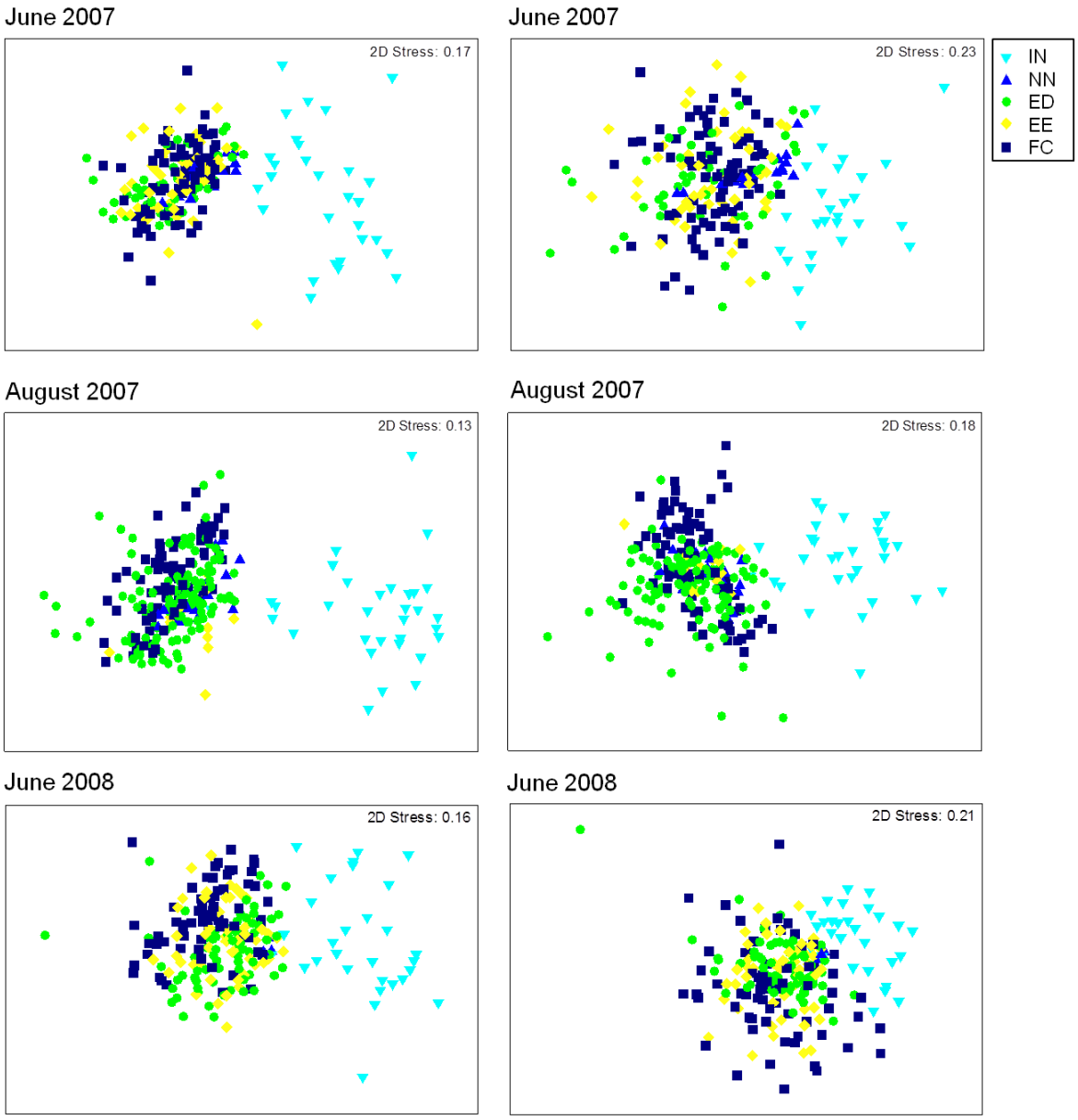


Figure 2.5. Non-metric multidimensional scaling plots illustrating horizontal structure in larval assemblages consisting of all taxa (left) and only of reef fishes (right) across each of three sampling periods. Stress values are indicated in the upper-right corner of each plot. Samples color-coded by water mass. IN = inshore, NN = nearshore/no eddy, ED = eddy, EE = eddy edge, and FC = Florida/Loop Current.

Figure 2.6. Mean (± SE) larval concentration of all taxa combined shown by depth for each water mass during each of three sampling periods. IN = inshore, NN = nearshore/no eddy, ED = eddy, EE = eddy edge, and FC = Florida/Loop Current. N/A indicates that no samples were collected at these depths.

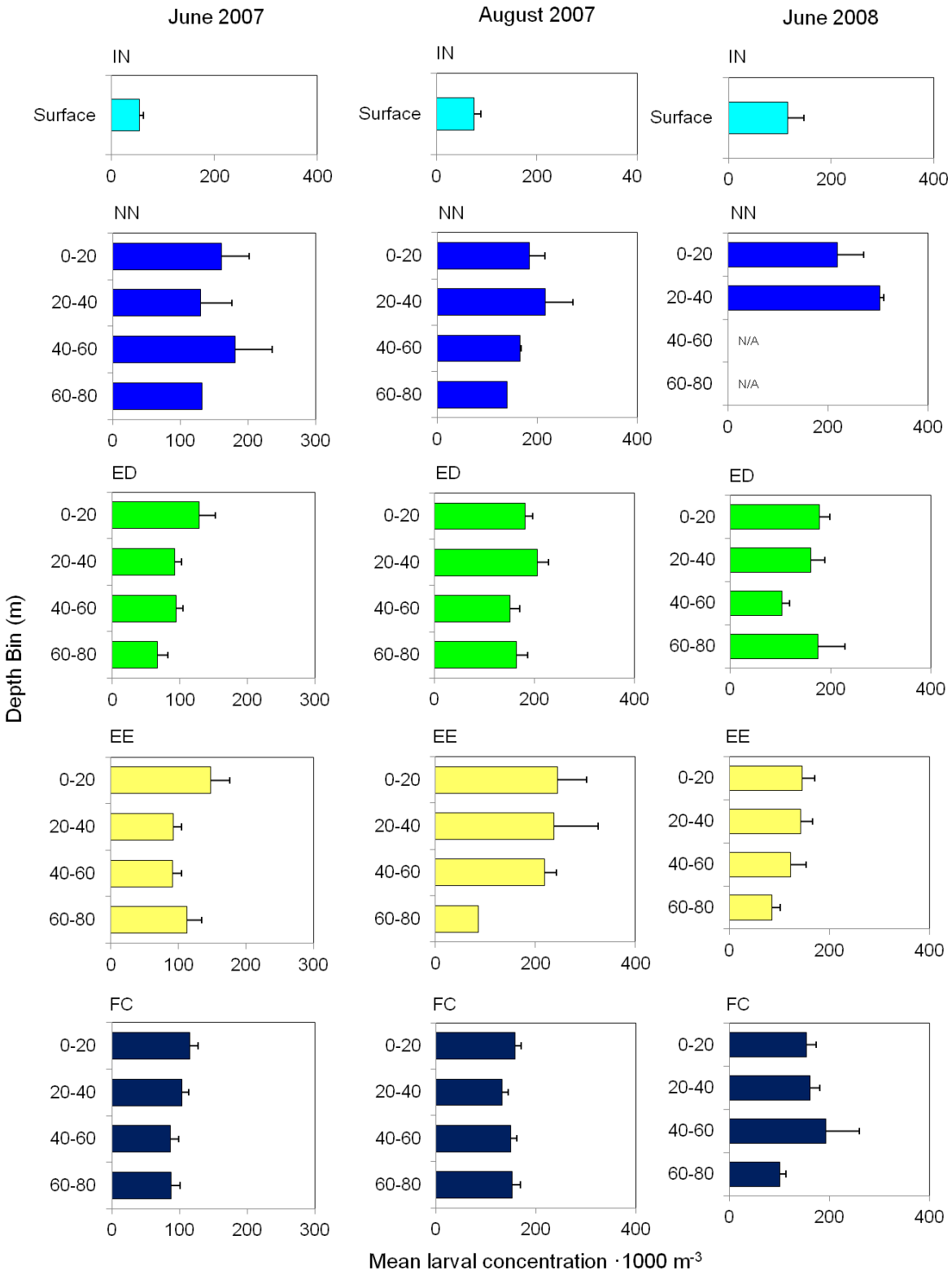

June 2007
August 2007
June 2008
IN
Surface
NN
0-20
20-40
40-60
60-80
N/A
ED
EE
FC
Depth Bin (m)
Mean larval concentration ·1000 m-3

Figure 2.7. Mean (± SE) larval concentration of reef fishes combined shown by depth for each water mass during each of three sampling periods. IN = inshore, NN = nearshore/no eddy, ED = eddy, EE = eddy edge, and FC = Florida/Loop Current. N/A indicates that no samples were collected at these depths.

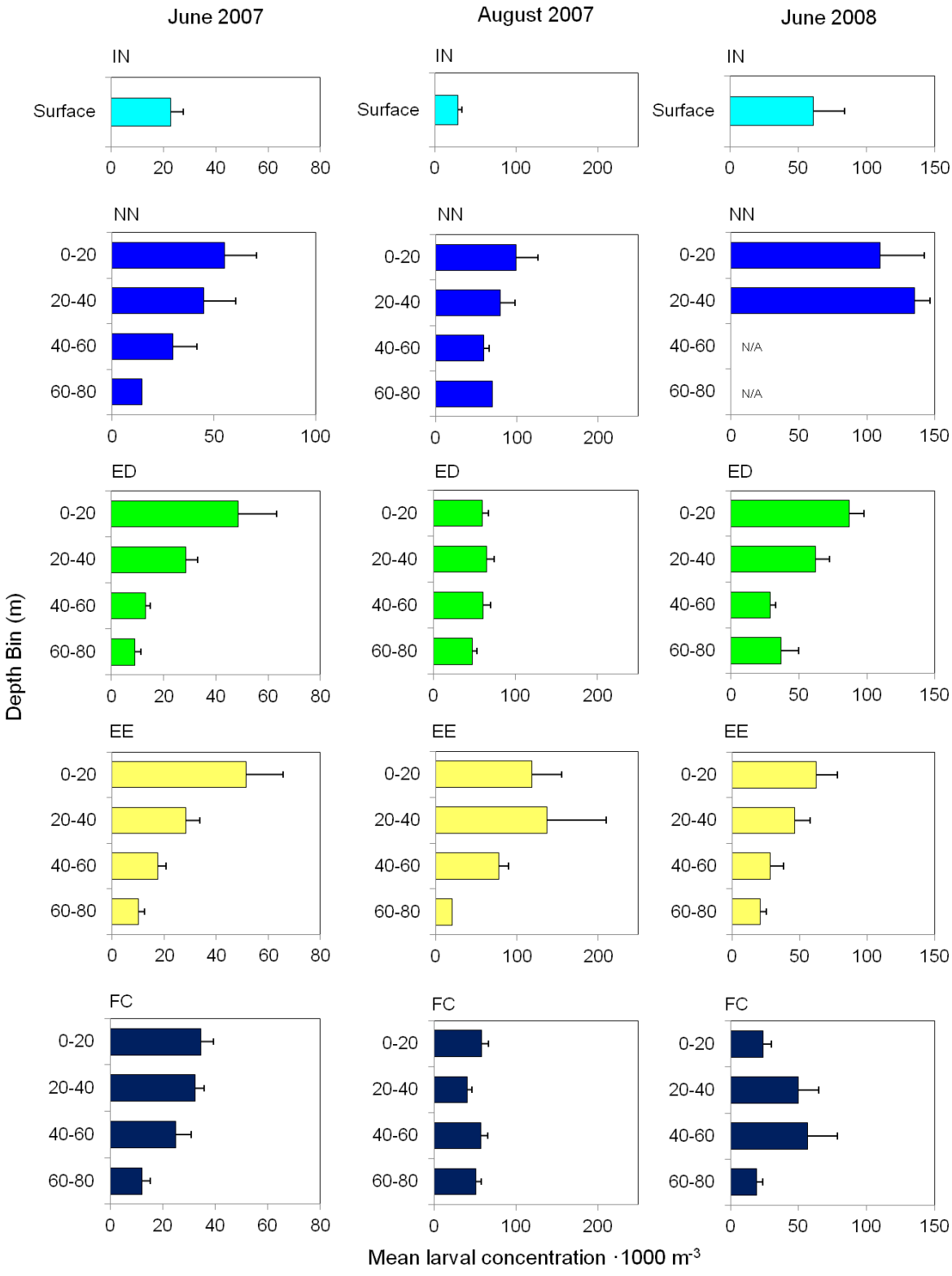

June 2007
August 2007
June 2008
IN
Surface
0
20
40
60
80
0
100
200
0
50
100
150
NN
0-20
20-40
40-60
60-80
0
50
100
0
100
200
N/A
N/A
ED
EE
FC
Depth Bin (m)
Mean larval concentration ·1000 m-3

Figure 2.8. Mean (± SE) larval abundance of all taxa combined for each water mass during each of three sampling periods. IN = inshore, NN = nearshore/no eddy, ED = eddy, EE = eddy edge, and FC = Florida/Loop Current. Letters denote significant differences resulting from a Kruskal-Wallis test.

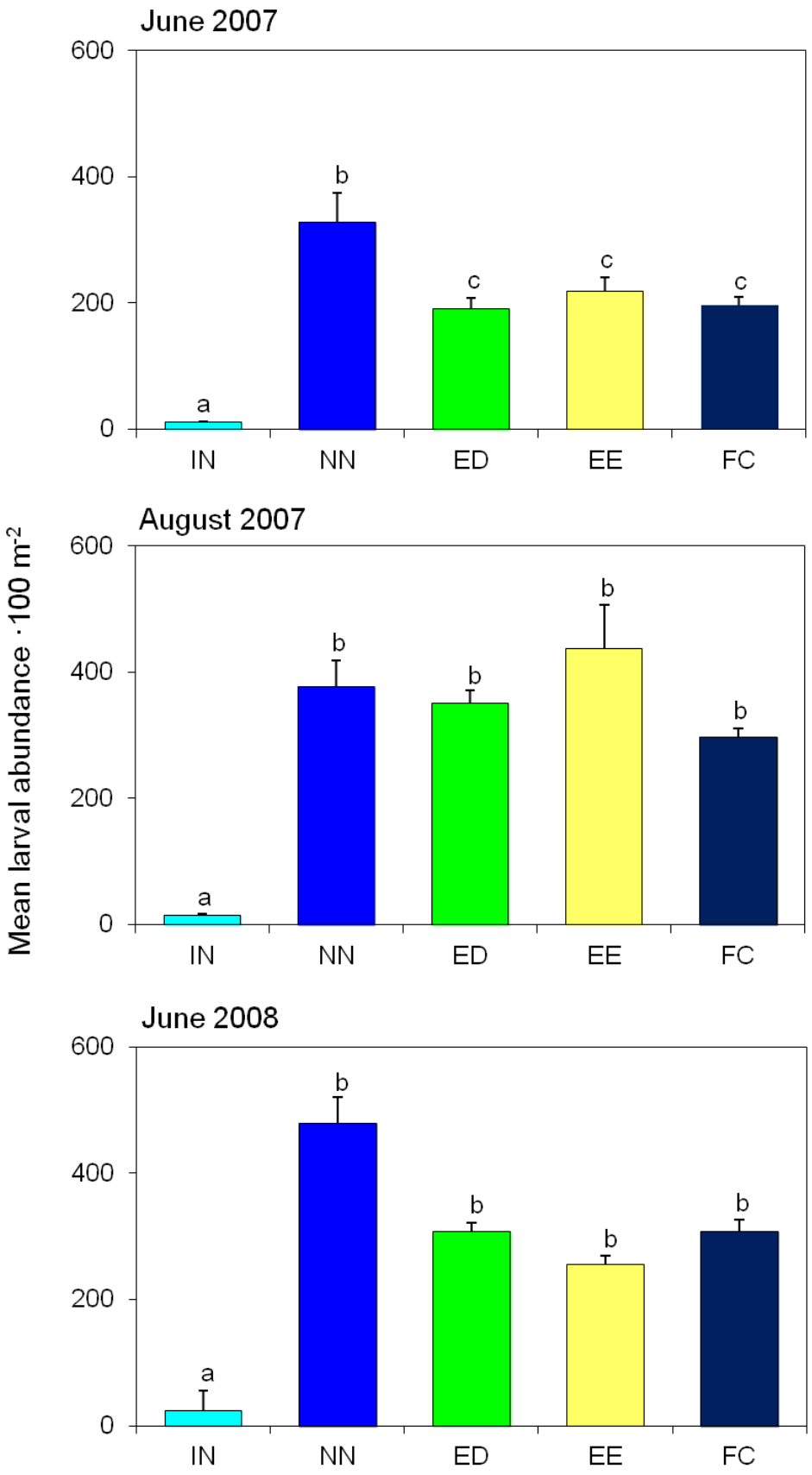
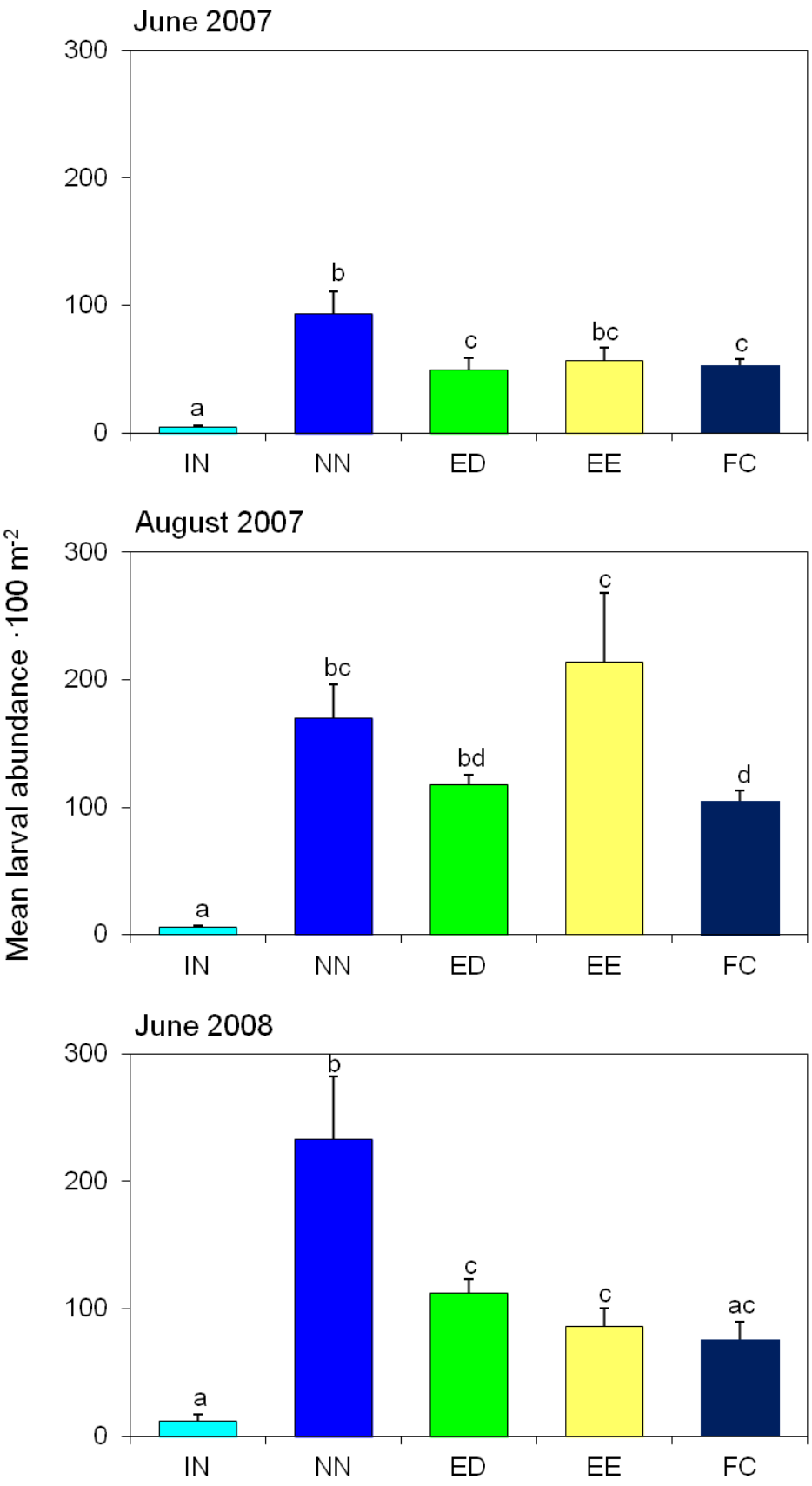

June 2007
600
400
200
0
a
b
c
c
c
IN
NN
ED
EE
FC
August 2007
Mean larval abundance ·100 m-2
600
400
200
0
a
b
b
b
b
IN
NN
ED
EE
FC
June 2008
600
400
200
0
a
b
b
b
b
IN
NN
ED
EE
FC

Figure 2.9. Mean (± SE) larval abundance of reef fishes combined for each water mass during each of three sampling periods. IN = inshore, NN = nearshore/no eddy, ED = eddy, EE = eddy edge, and FC = Florida/Loop Current. Letters denote significant differences resulting from a Kruskal-Wallis test.


June 2007
300
200
100
0
a
b
c
bc
c
IN
NN
ED
EE
FC
August 2007
Mean larval abundance ·100 m-2
300
200
100
0
a
bc
bd
c
d
IN
NN
ED
EE
FC
June 2008
300
200
100
0
a
b
c
c
ac
IN
NN
ED
EE
FC

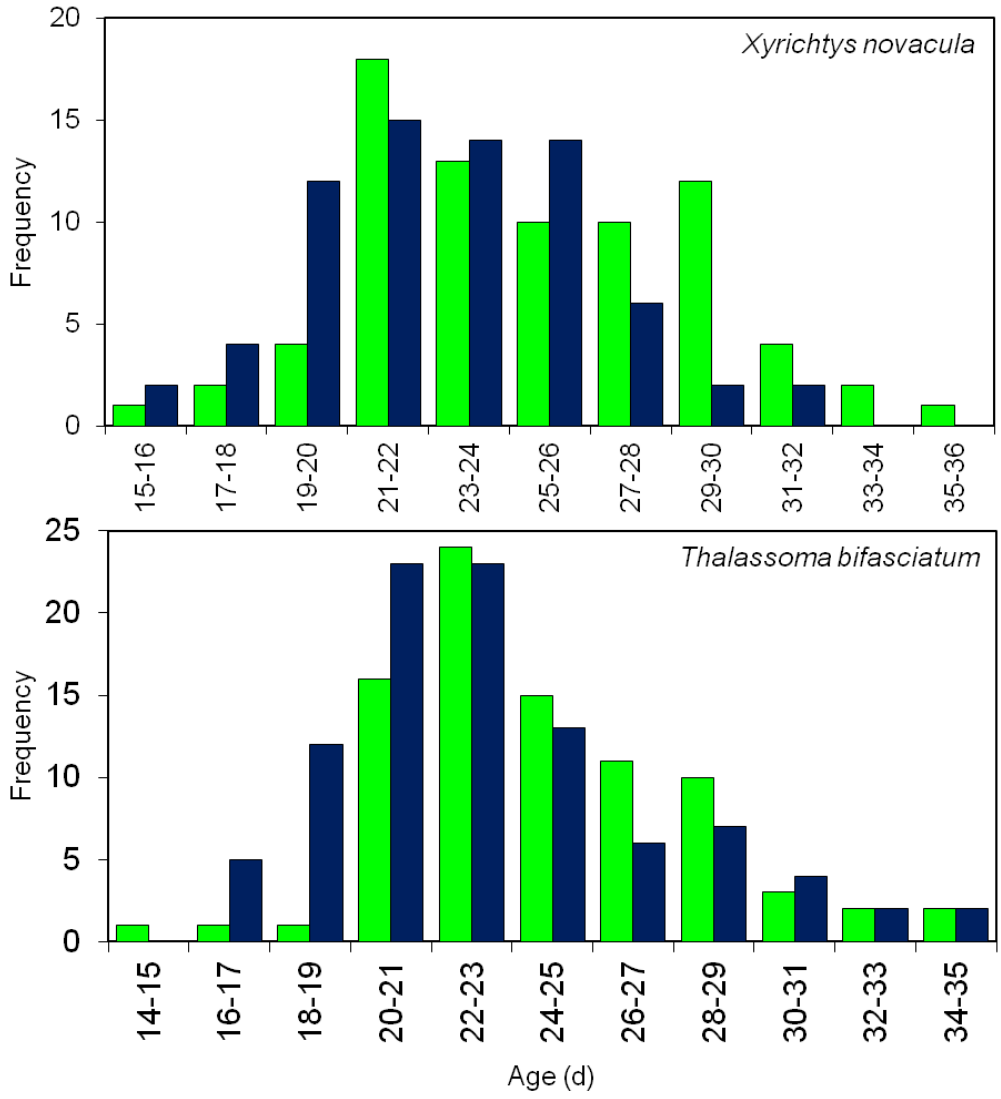
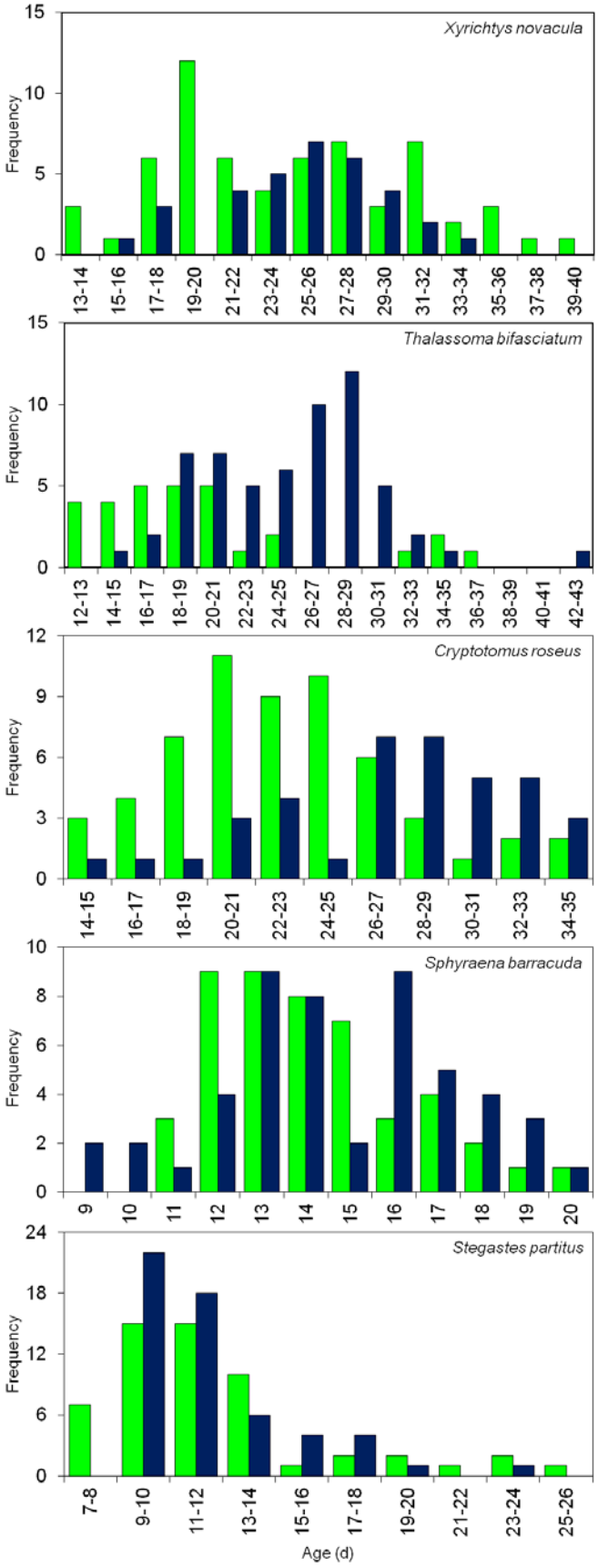


Figure 2.10. Age distributions for larvae sampled in ED (green) versus FC (blue) water masses in June 2007. ED = eddy and FC = Florida/Loop Current.

Figure 2.11. Age distributions for larvae sampled in ED (green) versus FC (blue) water masses in August 2007. ED = eddy and FC = Florida/Loop Current.


Xyrichtys novacula
Frequency
13-14
15-16
17-18
19-20
21-22
23-24
25-26
27-28
29-30
31-32
33-34
35-36
37-38
39-40
Thalassoma bifasciatum
12-13
14-15
16-17
18-19
20-21
22-23
24-25
26-27
28-29
30-31
32-33
34-35
36-37
38-39
40-41
42-43
Cryptotomus roseus
Sphyraena barracuda
Stegastes partitus
7-8
9-10
11-12
13-14
15-16
17-18
19-20
21-22
23-24
25-26
Age (d)

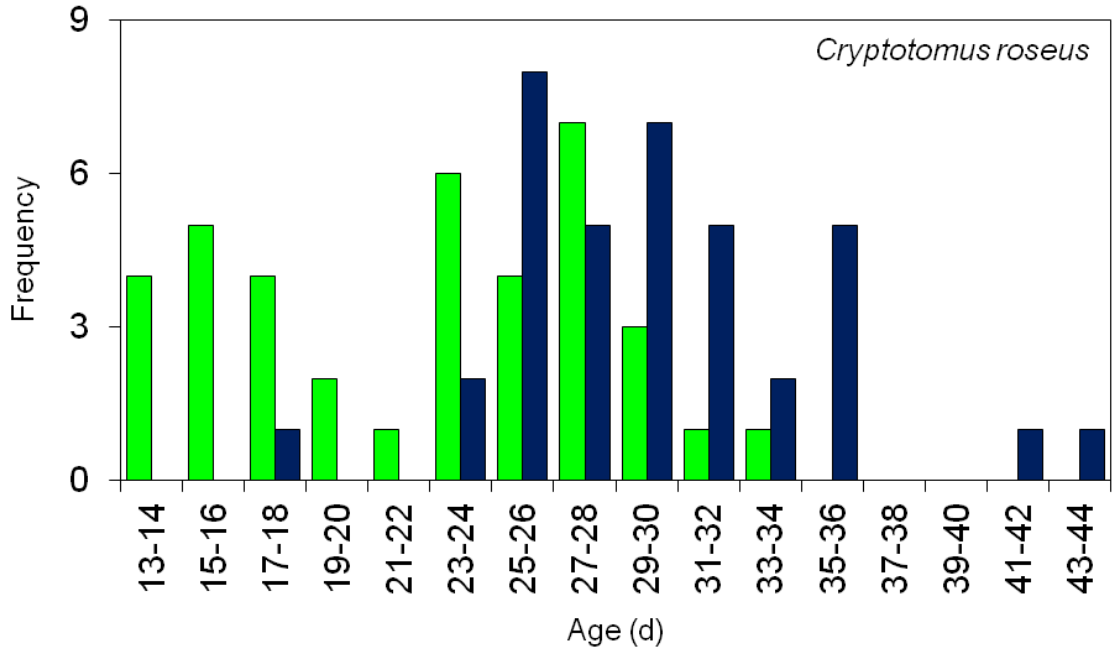


Figure 2.12. Age distributions for larvae sampled in ED (green) versus FC (blue) water masses in June 2008. ED = eddy and FC = Florida/Loop Current.

Chapter 3. Influence of mesoscale eddies on larval reef fish distributions and growth rates

Background

Mesoscale eddies as "ocean triads"

Mesoscale eddies (ME) are ubiquitous features in the world's oceans with circulation patterns that are both spatially and temporally dynamic. With diameters on the order of hundreds of kilometers and temporal scales ranging from weeks to months, the physical processes associated with MEs can have major impacts on biological systems (McGillicuddy et al. 1998, Bakun 2006). Specifically, the dynamics of MEs may generate planktonic habitats that fulfill the requirements of the "ocean triad hypothesis" (Bakun 1996). According to this hypothesis, the survival of fish larvae and subsequent recruitment success is contingent upon the co-occurrence of three key processes: nutrient enrichment, concentration of prey fields, and retention of fish larvae near suitable settlement habitat.

MEs exhibit zones of upwelling and divergence as well as downwelling and convergence, with the location of such zones driven by eddy rotation (i.e. cyclonic versus anticyclonic) and stage of development ("spinning up" versus "spinning down", Bakun 2006). In zones of upwelling, nutrients are injected into surface waters leading to increases in primary production which are particularly important in otherwise oligotrophic environments (McGillicuddy et al. 1998). In zones of downwelling and convergence, planktonic organisms capable of maintaining vertical position accumulate. Thus, MEs not only drive increases in production, they can also concentrate prey fields. In addition, the flow fields of MEs embedded within larger scale current patterns can significantly alter transport pathways and affect levels of local-retention. For instance,

fish larvae entrained within a ME propagating along the shoreward side of a western boundary current may be retained closer to shore, avoiding advection offshore and rapid transport downstream. This potential for enhanced retention completes the sequence of an "ocean triad." Thus, in terms of nutrient enrichment, concentration of prey, and retention near suitable settlement sites, MEs represent potentially important habitat for larval fishes.

An increasing body of empirical data is consistent with the notion that MEs can function as "ocean triads." Numerous studies have shown how the upwelling dynamics of eddies can support increased primary productivity (Yoder et al. 1981, McGillicuddy et al. 1998, Hitchcock et al. 2005, Crawford et al. 2007). Importantly, these increases in primary production can be transferred to higher trophic levels (copepods: Lee et al. 1994, Lane et al. 2003, micronekton: Sabarros et al. 2009, penguins: Cotte et al. 2007, frigate birds and tunas: Kai and Marsac 2010). Predators exploiting prey populations in MEs have been frequently observed feeding in areas of convergence (e.g., eddy edges, Kai and Marsac 2010, Sabarros et al. 2009), suggesting that both the nutrient enrichment and concentration of prey provided by MEs are important to a diversity of organisms. Several studies also underscore the importance of MEs in the retention of both zooplankton and ichthyoplankton (Lobel and Robinson 1986, Chiswell and Roemmich 1998, Condie et al. 2011). However, once fish larvae are entrained into a ME they can be transported towards as well as away from suitable habitat (Mackas and Coyle 2005, Sponaugle et al. 2005, Adams et al. 2011). In either case, these mesoscale features can impose significant variability upon patterns of larval settlement and recruitment (Myers and Drinkwater 1989, Sponaugle et al. 2005, Satoh 2010).

Mesoscale eddies in the Straits of Florida

The passage of cyclonic MEs through the Straits of Florida (SOF) is well-documented (Lee et al. 1992, Lee et al. 1994, Fratantoni et al. 1998, Hitchcock et al. 2005, Kourafalou and Kang 2012). These eddies form and propagate along the front of the Loop Current (LC) as it flows in a large meander through the Gulf of Mexico (Fratantoni et al. 1998). Upon entering the SOF, the LC becomes the Florida Current (FC) and MEs are often referred to regionally as 'Tortugas eddies'. These MEs significantly alter the oceanographic environment, particularly in the western SOF where the continental shelf is wider and eddy propagation speeds are slower than those in the eastern SOF. Thus, residence times for eddies in the western SOF can be on the order of weeks. As the SOF narrows in the vicinity of the middle Keys, the MEs elongate, speed up, and sheer apart, often forming a series of sub-mesoscale eddies. The passage of a ME through the SOF leads to increased nutrient levels at the eddy core, increased primary production, and increased abundances of copepod nauplii and slipper lobster larvae (Lee et al. 1992, Lee et al. 1994, Hitchcock et al. 2005). This collective research suggests that MEs in the SOF may serve as "ocean triads" in terms of nutrient enrichment and concentration of prey, and there has been much speculation upon the role that MEs play on the delivery of fish larvae to reefs of the Florida Keys. While research has shown that the passage of eddies is associated with large pulses of settlement to reefs in the upper Keys (Sponaugle et al. 2005, D'Alessandro et al. 2007), there is a paucity of data based on direct sampling of ichthyoplankton within MEs. To assess the role of MEs on the supply and settlement of reef fish to the Florida Keys, data are needed on the composition

and abundances of the larval assemblages in MEs as well as on relative growth rates of larvae inside and outside of these eddies.

Effects of MEs on larval assemblages, abundances, and growth

The larval assemblages associated with MEs will depend upon the extent to which the timing and location of spawning is coincident with the formation or passage of an eddy and the chance encounter of a ME with another water mass which contains fish larvae. Once larvae are entrained in an eddy, they must feed and avoid predation to survive. Thus, multiple factors, including entrainment and subsequent survival, will ultimately shape the larval assemblage present in a given eddy. Depending on the regularity of MEs (e.g., Wu and Chiang 2007) and how this timing interacts with life history strategies of fish populations (e.g., timing and location of spawning), certain components of the eddy larval assemblage may be consistent and predictable. However, other constituents of the eddy larval assemblage may appear and disappear episodically. Regardless, it is likely that the larval assemblage in an eddy will be significantly different from that in surrounding waters since MEs alter both the physical and biological environment as they propagate (e.g., Ring Group 1981, Paterson et al. 2008, Govoni et al. 2010, Kuo and Chern 2011). For example, cyclonic eddies can increase the intensity of the thermocline and shift it to a shallower location in the water column (Chen et al. 2011). In addition, water masses entrained into a propagating eddy can be modified as that water mass interacts with the dynamics of the ME (e.g., chlorophyll *a*, Kasai et al. 2002). Thus, eddy larval assemblages experience an environment unique from that found in surrounding waters.

Eddies also have the potential to alter patterns of larval abundance. Retention and concentration of larvae in zones of convergence within an eddy may increase abundances relative to surrounding waters. In addition, larvae entrained in the productive waters of an eddy may be buffered from starvation and, therefore, experience less mortality. However, it has also been shown that many marine predators target high productivity "hot spots" such as MEs and so predation may be more intense for fish larvae in eddies (Cotte et al. 2007, Sabarros et al. 2009, Kai and Marsac 2010). Patterns of larval abundance will ultimately be shaped by the timing and strength of entrainment, retention, and survival. Depending on the interaction of these factors, patterns of larval abundance will most likely be taxon-specific and spatially and temporally variable.

Finally, because of the increased productivity associated with MEs, these planktonic habitats likely provide enhanced feeding opportunities and, thus, may lead to faster growth in larval fishes. Productivity within an eddy will likely vary over time as the input of nutrients is balanced by grazing or sinking of phytoplankton (Kasai et al. 2002). Thus, the prey field of fish larvae (i.e., secondary productivity) should vary over time as well (Govoni et al. 2010). Recent work has shown that many larval reef fishes have specific dietary preferences (Llopiz and Cowen 2009). Therefore, for MEs to enhance larval fish feeding there must be increases in abundance of particular food items. For a range of larval reef fishes this would include calanoid, harpacticoid, and cyclopoid copepods, copepod nauplii, and appendicularians (Llopiz and Cowen 2009). Due to the complex trophic dynamics in eddies, which will vary temporally and spatially, the feeding environment for larval fishes may also be variable. To date, the hypothesis that

residence in an eddy leads to higher larval growth rates is largely untested (for an exception see Nakata et al. 2000).

The objective of the current study was to use direct sampling of MEs in the SOF to determine the influence of eddies on larval reef fish (1) assemblages, (2) abundances, and (3) growth rates. Patterns in larval distribution and growth could have significant implications for transport of larvae through the SOF, retention of larvae near suitable settlement habitat, and survival of larvae to the juvenile stage. The overarching goal of this study was to elucidate the role of MEs in shaping settlement and recruitment of reef fishes in the Florida Keys.

Materials and Methods

Field sampling

Sampling was conducted aboard the R/V Walton Smith during three 16-day cruises in the summers of 2007 (May 29 - June 13 and July 30 - August 13) and 2008 (June 17 - July 1). During each cruise, ichthyoplankton samples were collected along ten cross-shelf transects (see Chapter 2 Figure 2.1). Transects spanned the SOF, from the upper Keys to the Marquesas, and intercepted the LC as it entered the SOF. Along each transect ten stations were sampled, with four stations inside or over the reef tract and six stations outside the reef tract, extending into the FC. In the summer of 2007 additional stations were sampled after all transects were completed on a zigzag track that ran alongshore from the lower to the upper Keys. At each station an ichthyoplankton tow was completed using one of two net types as determined by bottom depth. A modified Multiple Opening Closing Net and Environmental Sensing System (MOCNESS, Guigand et al. 2005) was used outside of the reef tract while an inshore frame net (i.e., modified

neuston net) was employed at the shallower stations. The MOCNESS sampled from discrete 20 m depth bins down to 80 m using paired nets (4 m^2 and 1 m^2) fitted with 1-mm and 150-μm mesh, respectively. The inshore frame net fished approximately 1 m below the surface using paired nets (2 m^2 and 0.5 m^2) fitted with 1-mm and 150-μm mesh, respectively. Flowmeters were attached to both the MOCNESS and the inshore frame net to determine the volume sampled during each net tow. All ichthyoplankton tows were conducted during daylight hours, excluding dawn and dusk. Samples were preserved immediately in 95% ethanol, and transferred to 70% ethanol upon returning to the laboratory. All ichthyoplankton samples collected with the large-mesh nets (i.e., 1 mm) were processed by separating all fish larvae from other plankton, and identifying each specimen to the lowest possible taxonomic grouping with reference to a regional ichthyoplankton guide (Richards 2006). We limited our analyses spatially to samples collected along transects in the western SOF (i.e., offshore of the lower Keys, Marquesas Keys, and in the LC). This was based on the observation that MEs, the focus of our study, form more coherent structures and have longer residence times in the western SOF.

The water column was sampled using a ship-mounted 76.8 kHz RD Instruments Acoustic Doppler Current Profiler (ADCP). Sensors attached to the plankton sampling system collected information on temperature, salinity, and fluorescence. Two Lagrangian drifters drogued at 15 m were deployed during each cruise to aid in the delineation of MEs (Technocean).

Otolith analysis

Based on sample sizes and the ability to identify individuals to the species level five species of reef fish were chosen for otolith analysis: *Xyrichtys novacula* (pearly

razorfish), *Thalassoma bifasciatum* (bluehead wrasse), *Cryptotomus roseus* (bluelip parrotfish), *Sphyraena barracuda* (great barracuda), and *Stegastes partitus* (bicolor damselfish). Otolith analysis was conducted on a subset of fish from each species to obtain growth rates and ages. The abundance and size distribution of the fish used for otolith analysis was roughly proportional to that of the larvae in each sample. Standard length (SL) or notochord length (NL) was measured to the nearest 0.01 mm for each fish using a Leica MZ12 dissecting microscope, a Cool Snap-Pro monochrome digital camera, and Image-Pro Plus 4.5 image analysis software (Media Cybernetics). Sagittal (*X. novacula*, *T. bifasciatum*, and *C. roseus*) or lapillar (*S. partitus*) otoliths were dissected from each sample and stored in immersion oil ~ 7-14 d to facilitate reading. The lapillar otoliths of *S. barracuda* were dissected and sectioned to facilitate reading. Specifically, each otolith was mounted in crystal-bond thermoplastic glue on a glass microscope slide and polished down to the primordium (i.e., otolith core; using P2000 silicon-carbide abrasive paper, Nihonkenshi; D'Alessandro et al. 2010). All otoliths from a given species were analyzed by a single reader. Otoliths were read along the longest axis at 400X magnification (with the exception of *S. barracuda* lapilli which were read at 1000X magnification) through a Leica DMLB microscope and with the aid of the digital camera and Image-Pro Plus software. All otoliths were read at least twice, and if the reads differed by ≤ 5%, one read was randomly chosen for analysis. If reads differed by > 5%, a third read was conducted. This third read was then compared to the first two reads. If either comparison differed by ≤ 5%, one read from that comparison was randomly chosen for analysis; otoliths where all reads differed by > 5% were removed from any further analysis (Sponaugle 2009).

Data analysis

The presence and position of MEs in the SOF was determined using a suite of physical data. Eddies were first identified and their approximate location determined using a combination of satellite images, model outputs, and current fields. Then, station locations and drifter tracks were overlaid onto plots of temperature-at-depth contours. The signal of upwelling at the core of each eddy was clearly visible in these plots as a low temperature isotherm at 50 m (June 2007) or 70 m (August 2007 and June 2008), which was consistent with eddy locations determined in the first step (e.g., satellite imagery). This upwelling of cold water in the core has been previously documented for MEs in the SOF (Lee et al. 1992, Lee et al. 1994). Stations falling within the 24°C isotherm (i.e., the cold eddy core) were classified as eddy (ED) stations, and those falling outside the 25°C isotherm were designated no eddy (NE) stations. As it is challenging to delineate precise eddy boundaries, stations outside of the cold-core but potentially still located within the eddy (i.e., stations between the 24°C and 25°C isotherms) were excluded from the analysis. Consequently, our ED and NE groupings were conservative and also did not include the areas of convergence potentially located at the eddy edges. The NE grouping corresponds to the FC stations in Chapter 2 that are located on the LK, MQ, and LC transects. To corroborate the station designations and determine the validity of the groupings, temperature profiles were plotted for each station and compared between the ED and NE groups.

Temperature, salinity, and fluorescence values were calculated for each station by averaging over the water column (i.e., 2 - 80 m). Average surface current velocity was calculated using the first bin of data obtained with the ADCP (i.e., 8 - 24 m). Finally,

plankton displacement volume was determined using standard techniques (Postel et al. 2000) for samples from the small-mesh nets (i.e., 150 μm) collected from the most shallow depth bin (i.e., 0 - 20 m) at each station for the top 20 m of the water column. To compare the environments experienced by ED and NE fish, temperature, salinity, fluorescence, current speed, and plankton displacement volume were compared between ED and NE stations using one-way ANOVAs.

Larval counts were standardized to the volume of water sampled by each net. Resulting abundances were $\log_{(x+1)}$ transformed to reduce the influence of the most common taxa and families contributing to <5% of any one sample were removed to reduce the influence of the most rare taxa on the interpretation of data. Larval reef fish assemblages (in contrast to all taxa assemblages) were compared between ED and NE groups by first creating a Bray-Curtis similarity matrix between station pairs and then performing an ANOSIM analysis (Primer v6, Clarke and Gorley 2006). ANOSIM is analogous to ANOVA in that it compares within-group variation (i.e., similarities) to between-group variation (i.e., similarities). This is accomplished using the Bray-Curtis matrix and a non-parametric permutation test, thus, assumptions of normality and homoscedasticity are not required (Clarke 1993). The ANOSIM procedure calculates an R statistic that generally ranges in value from 0 to 1, where 1 signifies that all samples within a group are more similar to each other than they are to any sample from another group. Conversely, an R statistic of 0 indicates that similarities between samples within a group are the same as similarities between samples from different groups. As the results of a permutation test are influenced by sample size, it is important to examine both the p-value and R statistic generated from each ANOSIM. Comparisons among R statistics can

often be more biologically- relevant than comparisons among p-values, and statistically significant R statistics with near-zero values should be interpreted with caution. In cases where ANOSIM analyses indicated significant difference between ED and NE larval assemblages, we employed the SIMPER procedure to identify the taxa responsible for these differences. SIMPER uses the Bray-Curtis similarity matrix to determine percent contributions from each taxon to the differences between groups In addition to these comparisons between ED and NE assemblages we were able to investigate the temporal variation in an ED assemblage using Eddy 2. Eddy 2 was sampled in June and August 2007 so we examined differences in larval assemblages between sampling periods for ED stations from Eddy 2 using ANOSIM and SIMPER.

Larval distributions of each target species were compared between ED and NE groups using the delta approach (Serafy et al. 2007). This method deals with the high abundance of zero values in our data by first analyzing patterns in larval frequency of occurrence and then, for all positive samples, examining larval abundances. Frequency of occurrence was calculated for each 20 m depth bin and species-specific distributions were compared between ED and NE groups using two-way chi-square tests. Mean larval abundance was compared between ED and NE groups for each 20 m depth bin using Kruskal-Wallis tests as data did not conform to assumptions of normality and homoscedasticity.

To compare larval growth between ED and NE groups, growth of each individual was averaged over the last three full days of larval life. This measure of "recent growth" was used because we could not determine when each fish became entrained in an eddy, so the most parsimonious approach was to compare the most recent growth, averaging

this over several days to reduce noise. This measure of recent growth was then compared between groups using ANCOVA with age as a covariate. In instances where a significant interaction between age and group (i.e., ED and NE) precluded the interpretation of ANCOVA results, ED and NE fish were split into a young group (youngest half of the samples) and an old group (oldest half of the samples) and an ANCOVA conducted separately for each age group to compare ED and NE fish, also with age as a covariate. If a significant interaction between age and group remained, further analysis did not proceed.

Results

Identification of eddies

During our three sampling periods in the summers of 2007 and 2008, we identified a total of five MEs (Figure 3.1). Though eddies propagated continuously through the study area, their positions in the western SOF near the Dry Tortugas and lower Keys were roughly similar across sampling periods. Eddy 2 was sampled twice during the study as it was located near the Dry Tortugas during June 2007 and off the lower Keys in August 2007. Satellite images and model outputs indicated the presence of all five eddies (Appendices 1-2). Current fields, drifter tracks, and plots of temperature-at-depth contours allowed us to determine eddy positions at a finer scale (Appendices 3-4). The temperature-at-depth contour plots showed clear signals of the cold-cores produced by upwelling, typical of cyclonic eddies. Due to seasonal changes in overall temperature in the region, temperature contours at 50 m depth best identified the signal of the eddy core in June 2007. In August 2007 and June 2008, the signal of the eddy core in the temperature contours was stronger at 70 m depth. We identified 18 ED and 16 NE

stations for the June 2007 sampling period, 29 ED and 7 NE stations in August 2007, and 20 ED and 6 NE stations in June 2008. Plots of temperature profiles at each station demonstrate the clear differentiation between ED and NE stations (Figure 3.2). Although temperatures across stations are similar at the surface, there is a clear temperature signal at depth in the stations impacted by the upwelling of cool water.

Table 3.1 further illustrates the unique environments inside and outside of the sampled MEs. Mean temperatures were lower (ED range: 24.10°C – 25.89°C; NE range: 26.17°C – 28.36°C) and mean salinities higher (ED range: 36.39 – 36.43; NE range: 36.18 – 36.31) in the ED stations, due to the upwelling of cold, salty water in these cyclonic MEs. In addition, average current speeds were faster in the NE stations (range: 68.06 $cm \cdot s^{-1}$ – 106.84 $cm \cdot s^{-1}$) where flow was mainly influenced by the FC and LC. Mean current speeds observed for the ED stations ranged from 32.41 $cm \cdot s^{-1}$ to 52.66 $cm \cdot s^{-1}$. Although physical environments differed consistently between ED and NE stations, patterns in the biological environment were variable (Table 3.1). There were no significant differences in fluorescence between ED and NE stations for any cruise. Yet we observed a significantly larger volume of plankton in ED stations during the August 2007 sampling period (ED mean: 0.092 $mL \cdot L^{-1}$; NE mean: 0.045 $mL \cdot L^{-1}$).

Larval assemblages

Across all three sampling periods, 77,670 fish larvae were sampled at ED and NE stations. Of these larvae, 21,420 were reef fishes (Table 3.2). During the June 2007 sampling period, we collected 2,285 and 1,684 reef fish at ED and NE stations, respectively. The largest number of reef fish larvae was sampled in August 2007, with

7,361 collected at ED stations and 1,746 at NE stations. Finally, we collected 3,791 reef fish larvae at ED stations and 663 at NE stations in June 2008.

ANOSIM analyses which are based on presence/absence as well as abundance of taxa revealed that ED reef fish assemblages differed significantly from NE assemblages for each sampling period, with the greatest difference between assemblages evident in June 2008 (Table 3.3). Results of tests where larval abundances were averaged across the water column were similar to results from tests conducted separately on samples from each depth bin. In August 2007 and June 2008 all NE stations were located along transects intercepting the LC, and therefore geographically distant (separated by at least 65 km) from ED stations off the lower Keys. The differences between ED and NE assemblages were much greater in June 2008 (R statistic = 0.655, $p = 0.001$) than they were in August 2007 (R statistic = 0.271, $p < 0.05$), suggesting that the differences between ED and NE assemblages were not driven primarily by geographical differences among sampling stations.

These differences between ED and NE reef fish assemblages were driven largely by changes in abundance of certain families between groups (Figure 3.3). The ten families listed for each sampling period in Figure 3.3 account for approximately half of the variation between ED and NE larval assemblages (June 2007: 47.97%, August 2007: 65.17%, June 2008: 64.71%). In June 2007, larvae of the families Acanthuridae and Balistidae were more abundant at NE stations while larvae of Gerreidae, Holocentridae, Carapidae, Sphyraenidae, Monacanthidae, Apogonidae, Pomacentridae, and Labridae were more abundant at ED stations. In August 2007 larvae of Acanthuridae, Pomacentridae, and Scaridae were more abundant at NE stations while larvae of

Scorpaenidae, Gobiidae, Antennariidae, Lutjanidae, Priacanthidae, Holocentridae, and Sphyraenidae were more abundant at ED stations. The pattern differentiating groups in June 2008 was most extreme, with larvae of Acanthuridae, Scaridae, and Pomacentridae more abundant at NE stations and larvae of Scorpaenidae, Priacanthidae, Gobiidae, Apogonidae, Callionymidae, Monacanthidae, and Triglidae more abundant at ED stations. Although the families distinguishing ED and NE assemblages changed during each sampling period, certain families were consistently important in delineating groups. Larvae of Acanthuridae and Scaridae were consistently more abundant at NE stations, while larvae of Holocentridae, Monacanthidae, Apogonidae, Scorpaenidae, Gobiidae, and Priacanthidae were more abundant at ED stations.

The larval reef fish assemblage present in Eddy 2 was significantly different between the June and August 2007 sampling periods (R statistic = 0.867, $p = 0.001$). In fact, the R statistic resulting from this temporal comparison was higher than any R statistic resulting from comparisons between ED and NE assemblages. Thus, the larval assemblage of Eddy 2 changed substantially as this ME propagated from its position off of the Dry Tortugas to a location offshore of the lower Keys. This temporal difference between larval assemblages in Eddy 2 appears to be driven primarily by the increase in abundance of a variety of reef fish families in the August 2007 sampling period (Figure 3.4). Although larvae of Acanthuridae, Triglidae, and Antennariidae decreased in abundance from June to August 2007, all other reef fish families contributing to the difference between assemblages increased in abundance. In fact, larvae of Holocentridae, Tetraodontidae, and Lutjanidae were absent from Eddy 2 in June 2007, in contrast to

Eddy 2 stations in August 2007. Larvae of Gobiidae and Callionymidae were particularly abundant in Eddy 2 in August 2007.

Larval abundances

For all five reef fishes examined, patterns in frequency of occurrence were similar to patterns of larval abundance across depth bins and sampling periods, with several exceptions (Figures 3.5-3.9). The main exception to this pattern can be seen during the 2007 sampling periods when both *X. novacula* and *C. roseus* had relatively high frequency of occurrence coupled with low abundances (Figures 3.5 and 3.7). Distributions of frequency of occurrence were consistently different between ED and NE groups (Table 3.4). These differences were driven in part by the tendency of certain species to occur more frequently in either ED or NE stations. For instance, *T. bifasciatum* occurred more often in NE stations in August 2007 and June 2008, while *X. novacula* occurred more frequently in ED stations in June 2008 (Figures 3.5 and 3.6). Differences in frequency of occurrence were also due to a shift in depth distributions between ED and NE stations. This is exemplified by the distributions of *C.* roseus and *S. partitus* in June 2007 (Figures 3.7 and 3.9). While *C. roseus* occurred more often in the upper two depth bins of the ED stations, their distribution was shifted to the intermediate depth bins of NE stations. Similarly, the highest frequencies of occurrence for *S. partitus* were shallower in ED stations compared to NE stations.

Larval abundance was not consistently different between ED and NE stations (Table 3.5), though some trends were evident in the data. *Xyrichtys novacula* tended to have higher abundances at ED stations while *T. bifasciatum* tended to be more abundant at NE stations (Figures 3.5 and 3.6). Interestingly, the trend for *S. partitus* changed

among sampling periods with higher abundances at ED stations in June 2007 and higher abundances at NE stations in August 2007 and June 2008 (Figure 3.9). Patterns in larval abundance across depth bins were species-specific and often temporally variable. These patterns ranged from a uniform abundance across depth bins (e.g., *X. novacula* at NE stations in June 2007) to highly skewed distributions with maximum abundance in the most shallow or deepest depth bin (e.g., *S. barracuda* in all sampling periods, *X. novacula* at NE stations in August 2007, respectively).

Larval growth

Sample sizes permitted tests of growth differences between ED and NE fish for *X. novacula* and *T. bifasciatum* in June and August 2007, for *C. roseus* in August 2007 and June 2008, and for *S. barracuda* and *S. partitus* in August 2007. Of these eight tests, three (i.e., *T. bifasciatum*, *C. roseus*, and *S. barracuda* from August 2007) resulted in a significant interaction between age and group necessitating the division of samples into old and young groups for separate ANCOVA analysis. After dividing samples, only one significant interaction between age and group remained (i.e., *T. bifasciatum* young fish) so this group was removed from the analysis.

Across sampling periods, for four of the five species of reef fishes examined, consistently higher recent growth was associated with eddies. *Xyrichtys novacula* ED fish had significantly faster growth than NE fish in June and August 2007 (Table 3.6, Figure 3.10). *T. bifasciatum* ED fish from June 2007 and the old age group from August 2007 exhibited significantly faster growth than NE fish. In August 2007, growth of young *C. roseus* larvae did not differ between ED and NE groups yet old ED larvae from the same sampling period and ED larvae from June 2008 had faster growth than NE larvae. For *S.*

barracuda, although there was no difference in the old group, young ED larvae grew significantly faster than young NE larvae. Finally, recent growth of *S. partitus* did not differ significantly between ED and NE larvae.

Discussion

Eddy characteristics

For all sampling periods during the summers of 2007 and 2008, the physical parameters of ED stations differed consistently from those of NE stations. Specifically, ED stations had lower temperatures and higher salinities at depth due to the upwelling of cold, salty water. This signature of upwelling is consistent with previous findings for MEs in the SOF (Lee et al. 1992, Lee et al. 1994). In addition, the slower current speeds observed in ED stations are typical of those found previously in the flow fields of MEs in the region (Fratantoni et al. 1998, Lee et al. 1992, Lee et al.1994). In contrast to these distinct physical differences, biological parameters (i.e., fluorescence and plankton volume) did not differ consistently between ED and NE groups. Given the temporally and spatially variable dynamics of productivity in MEs, the patterns we observed in fluorescence and plankton volume are not entirely surprising. Previous work has shown that productivity is often highest in the early stages of eddy formation (Bibby et al. 2008). However, nutrient injections throughout the life of an eddy from sub-mesoscale processes, the entrainment of a nutrient-rich water mass, or variable grazing by zooplankton can also impact patterns of primary productivity (Moore et al. 2007, Lehahn et al. 2011). Govoni et al. (2010) tracked a cyclonic ME as it propagated along the southeast shelf of the United States. They found that chlorophyll *a* concentrations decreased over the 5 d sampling period presumably due to grazing. In this same study,

zooplankton displacement volume did not change significantly across days, but certain zooplankton taxa important in the diets of fish larvae did increase in concentration. Thus, the snapshot provided by fluorometry data and plankton samples will be affected by the interaction between timing of sampling and the trophic dynamics of the eddy. As previous work has shown increased primary productivity at the core of a ME in the SOF (Hitchcock et al. 2005), it is possible that high levels of grazing in the eddies we sampled had reduced fluorescence levels at ED stations making them comparable to NE stations at the time of sampling. In addition, although we did not see consistently higher zooplankton displacement volume at ED stations, it is possible that taxon-specific concentrations of zooplankton are different inside and outside of the MEs we sampled. Such differences will be particularly important if prey items of reef fish larvae have higher concentrations at ED stations. Previous work in the SOF has demonstrated that higher abundances of copepod nauplii, *Oithona* spp., and calanoid copepodites (at night) were associated with a sub-mesoscale eddy off the lower Keys (Lane et al. 2003). Though *Oithona* spp. are marginally important to the diets of reef fish larvae, copepod nauplii are primary constituents, particularly in the small size classes, for larvae of Lutjanidae, Acanthuridae, *Xyrichtys* spp., *Halichoeres* sp., and Mullidae (Llopiz and Cowen 2009). In addition, calanoid copepods are important constituents of the diets of larval *Serranus* spp., *Halichoeres* spp., Mullidae, and *Stegastes* spp. An alternative to the explanation of trophic dynamics and timing of sampling is that the productivity generated by the eddies we sampled was concentrated in zones of convergence at the eddy periphery. Thus, the stations exhibiting high fluorescence and plankton volume (i.e., eddy edge stations)

would not have been included in our ED group. Unfortunately, because eddy edges are harder to precisely and objectively define, we cannot address this possible explanation.

Larval assemblages

Larval reef fish assemblages differed consistently between ED and NE stations during all three of our sampling periods. This finding is comparable with a number of other studies focusing on larval fish assemblages in eddies in geographically diverse locations (southwestern Australia, Muhling et al. 2007, Holliday et al. 2011; Gulf of Alaska, Atwood et al. 2010; Gulf of California, Contreras-Catala et al. 2012). Specifically, ANOSIM analysis of larval assemblages between a cyclonic and anti-cyclonic eddy off the coast of southwestern Australia produced an R statistic of 0.180 (Muhling et al. 2007), with no significant differences among larval assemblages from the center, body, and perimeter of the cyclonic eddy. In another study examining anti-cyclonic eddies in the Gulf of Alaska over a three-year period, Atwood et al. (2010) found consistent differences in larval assemblages among eddy, basin, and shelf samples. Differences between assemblages in the center of an anti-cyclonic eddy and shelf assemblages off of southwestern Australia, (i.e., R statistic = 0.160) were comparable to differences between our ED and NE stations, but differences between the oceanic assemblage and all others were much greater than those we observed (i.e., R statistic $\geq$ 0.8; Holliday et al. 2011). Finally, in the Gulf of California, the larval assemblage in an anti-cyclonic eddy was distinct from that found in the neighboring water mass (Contreras-Catala et al. 2012). Thus, our results are consistent with an accumulating body of empirical data illustrating that the larval assemblages found in MEs are distinct from those in surrounding water masses.

In addition to comparisons of larval reef fish assemblages inside and outside of eddies, we were able to examine temporal variation in the larval assemblage of Eddy 2 which was sampled in June 2007 and again in August 2007. The difference in Eddy 2 larval assemblages between sampling periods was greater than the differences we observed for all comparisons of ED and NE stations. Thus, as Eddy 2 propagated east from its location near the entrance of the SOF to a position offshore of the lower Keys, its larval reef fish assemblage changed dramatically. Although many of the same families were present in the Eddy 2 assemblages in June and August 2007, all but three families were found in greater abundance in August. Age distributions of two species of larval reef fishes, *T. bifasciatum* and *X. novacula*, sampled from Eddy 2 indicate that the increases in abundances were due to input from spawning (Appendix 5). Eddy 2 contained a large number of young larvae in August 2007, yet based on average pelagic larval durations, larvae present in Eddy 2 in June 2007 would have settled well before the subsequent sampling period. It is possible that spawning output of adult fish increased as water temperatures warmed between June and August. Alternatively, overall spawning output along the main reef tract of the Florida Keys may be greater than that for deep reefs in the vicinity of Eddy 2 when it was located off of the Dry Tortugas; however, empirical data on spawning output is required to test this hypothesis. The importance of adult spawning behaviors in structuring larval fish assemblages is well-recognized (Olivar 1990, Leis 1993, Grothues and Cowen 1999, Muhling et al. 2008) and adult spawning behaviors were likely driving the observed temporal changes in larval assemblages in Eddy 2 as it propagated from west to east through the SOF.

Larval abundances

For the five species of reef fish examined, we found that frequency of occurrence was consistently different between ED and NE stations. Differences between ED and NE stations resulting from shifts in depth distributions between groups can be explained, in part, by variations in age distributions. Specifically, for *T. bifasciatum* and *C. roseus* in August 2007 and for *C. roseus* again in June 2008, the age of fish was significantly younger in ED stations than NE stations (see Chapter 2). Previous work in the SOF has shown evidence of ontogenetic vertical migrations for a number of reef fishes, including *T. bifasciatum* (Huebert et al. 2011). This may explain the tendency for young fish in ED stations to occur more frequently in the shallower depth bins while older fish in NE stations were distributed deeper in the water column. In cases where certain species occurred more often in either ED or NE stations, this pattern was mirrored by trends in larval abundance. Yet there were no consistently significant differences in larval abundance between ED and NE stations. Holliday et al. (2011) found that mean abundances of larval fish were higher in the center and perimeter of an anti-cyclonic eddy than they were in oceanic stations. However, they were examining abundances of all fish larvae together while we were examining species-specific patterns in abundance.

We did see a trend in which *X. novacula* abundances were higher in ED than NE stations and *T. bifasciatum* abundances were higher in NE stations. These contrasting patterns in abundance coupled with the differences we observed between ED and NE stations in frequency of occurrence could result from differences in the entrainment process or species-specific mortality of larvae once they are entrained. As *T. bifasciatum* spawn daily along the reefs of the Florida Keys, it is surprising that their larvae are more

abundant in NE stations which were generally located farther offshore. However, this finding is consistent with another study conducted in the SOF (just north of our study area) in which higher abundances of *T. bifasciatum* were observed at offshore stations (Sponaugle et al. 2009). Thus, newly-spawned *T. bifasciatum* larvae which were likely spatially and temporally coincident with MEs during our study, were either advected through or around the eddy to offshore waters (i.e., not entrained) or did not survive inside the eddy due to starvation or predation. *T. bifasciatum* and *X. novacula*, both species in the wrasse family, have similar diets consisting primarily of copepods (i.e., a combination of *Farranula*, *Oncaea*, and harpacticoids; Llopiz and Cowen 2009). The main difference between these species is the additional contribution of nauplii and calanoid copepods to the diets of small size classes (i.e., 3-6 mm) of *X. novacula*. If this subtle difference allows *X. novacula* larvae to better exploit prey items found in MEs, they may be less likely to starve during the vulnerable early stages of larval life (e.g., first feeding). Species-specific predation could also result in the contrasting patterns of occurrence and abundance that we observed. The morphologies of *X. novacula* and *T. bifasciatum* are similar as these species are closely-related. Both species are lacking structures, such as robust spines and armor, thought to be adaptations for defense against predation. However, data on predation of fish larvae in the plankton is scarce, making it difficult to speculate on species-specific vulnerabilities to predation in MEs.

Larval growth

To our knowledge, this is the first study using otolith-derived growth measures to examine fish larvae directly sampled from MEs. In seven out of the ten possible comparisons of recent larval growth between ED and NE stations, we found that growth

was significantly faster in larvae sampled from ED stations. Our finding of faster growth associated with residence in MEs is consistent across three sampling periods over two summers and across four species of reef fish from three different families. This finding is similar to that of a study on nutritional condition (i.e., RNA/DNA ratios) of anchovy larvae, showing that larvae in the 6-8 mm size class were of higher condition in a frontal eddy of the Kuroshio Current than they were in inshore and offshore stations (Nakata et al. 2000). There was, however, no difference in condition among eddy, inshore, and offshore stations for the larger size class (i.e., 9-11 mm). The larvae in our study ranged in size from ~ 3 to 11 mm (SL) and larvae of all sizes exhibited faster growth in MEs. Whether this difference between studies is due to oceanographic differences, species-specific effects of MEs on larval growth (i.e., anchovy versus reef fish), or to methodological differences (i.e., RNA/DNA ratios versus otolith-derived growth) is unknown.

While there are few studies comparing condition and growth of fish larvae sampled inside and outside of eddies, a large body of empirical data points to likely trophic mechanisms of fast growth for larval fish in eddies. High levels of primary and secondary productivity have been identified in MEs across a range of geographic locations (Gulf Stream, Yoder et al. 1981; Kuroshio Current, Kasai et al. 2002; Gulf of Alaska, Crawford et al. 2007; subtropical North Atlantic and Pacific Oceans, Bibby et al. 2008; southeast United States shelf, Govoni et al. 2010). Similarly, MEs in the SOF have been shown to be highly productive, with increased levels of nutrients, chlorophyll *a*, and copepod abundances (Lee et al. 1992, Lee et al. 1994, Hitchcock et al. 2005). As copepods serve as food items for a variety of larval reef fish (Llopiz and Cowen 2009),

the productivity found in MEs of the SOF can explain the enhanced growth we observed for four species of larval reef fish sampled from these eddies.

Implications for retention and recruitment of reef fish in the SOF

MEs are dominant features in the oceanographic environment of the SOF, and our study provides evidence that these eddies directly impact distributions and growth of larval reef fishes. Specifically, the finding that larval assemblages are different inside and outside of eddies has implications for patterns of local-retention. Families of fish larvae that were consistently more abundant in ED assemblages across sampling periods may be more likely to experience enhanced local retention as they are entrained in the re-circulating currents of MEs. The opposite is true for families that were consistently more abundant in NE assemblages as these larvae were often sampled from the FC where they would likely be transported to downstream locations. The temporal changes we observed in the assemblage of Eddy 2 lend support to the role of MEs as a retention mechanism for locally-spawned reef fish larvae. While the assemblage of Eddy 2 consisted of a variety of families with relatively low abundances when it was positioned at the entrance to the SOF, presumably locally-spawned larvae were added to the assemblage by the time this eddy was sampled offshore of the lower Keys approximately two months later. As these larvae were not in Eddy 2 as it entered the SOF, they had to be entrained in the eddy as it propagated to the east. Thus, larvae had to be entrained from either the FC, where most NE stations were located, or from nearshore waters. The dissimilarity between the assemblage of Eddy 2 in August 2007 (i.e., when it was located offshore of the lower Keys) and the NO ED assemblages observed across sampling periods, supports an origin for Eddy 2 larvae from nearshore waters. Thus, it appears that locally-spawned larvae are

being entrained into MEs as they propagate slowly through the western SOF, and the consistent differences between ED and NE larval assemblage across sampling periods suggest that these entrained larvae may remain in the ED. Future work should focus on the evolution of larval assemblages in MEs in SOF to further elucidate their role in local retention as well as the specific mechanisms involved.

The enhanced growth of larvae associated with MEs has implications for recruitment of reef fish to the Florida Keys reef tract. Faster growth during the larval stage or higher settlement condition has been shown to lead to increased survival in juveniles on the reef in the Florida Keys (Grorud-Colvert and Sponaugle 2011, Rankin and Sponaugle 2011, D'Alessandro and Sponaugle in review) and elsewhere (Searcy and Sponaugle 2001, Vigliola and Meekan 2002). Thus, these fast-growing larvae residing in MEs may subsequently settle to the reef and preferentially survive. Logerwell and Smith (2001) found that highest abundances of sardine 'survivors' (i.e., older larvae found in aggregations) were associated with eddies located offshore of the California coast, providing additional support to the idea that residence in eddies improves survival. Tracking cohorts from the pelagic environment (during the passage of an eddy) to the reef tract would help to resolve the ultimate effects of the enhanced growth of fish larvae in ME on recruitment. If fast-growing larvae from MEs do, in fact, preferentially survive as juveniles on the reef, larvae retained in eddies may, regardless of patterns of abundance, contribute disproportionately to the replenishment of reef fish populations.

Table 3.1. Comparison of environmental variables between ED and NE stations. Mean (± SE) values are given for each variable across sampling periods. Significance values are based on one-way ANOVAs. ED = eddy and NE = no eddy. * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$, ns = not significant.

	June 2007			August 2007			June 2008		
	ED	NE	p	ED	NE	p	ED	NE	p
Temperature (°C)	24.10 (0.30)	26.17 (0.12)	***	26.89 (0.15)	28.36 (0.19)	***	25.89 (0.24)	28.30 (0.03)	***
Salinity	36.40 (0.02)	36.31 (0.01)	***	36.39 (0.01)	36.28 (0.03)	***	36.43 (0.01)	36.18 (0.02)	***
Surface current speed	32.41 (3.30)	68.06 (9.68)	**	52.66 (8.14)	71.69 (14.74)	ns	47.36 (9.72)	106.84 (18.08)	**
Fluorescence (volts)	0.145 (0.004)	0.138 (0.002)	ns	0.119 (0.001)	0.120 (0.003)	ns	0.145 (0.006)	0.164 (0.012)	ns
Plankton displacement volume ($mL \cdot L^{-1}$)	0.095 (0.004)	0.082 (0.005)	ns	0.092 (0.004)	0.045 (0.004)	***	0.091 (0.010)	0.110 (0.026)	ns

Table 3.2. Mean larval concentrations (m^{-3}) for all reef fishes sampled in eddy (ED) and no eddy (NE) stations across three sampling periods.

		June 2007		August 2007		June 2008		All Cruises	
Family	Species	ED	NE	ED	NE	ED	NE	ED	NE
Acanthuridae	*Acanthurus* spp.	1.62	4.52	1.26	2.47	2.81	8.48	1.52	4.65
Antennariidae	spp.	2.24	1.24	7.12	2.70	1.11		5.20	1.82
Apogonidae	spp.	3.08	2.58	4.22	1.30	3.74	1.16	3.84	1.83
Aulostomidae	*Aulostomus maculatus*		0.98		0.96		2.13		1.16
Balistidae	spp.	2.13	2.99	0.82	0.90	1.20	1.11	1.44	2.34
Blenniidae	spp.	0.63	1.99					0.63	1.99
Suborder: Blennioidei	spp.		1.83			1.09		1.09	1.83
Callionymidae	spp.	1.32	1.77	5.77	3.47	5.17	1.30	4.42	2.29
Carapidae	spp.	3.44	1.97	3.29		2.58		3.10	1.97
Chaetodontidae	*Chaetodon* spp.	1.79	0.84	1.04	1.09	0.94		1.30	0.91
Cirrhitidae	*Amblycirrhitus* spp.	0.87	1.47	0.81	0.78			0.85	1.24
Dactylopteridae	*Dactylopterus volitans*	1.49		0.97	0.85	0.93	1.05	1.21	0.92
Diodontidae	spp.	0.73	1.96		0.77			0.73	1.66
Fistulariidae	*Fistularia* spp.	1.19	0.74	0.74		0.94		0.83	0.74
Gerreidae	spp.	3.37	0.93	4.11		7.73		4.40	0.93
Gobiidae	spp.	2.99	2.43	16.48	5.48	19.02	4.31	14.57	3.80
Haemulidae	spp.	0.87	2.03	1.04	0.82	2.12	2.05	1.14	1.59
Holocentridae	spp.	7.68	1.55	5.73	4.05	1.65		5.30	2.55
Kyphosidae	*Kyphosus* spp.			0.73				0.73	
Labridae	*Bodianus* spp.			0.84				0.84	
	Clepticus parri	0.61	1.25	0.89	1.38		1.67	0.81	1.33
	Decodon puellaris	0.84	0.58	2.61		1.19		2.10	0.58
	Doratonotus spp.	1.78	1.79	0.81	0.76	1.20	1.22	1.26	1.45
	Halichoeres spp.	1.75	1.90	1.47	1.65	1.10	0.99	1.47	1.61
	Thalassoma bifasciatum	6.30	5.85	1.36	4.11	1.93	2.63	3.76	4.44
	Xyrichtys spp.	4.04	2.69	6.38	5.96	4.97	0.84	5.44	3.69
	spp.	1.45	1.20	1.29	0.89		1.05	1.33	1.01

Table 3.2. (*continued*)

		June 2007		August 2007		June 2008		All Cruises	
Family	Species	ED	NE	ED	NE	ED	NE	ED	NE
Lutjanidae	*Etelis oculatus*			1.16	0.83	0.97	1.24	1.13	0.97
	Lutjaninae spp.	0.65	1.05	1.53	0.77	3.06	0.92	1.80	0.96
	Lutjanus spp.	0.67	0.83	1.32	2.30	1.03	0.96	1.11	1.36
	Pristipomoides spp.	1.29	1.52	3.34		2.64		2.93	1.52
	Rhomboplites aurorubens	0.96	0.92	3.54		2.71		3.02	0.92
	spp.	2.05	1.60	4.08	2.92	3.51	1.26	3.53	1.90
Microdesmidae	spp.	1.78	0.83	1.24		2.76		1.55	0.83
Monacanthidae	spp.	2.80	1.09	2.53	2.24	5.85	1.39	3.75	1.54
Mullidae	spp.	8.91	2.30	1.16	0.79	2.26	0.91	6.30	1.33
Opistognathidae	spp.	0.89				19.79		6.29	
Ostraciidae	spp.	0.86	0.85					0.86	0.85
Pomacanthidae	spp.	1.40	1.53	1.21	1.26	0.89	2.71	1.20	1.60
Pomacentridae	*Abudefduf* spp.	1.21		1.05	0.79			1.09	0.79
	Chromis spp.	0.90	0.84		0.80		3.26	0.90	1.55
	Stegastes spp.	3.02	1.20	1.51	5.12	1.01	7.24	2.20	3.86
	spp.	2.74	3.37	1.74	0.74	2.24	1.07	2.27	2.36
Priacanthidae	spp.	2.36	1.42	4.53	1.75	4.63	1.42	4.25	1.56
Scaridae	*Cryptotomus roseus*	1.20	1.30	7.51	2.61	3.59	5.48	5.83	2.69
	Scarus spp.	0.94	1.08	2.53	2.75	1.12	1.30	2.25	1.80
	Sparisoma spp.	3.25	2.23	3.31	25.17	2.25	8.89	3.14	11.71
	spp.	0.99		1.62	1.35	0.98	1.42	1.45	1.38
Scorpaenidae	spp.	2.00	2.82	4.40	2.06	8.50	1.75	5.02	2.51
Serranidae	spp.	3.26	2.73	2.61	3.23	2.86	2.79	2.85	2.86
Sphyraenidae	spp.	2.35	1.57	4.00	3.62	3.08	2.14	3.36	2.58
Syngnathidae	spp.		0.84	0.85	1.26	1.47	0.97	0.95	0.89
Tetraodontidae	spp.	2.65	1.69	2.77	1.97	4.49	1.04	3.32	1.64
Triacanthodidae	spp.	0.80	1.25		1.29	1.03		0.92	1.27
Triglidae	spp.	1.40	1.20	1.62	1.92	3.20		2.14	1.54

Table 3.3. ANOSIM results for comparisons of larval reef fish assemblages between eddy (ED) and no eddy (NE) groups. Tests were conducted for all depths combined (i.e., abundances averaged over the water column) and across each 20 m depth bin. * $p < 0.05$, ** $p < 0.01$, *** $p = 0.001$, ns = not significant.

	June 2007	August 2007	June 2008
Groups	R statistic	R statistic	R statistic
All Depths	0.203 **	0.271 *	0.655 ***
0-20	0.180 ***	0.246 *	0.761 ***
20-40	0.150 **	0.415 **	0.688 ***
40-60	0.318 ***	0.309 **	0.479 **
60-80	0.220 ***	0.250 *	0.366 **

Table 3.4. Results of two-way chi-square tests comparing frequency of occurrence distributions across depth bins between eddy (ED) and no eddy (NE) stations. Chi-square test statistics, degrees of freedom (df), and p-values for each test are shown for five species of reef fishes across three sampling periods. Significant results are in bold and ns = non-significant.

Taxon	June 2007			August 2007			June 2008		
	Chi-square	df	p-value	Chi-square	df	p-value	Chi-square	df	p-value
Xyrichtys novacula	7.77	3	**<0.05**	26.86	3	**<0.001**	42.60	3	**<0.001**
Thalassoma bifasciatum	1.40	3	ns	22.14	3	**<0.001**	20.49	3	**<0.001**
Cryptotomus roseus	37.20	3	**<0.001**	31.94	3	**<0.001**	15.44	3	**<0.01**
Sphyraena barracuda	8.55	2	**<0.05**	20.92	3	**<0.001**	17.72	2	**<0.001**
Stegastes partitus	51.68	3	**<0.001**	9.57	3	**<0.05**	2.31	1	ns

Table 3.5. Results of Kruskal-Wallis tests comparing larval abundances between eddy (ED) and no eddy (NE) groups for five species of reef fish across each of three sampling periods. Tests were conducted on abundances averaged across the water column (All Depths) and on abundances across each 20 m depth bin. In cases where p-values are significant, they are in bold and the directionality of the result is given in parenthesis. E = ED and N = NE. Tests could not be conducted for comparisons with zero values; this is indicated by a dash.

Taxon	Depth	June 2007	August 2007	June 2008
Xyrichtys novacula	*All Depths*	0.703	0.041	0.133
	0-20	0.327	0.143	-
	20-40	0.902	**0.018 (E>N)**	-
	40-60	0.722	0.604	0.172
	60-80	0.701	0.775	-
Thalassoma bifasciatum	*All Depths*	0.185	**< 0.001 (E<N)**	0.634
	0-20	0.096	**0.005 (E<N)**	0.221
	20-40	0.440	**0.016 (E<N)**	**0.046 (E<N)**
	40-60	0.157	0.134	-
	60-80	0.317	0.221	-
Cryptotomus roseus	*All Depths*	0.289	0.206	0.181
	0-20	0.380	0.172	0.317
	20-40	0.288	0.288	0.439
	40-60	0.770	0.770	1.000
	60-80	-	0.831	0.050
Sphyraena barracuda	*All Depths*	0.130	0.910	0.166
	0-20	**0.021 (E>N)**	0.499	0.292
	20-40	0.317	1.000	0.297
	40-60	-	0.221	0.317
	60-80	-	-	-
Stegastes partitus	*All Depths*	0.700	**0.020 (E<N)**	0.157
	0-20	-	0.317	-
	20-40	0.770	-	-
	40-60	0.699	0.456	-
	60-80	-	**0.017 (E<N)**	0.180

Table 3.6. ANCOVA results for comparisons of recent growth between eddy (ED) and no eddy (NE) groups for five species of reef fish. Where significant interactions between age and group were present, samples were divided into young and old age groups and separate ANCOVAs were performed on each age group. If a significant interaction remained, analysis did not proceed; this is indicated by a dash. Significant results are in bold.

Taxon	Sampling Period	Age Group	ED vs. NE
Xyrichtys novacula	June 2007		**$p < 0.001$**
	August 2007		**$p < 0.001$**
Thalassoma bifasciatum	June 2007		**$p < 0.001$**
	August 2007	Young	-
		Old	**$p < 0.001$**
Cryptotomus roseus	August 2007	Young	$p = 0.094$
		Old	**$p < 0.001$**
	June 2008		**$p < 0.001$**
Sphyraena barracuda	August 2007	Young	**$p < 0.001$**
		Old	$p = 0.266$
Stegastes partitus	August 2007		$p = 0.899$

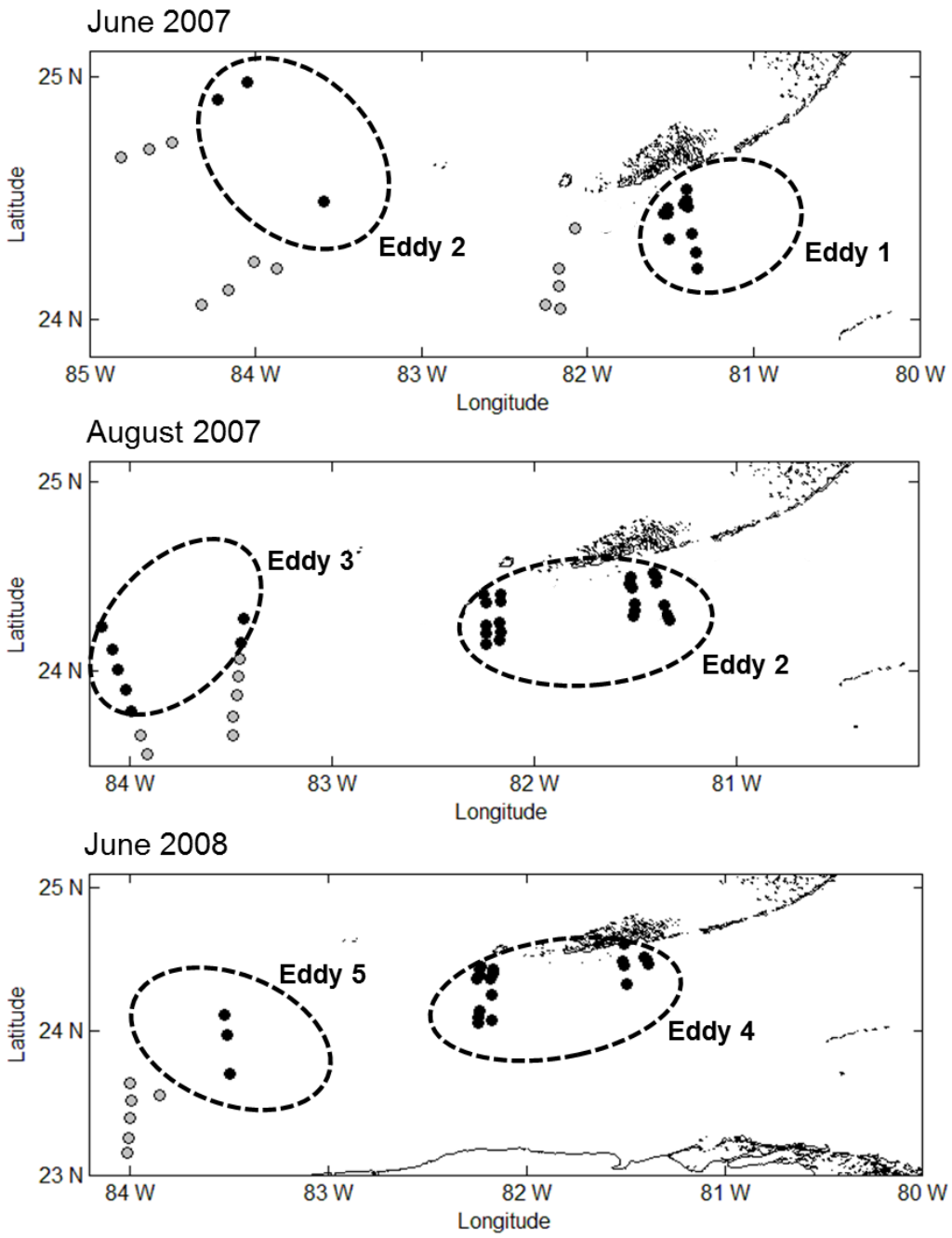


Figure 3.1. Map study area for each of the three sampling periods, illustrating locations of ED (black points) and NE (gray points) stations. Approximate positions of mesoscale eddies during each cruise are superimposed on the maps with dotted lines. Eddies are identified numerically in the order in which they propagated through the SOF. The current meter offshore of Looe Key Reef is denoted by a triangle. ED = eddy and NE = no eddy.

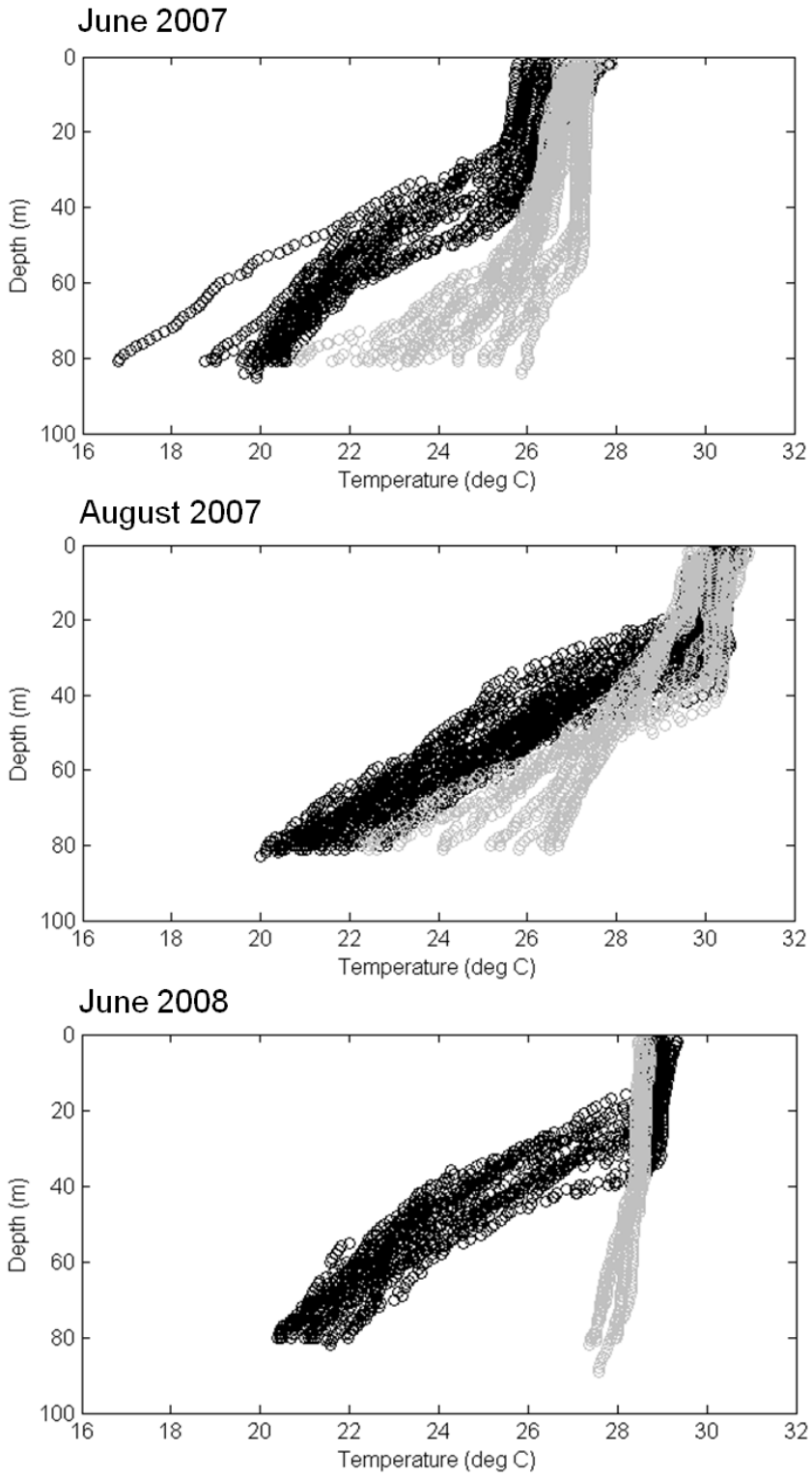
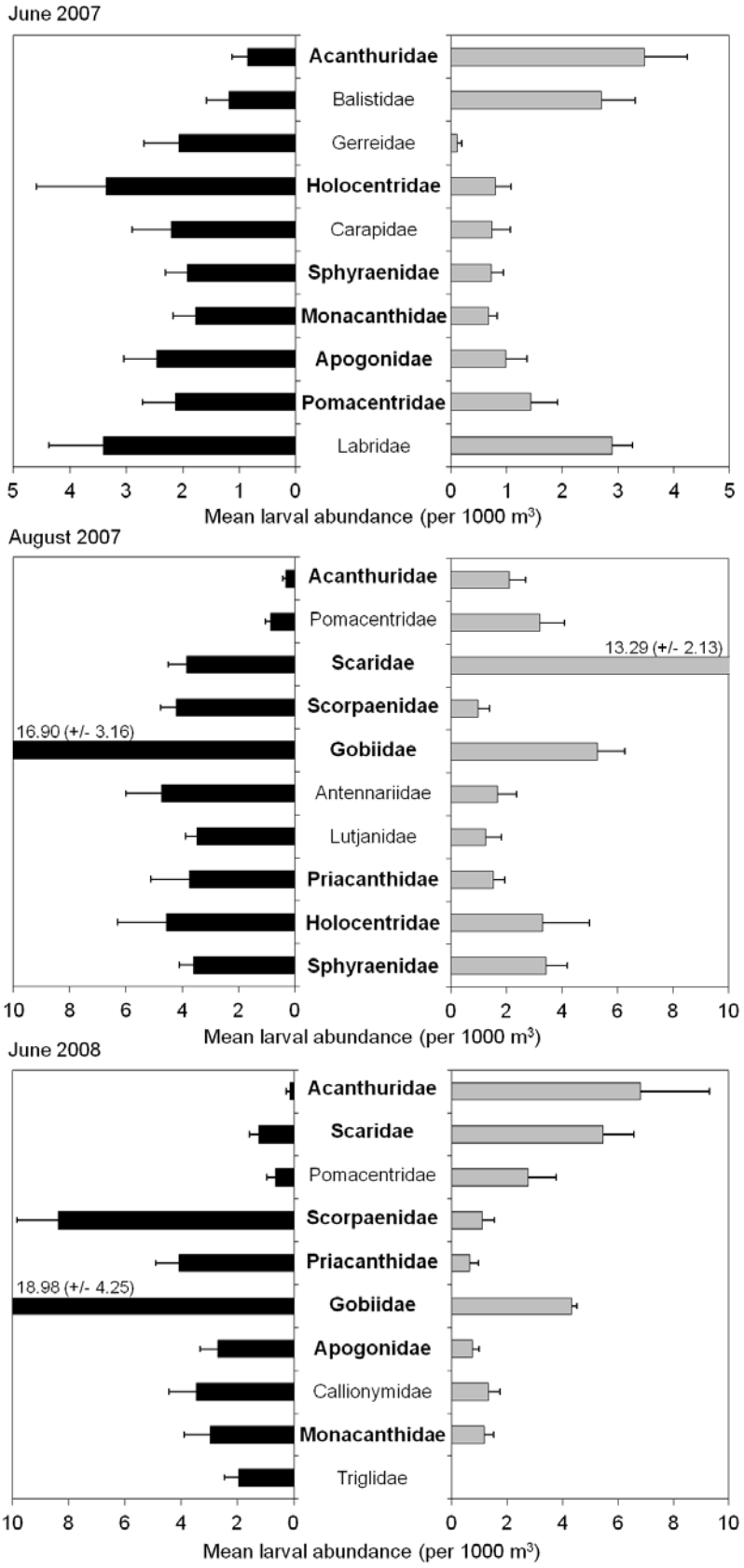


Figure 3.2. Temperature profiles of ED (black) and NE (gray) stations for each of three sampling periods showing distinct temperature signals at depth due to the upwelling of cold water at ED stations. ED = eddy and NE = no eddy.

Figure 3.3. Comparison of mean larval abundance (±SE) for the reef fish families accounting for approximately half of the variation between ED (black bars) and NE (gray bars) larval assemblages for each of three sampling periods. Larval abundances for each family were averaged over the water column. Families in bold exhibited consistent differences in abundance between ED and NE stations in more than one sampling period. ED = eddy and NE = no eddy.


June 2007
Acanthuridae
Balistidae
Gerreidae
Holocentridae
Carapidae
Sphyraenidae
Monacanthidae
Apogonidae
Pomacentridae
Labridae
5 4 3 2 1 0
0 1 2 3 4 5
Mean larval abundance (per 1000 m3)
August 2007
Acanthuridae
Pomacentridae
Scaridae
Scorpaenidae
Gobiidae
Antennariidae
Lutjanidae
Priacanthidae
Holocentridae
Sphyraenidae
16.90 (+/- 3.16)
13.29 (+/- 2.13)
10 8 6 4 2 0
0 2 4 6 8 10
Mean larval abundance (per 1000 m3)
June 2008
Acanthuridae
Scaridae
Pomacentridae
Scorpaenidae
Priacanthidae
Gobiidae
Apogonidae
Callionymidae
Monacanthidae
Triglidae
18.98 (+/- 4.25)
10 8 6 4 2 0
0 2 4 6 8 10
Mean larval abundance (per 1000 m3)

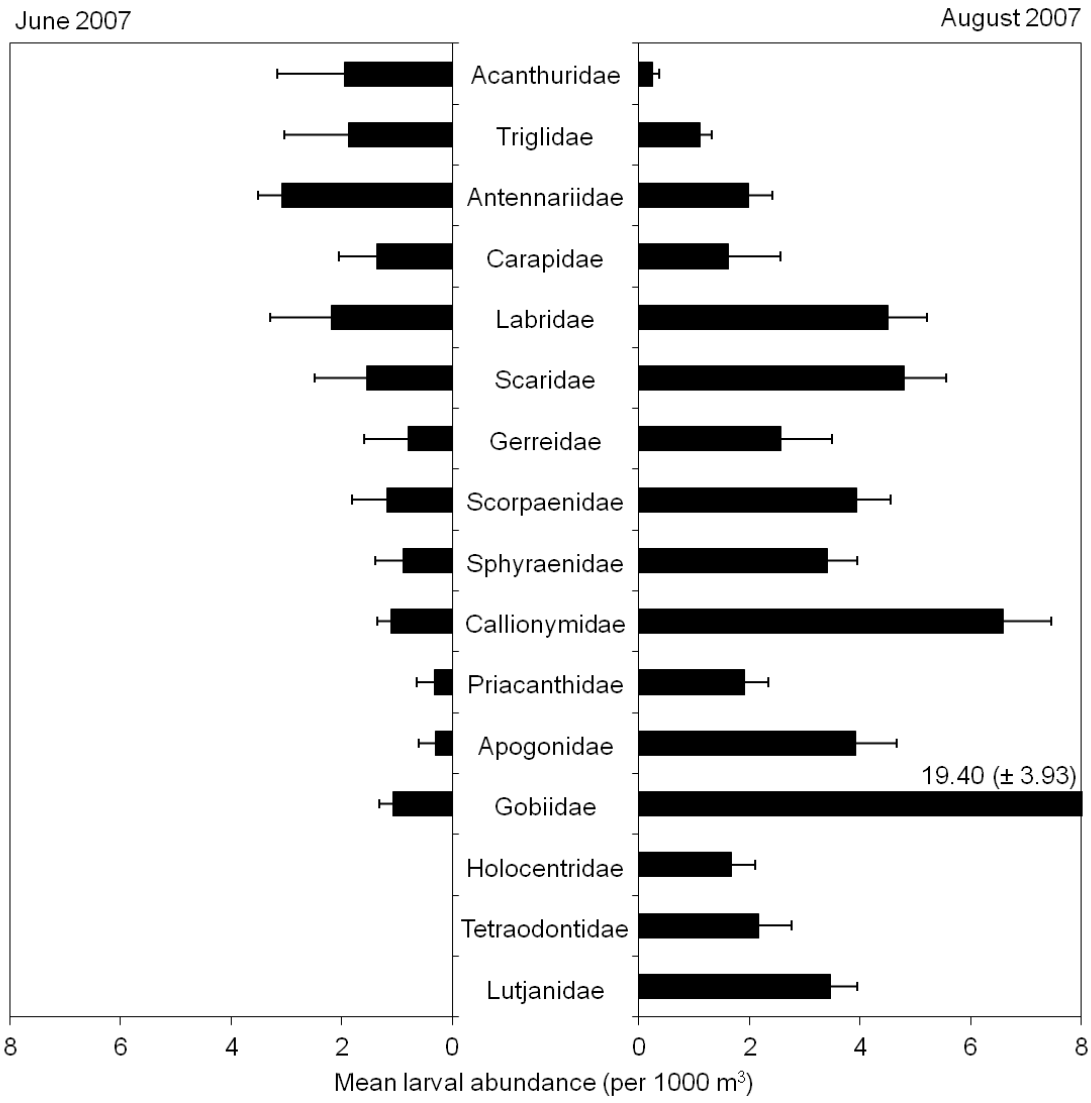


Figure 3.4. Comparison of larval reef fish assemblages in Eddy 2 between the June 2007 (left) and August 2007 (right) sampling periods. Mean larval abundance (±SE) averaged across the water column is shown for sixteen reef fish families that account for >90% of the variation between assemblages.

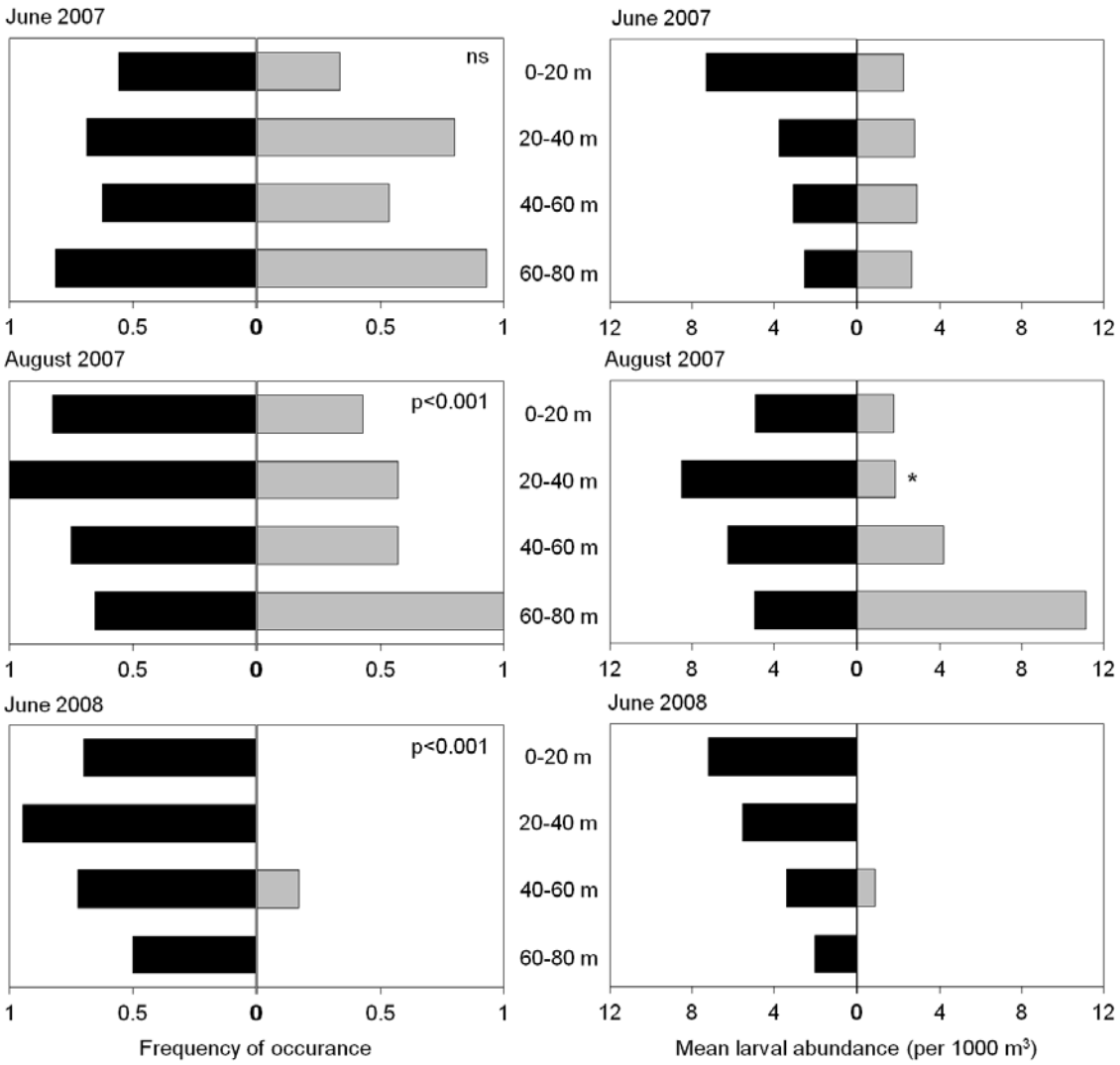


Figure 3.5. Frequency of occurrence and mean larval abundance at ED (black bars) and NE (gray bars) stations for *Xyrichtys novacula*. Data are shown across discretely-sampled 20 m depth bins for each of three sampling periods. Results of two-way chi-square tests shown as p-values on frequency of occurrence plots. Significant results for comparisons of larval abundance between ED and NE stations (Kruskal-Wallis tests conducted separately for each depth bin) are also shown. ED = eddy and NE = no eddy. *p<0.05, **p<0.01, and ***p<0.001.

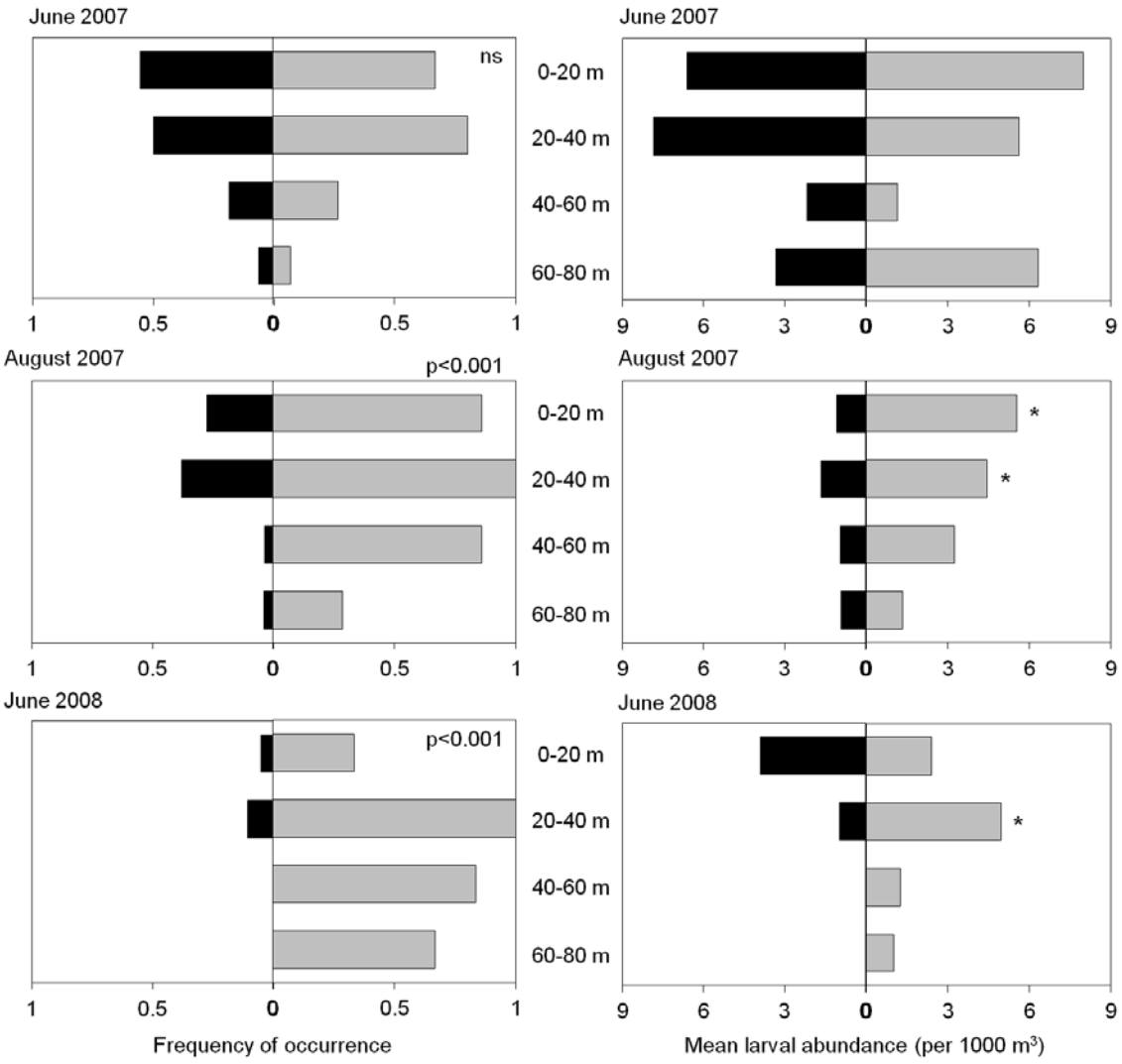


Figure 3.6. Frequency of occurrence and mean larval abundance at ED (black bars) and NE (gray bars) stations for *Thalassoma bifasciatum*. Data are shown across discretely-sampled 20 m depth bins for each of three sampling periods. Results of two-way chi-square tests shown as p-values on frequency of occurrence plots. Significant results for comparisons of larval abundance between ED and NE stations (Kruskal-Wallis tests conducted separately for each depth bin) are also shown. ED = eddy and NE = no eddy. *$p<0.05$, **$p<0.01$, and ***$p<0.001$.

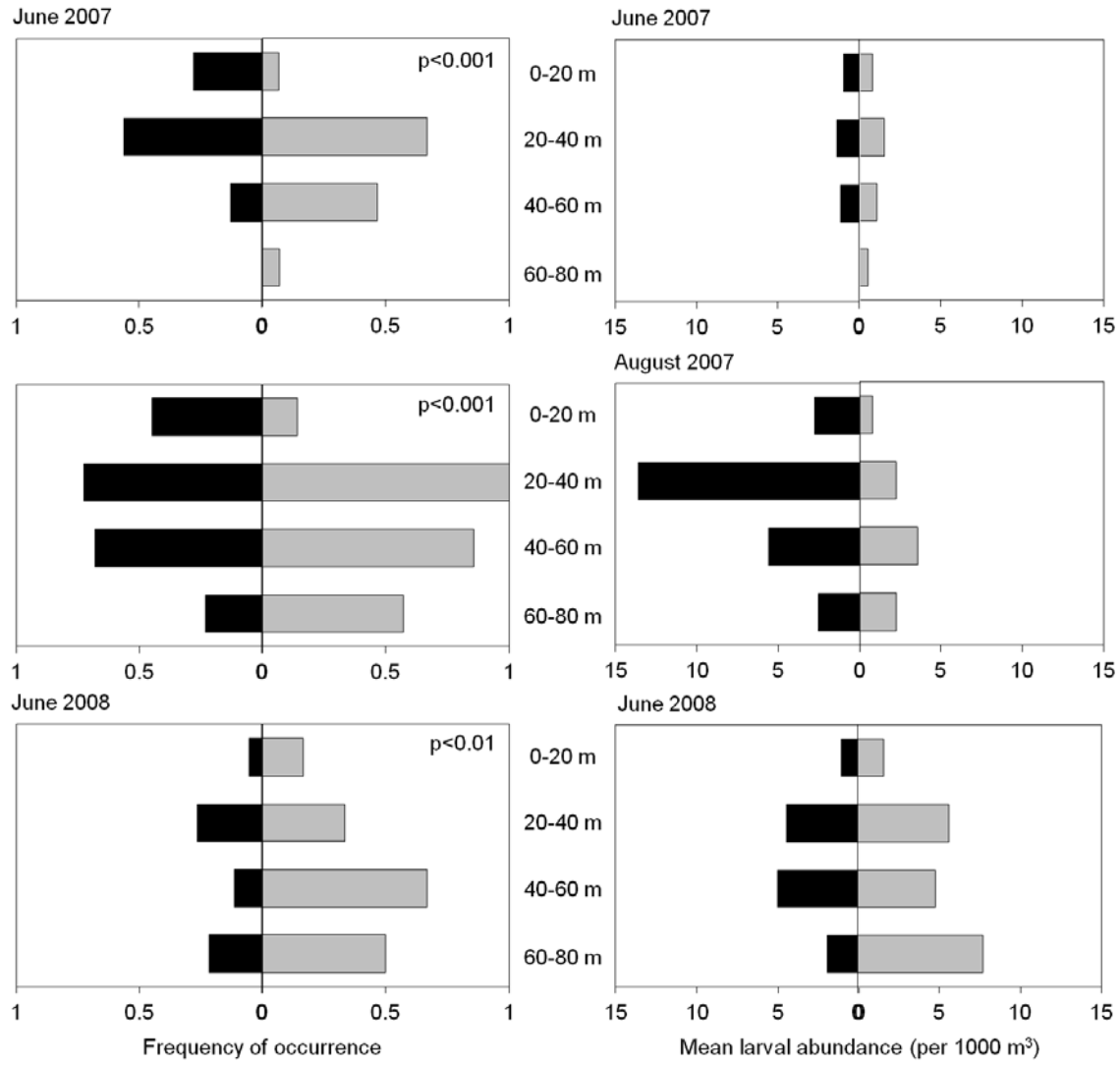


Figure 3.7. Frequency of occurrence and mean larval abundance at ED (black bars) and NE (gray bars) stations for *Cryptotomus roseus*. Data are shown across discretely-sampled 20 m depth bins for each of three sampling periods. Results of two-way chi-square tests shown as p-values on frequency of occurrence plots. Significant results for comparisons of larval abundance between ED and NE stations (Kruskal-Wallis tests conducted separately for each depth bin) are also shown. ED = eddy and NE = no eddy. *p<0.05, **p<0.01, and ***p<0.001.

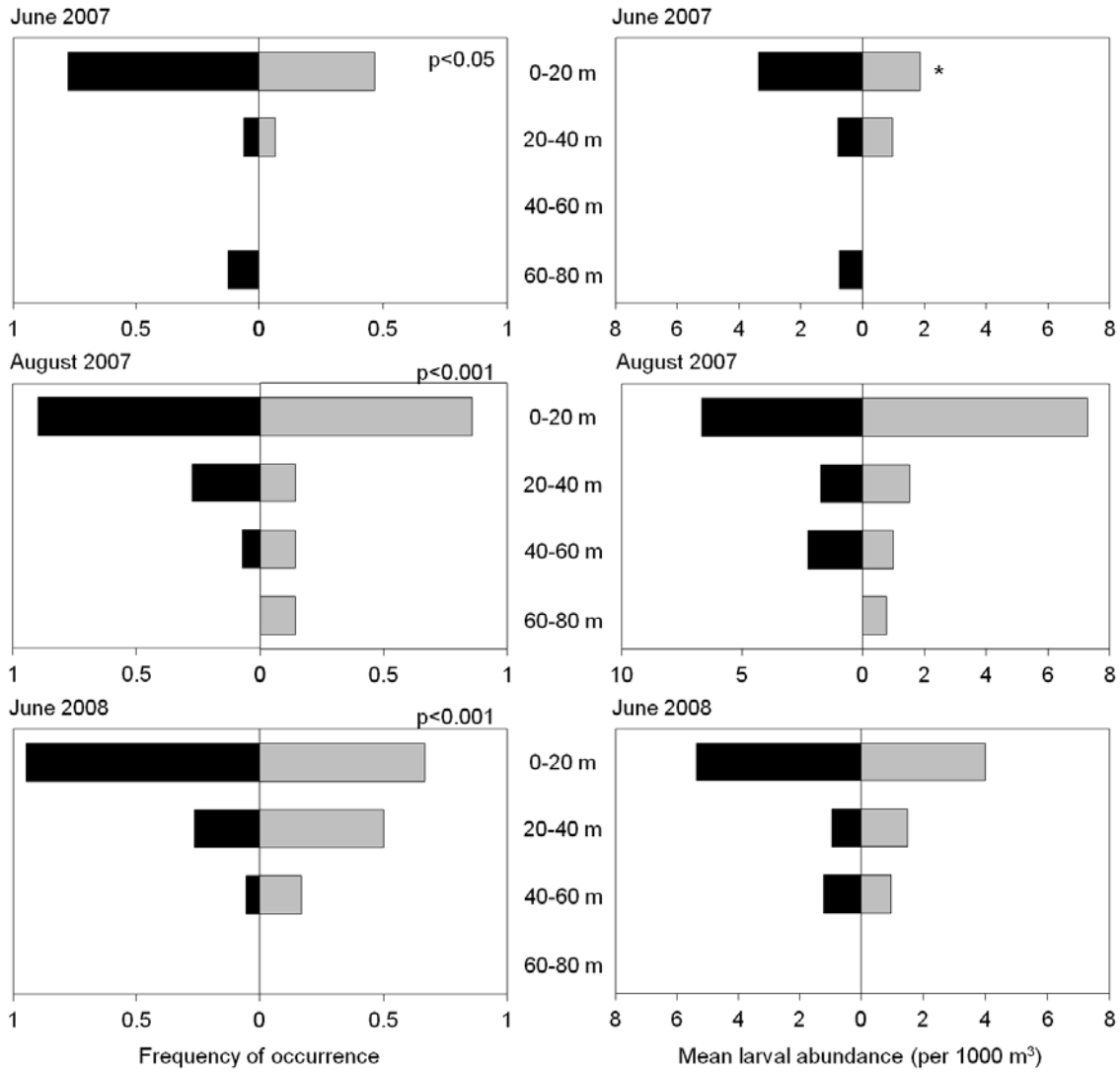


Figure 3.8. Frequency of occurrence and mean larval abundance at ED (black bars) and NE (gray bars) stations for *Sphyraena barracuda*. Data are shown across discretely-sampled 20 m depth bins for each of three sampling periods. Results of two-way chi-square tests shown as p-values on frequency of occurrence plots. Significant results for comparisons of larval abundance between ED and NE stations (Kruskal-Wallis tests conducted separately for each depth bin) are also shown. ED = eddy and NE = no eddy. *p<0.05, **p<0.01, and ***p<0.001.

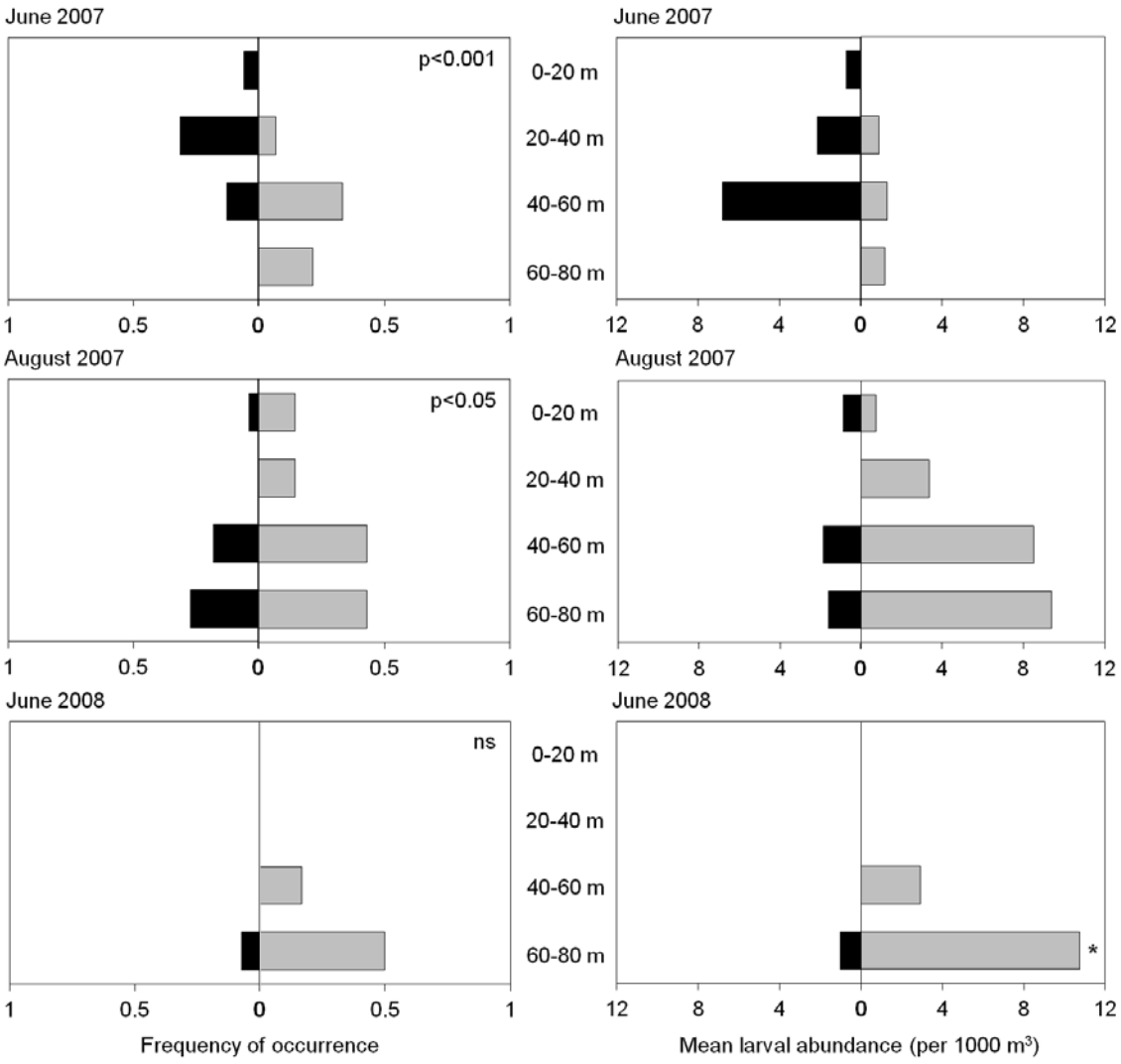
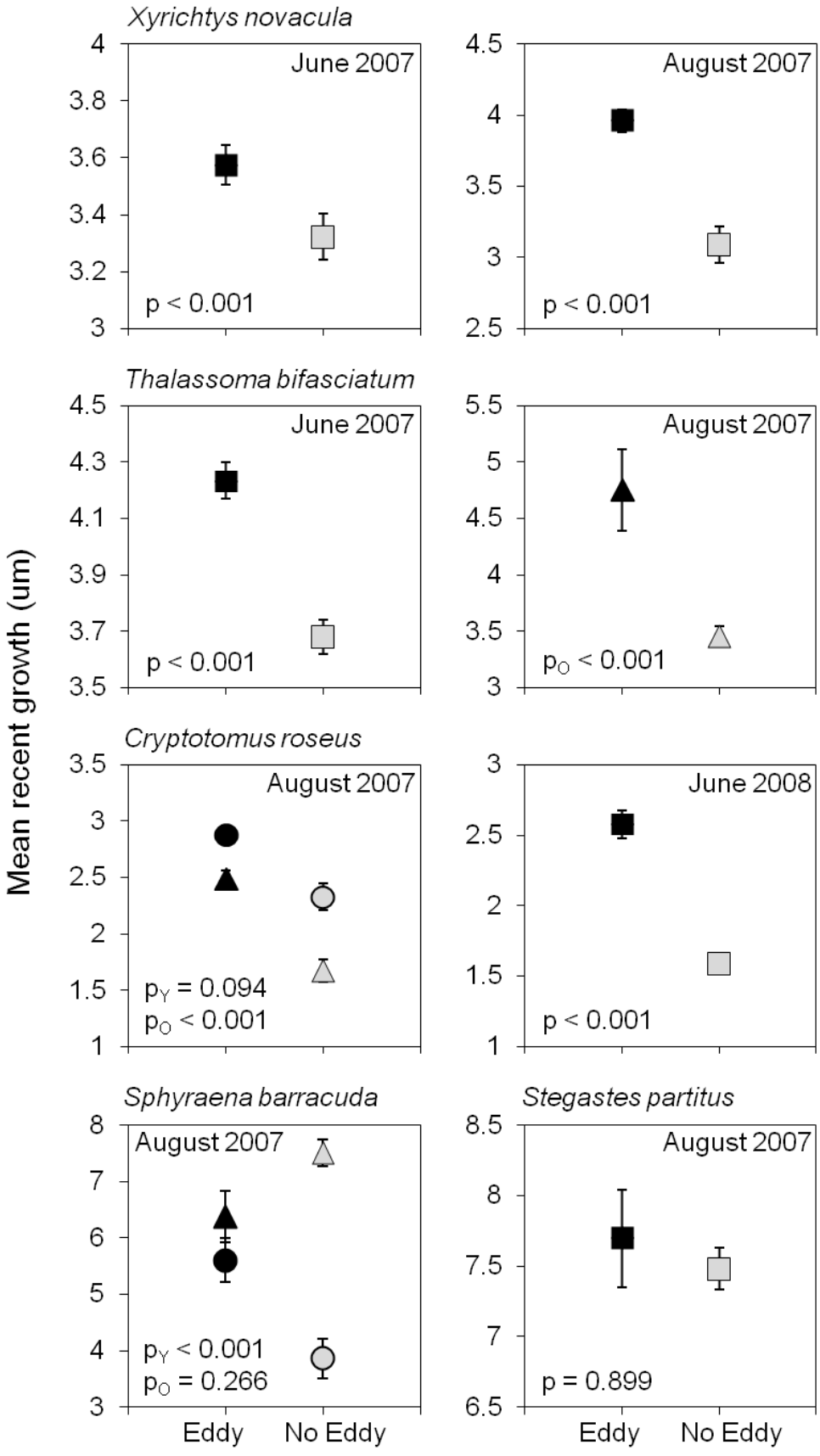


Figure 3.9. Frequency of occurrence and mean larval abundance at ED (black bars) and NE (gray bars) stations for *Stegastes partitus*. Data are shown across discretely-sampled 20 m depth bins for each of three sampling periods. Results of two-way chi-square tests shown as p-values on frequency of occurrence plots. Significant results for comparisons of larval abundance between ED and NE stations (Kruskal-Wallis tests conducted separately for each depth bin) are also shown. ED = eddy and NE = no eddy. *p<0.05, **p<0.01, and ***p<0.001.

Figure 3.10. Comparisons of recent larval growth between ED (black) and NE (gray) groups for *X. novacula* (June and August 2007), *T. bifasciatum* (June and August 2007), *C. roseus* (August 2007 and June 2008), *S. barracuda* (August 2007), and *S. partitus* (August 2007). Where significant interactions between age and group were present, samples were divided into young and old age groups and separate ANCOVAs were performed on each age group. ▲ = comparisons with all ages included, ■ = young age group only, and ● = old age group only. P-values from ANCOVAs are reported on each plot. p_Y = p-value for comparisons in young age groups and p_O = p-value for comparisons in old age groups. ED = eddy and NE = no eddy.


Xyrichtys novacula
June 2007
p < 0.001
August 2007
p < 0.001
Thalassoma bifasciatum
June 2007
p < 0.001
August 2007
pO < 0.001
Cryptotomus roseus
August 2007
pY = 0.094
pO < 0.001
June 2008
p < 0.001
Sphyraena barracuda
August 2007
pY < 0.001
pO = 0.266
Stegastes partitus
August 2007
p = 0.899
Mean recent growth (um)
Eddy
No Eddy
Eddy
No Eddy

Chapter 4. Growth and survival in two reef fish through the pelagic larval stage to settlement

Background

Mortality rates experienced by larval stages of marine fishes are extremely high and temporally variable, resulting from varying combinations of predation, starvation, and advection away from settlement habitat. Mortality is frequently selective, removing individuals with specific early life history traits (ELHTs; e.g., slow larval growth, small size-at-age) from the population (Hare and Cowen 1997, Sogard 1997, Takasuka et al. 2003), and this process can be environmentally-mediated and temporally variable (Gagliano et al. 2007, Grorud-Colvert and Sponaugle 2011, Rankin and Sponaugle 2011). Due to the complex nature of the life cycle of the vast majority of benthic marine organisms, including fishes, mortality impacting vulnerable larval stages significantly affects recruitment variability (e.g., Doherty and Fowler 1994) and can influence survival during subsequent life stages ('carry-over', e.g., Searcy and Sponaugle 2001). Thus, an understanding of the processes driving mortality throughout the larval stage, as well as the temporal and spatial variations within them, is crucial to our ability to describe, and in certain cases, predict patterns observed in juvenile and adult benthic populations.

The growth-mortality hypothesis has developed as a framework in which selective processes can be examined (Anderson 1988). Based on three mechanisms, the hypothesis states that: 1) if predation is size-dependent (e.g., gape-limited), then larvae that attain larger sizes-at-age will exhibit increased survival (i.e., 'bigger-is-better' mechanism, Miller et al. 1988), 2) faster growth rates will lead to reductions in mortality rates because larvae will spend less time at smaller sizes (i.e., 'growth-rate' mechanism, Ware 1975, Shepherd and Cushing 1980), and 3) shorter pelagic larval durations (PLD) will limit

exposure of the most vulnerable life stages to predation in the pelagic environment (i.e., 'stage-duration' mechanism, Houde 1987). Recent work on the pelagic larval stage of marine fishes suggests that, on average, small and/or slow-growing individuals are selectively lost from cohorts, supporting the 'bigger-is-better' and 'growth-rate' mechanisms of the growth-mortality hypothesis (Shoji and Tanaka 2006, Tanaka et al. 2006, Takasuka et al. 2003, 2004, and 2007; but see Sponaugle et al. 2011).

Much of the research examining mortality rates in the pelagic environment has focused on the relative contributions of predation and starvation (Bailey and Houde 1989, Leggett and Deblois 1994). Predation rates on larval fishes are determined by a combination of encounter, attack, and capture rates (O'Brien 1979, Fuiman 1989), which change throughout ontogeny and by predator type. As a consequence, predator-mediated selective mortality is typically temporally and spatially variable and can produce results that contrast expectations of the growth-mortality hypothesis (e.g., Takasuka et al. 2004, Litvak and Leggett 1992, Pepin at al. 1992). Evidence for the link between food availability and larval survival remains largely equivocal in part due to coarse definitions of larval fish prey, which may overlook specificity in larval diets (Llopiz and Cowen 2009). When such dietary preferences are accounted for, high prey abundances have been shown to lead to faster larval growth and larger sizes-at-age (Sponaugle et al. 2009).

In addition to mortality caused by predation and starvation, transport-related processes are integral to the survival of larval fishes (Iles and Sinclair 1982, Cowen and Sponaugle 1997). These transport-related processes, coupled with larval behaviors, can influence mortality rates indirectly by altering rates of growth or predation. Specifically, larvae entrained in a highly productive water mass may be buffered from starvation;

similarly, transport in waters with few predators may result in decreased probability of mortality during the larval stage. Transport-related processes also impact mortality rates directly as larvae can be advected away from suitable settlement habitat. This is particularly relevant to reef fish larvae that must locate and settle into benthic habitats that are patchily distributed and often widely dispersed. This has prompted an emphasis in the tropics on the importance of transport-processes to larval survival and recruitment variability (Cowen and Sponaugle 1997).

While larvae have long been considered passive drifters with dispersal trajectories directed solely by ocean currents (e.g., Roberts 1997), a large body of evidence now demonstrates that larvae have extensive behavioral and sensory capabilities that allow them to orient to their environment and influence dispersal trajectories (Kingsford et al. 2002, Leis 2006). Although mortality due to advection during the larval phase is certainly high, evidence for retention of larvae in the vicinity of parental habitats (Swearer et al. 2002) suggests that life history strategies and larval capabilities have evolved to help maximize survival during this potentially dispersive life stage.

Mortality of reef fish larvae in the SOF

In contrast to previously held views for oligotrophic environments, recent work shows that larval feeding success is high in the Straits of Florida (SOF) (Llopiz and Cowen 2009), and this feeding success has been related to prey availability (Sponaugle et al. 2009). While very little is known about the predator fields of larval fish in this region, some larval fish themselves have been shown to be piscivorous (Llopiz and Cowen 2009). In addition to mortality mediated by feeding and predation, the presence of a major western boundary current (i.e., the Florida Current, FC) in the SOF has major

implications for dispersal trajectories and, thus, the successful transport of larvae to suitable settlement habitats. Larvae in nearshore retention zones will be located closer to such habitats (e.g., the reef tract), while larvae entrained in the FC are more likely to be rapidly advected downstream. The cumulative mortality imposed upon larvae in the SOF will be influenced by variability in the dynamic oceanographic environment as differential transport or residence in water masses with contrasting productivity and predator fields will produce temporal and spatial variation in mortality rates.

An examination of selective mortality by tracking cohorts over time provides information about the types and timing of such processes important in determining overall mortality in the pelagic environment. In the present study, we examine patterns of selective mortality in relation to larval residence in particular water masses in the SOF. Specifically, our objective was to track cohorts of two reef fishes with contrasting life histories through the pelagic environment to the point of settlement to 1) identify the presence of selective mortality in different water masses, 2) determine which ELHTs are important to survival during the larval stage, and 3) establish when during this pelagic stage selective loss of particular traits occurs.

Materials and Methods

Field sampling

To track cohorts through time, we used ichthyoplankton tows to collect reef fish larvae with a broad size/age range from the plankton and light traps to collect late-stage larvae as they moved onshore to settle into benthic habitats. Ichthyoplankton tows were conducted aboard the R/V Walton Smith during three 16-day cruises carried out in the summers of 2007 (May 29 - June 13 and July 30 - August 13) and 2008 (June 17 - July

1). Based on the combined sample sizes of pelagic and settlement-stage larvae, the present study focused on tracking cohorts during the second cruise (i.e., August 2007). During the cruise, ichthyoplankton samples were collected along ten cross-shelf transects that spanned the SOF, from the upper Keys to the Marquesas, and intercepted the LC as it entered the SOF (Figure 4.1). Along each transect, ten stations were sampled, with four stations inside or over the reef tract and six stations outside the reef tract, extending into the FC. Additional stations were sampled after all transects were completed on a zigzag track that ran alongshore from the lower to the upper Keys.

At each station an ichthyoplankton tow was completed using one of two net types as determined by bottom depth. A modified Multiple Opening Closing Net and Environmental Sensing System (MOCNESS, Guigand et al. 2005) was used outside of the reef tract while an inshore frame net (i.e., modified neuston net) was employed at the shallower stations. The MOCNESS sampled from discrete 20 m depth bins down to 80 m using paired nets (4 m^2 and 1 m^2) fitted with 1-mm and 150-μm mesh, respectively. The inshore frame net fished approximately 1 m below the surface with 1-mm and 150-μm nets. Both the MOCNESS and the inshore frame net were fitted with flowmeters that were used to determine the volume sampled during each net tow. Sensors attached to the MOCNESS collected temperature and fluorescence data. All ichthyoplankton tows were conducted during daylight hours, excluding dawn and dusk. Samples were preserved immediately in 95% ethanol, and transferred to 70% ethanol upon returning to the laboratory.

During and after the cruise (i.e., August – September 2007), late-stage larvae were sampled from shore-based sampling stations corresponding to transect locations in the

UK and LK (see Figure 4.1). Late-stage larvae were sampled at two reefs in the upper Keys (PI: Pickles and SI: Sand Island) and at two reefs in the lower Keys (AS: American Shoal and LK: Looe Key) by deploying four replicate light-traps at each reef 1 m below the surface and 50 m apart. Traps fished from sunset to sunrise during a total of two 15-day periods that encompassed both the new and third-quarter lunar phases during which many coral reef fishes settle. Samples of settlement stage larvae were preserved immediately in 95% ethanol. Based on sample sizes of settlement-stage larvae, data analyses in the present study only included settlement-stage larvae collected from light traps in the lower Keys.

All ichthyoplankton samples collected with the large-mesh nets (i.e., 1 mm) and all light-trap samples were processed by separating all fish larvae from other plankton, and then identifying each specimen to the lowest possible taxonomic grouping with reference to a regional ichthyoplankton guide (Richards 2006).

Study species

Based on our ability to identify larvae to the species level and to obtain adequate sample sizes for tracking cohorts through time, we chose two species of reef fish for otolith analysis: *Stegastes partitus* (bicolor damselfish) and *Cryptotomus roseus* (bluelip parrotfish). Importantly, these species have contrasting life histories enabling the comparison of patterns of selective mortality, or lack thereof, between two life history strategies. Adults of *S. partitus* are common along the Florida Keys reef tract, though highest densities occur in piles of dead coral rubble at the reef base. This species is gonochoristic and females produce benthic eggs in nests that are subsequently guarded by males. Adults of *C. roseus* are found in seagrass beds adjacent to the reef tract. They are

sequential hermaphrodites, changing from female (i.e., the initial phase) to male (i.e., the terminal phase), and during spawning events planktonic eggs are released directly into the water column. The different modes of egg production (i.e., benthic and pelagic) observed in these study species may lead to differences in size- or development-at-hatching which can subsequently influence swimming abilities or orientation behaviors. While much species-specific information on such behaviors remains unknown, damselfish (i.e., family Pomacentridae) have been shown to be strong swimmers especially late in larval life (Leis 2006).

Otolith analysis

Sample sizes obtained from ichthyoplankton tows and light traps enabled us to track a single cohort of *S. partitus* and *C. roseus* during the summer of 2007. Due to low light-trap catches or a temporal mismatch of those catches with samples from ichthyoplankton tows, we were only able to track cohorts onshore to the lower Keys. Thus, we limited our analyses of samples from ichthyoplankton tows to those collected along transects in the western SOF (i.e., offshore of the lower Keys, Marquesas Keys, and in the LC) as these larvae would be more likely to settle to the lower Keys (in contrast to larvae collected farther downstream in the SOF). To compare otolith-derived ELHTs of larvae sampled 1) nearshore, but not in an eddy (NN, see Chapter 2), 2) nearshore, but at an eddy edge (EE, see Chapter 2), and 3) in an eddy (ED, see Chapter 2), where sample sizes allowed, only for *C. roseus*, we included larvae collected on transects in the middle and upper Keys, but these samples were treated separately and their downstream location addressed explicitly.

Otolith analysis was conducted on a subset of larvae from each species to obtain growth rates and ages. The abundance and size distribution of the subset of larvae used for otolith analysis was proportional to that of all larvae in each sample. Standard length (SL) or notochord length (NL) was measured to the nearest 0.01 mm for each larva using a Leica MZ12 dissecting microscope, a Cool Snap-Pro monochrome digital camera, and Image-Pro Plus 7.0 image analysis software (Media Cybernetics). Sagittal (*C. roseus*) or lapillar (*S. partitus*) otoliths were dissected from each sample and stored in immersion oil ~ 7-14 d to facilitate reading. All otoliths from a given species were analyzed by a single reader. Otoliths were read along the longest axis at 400X magnification through a Leica DMLB microscope and with the aid of the digital camera and Image-Pro Plus software. All otoliths were read at least twice, and if the reads differed by ≤ 5%, one read was randomly chosen for analysis. If reads differed by > 5%, a third read was conducted. This third read was then compared to the first two reads. If either comparison differed by ≤ 5%, one read from that comparison was randomly chosen for analysis; otoliths where all reads differed by > 5% were removed from any further analysis (Sponaugle 2009).

Environmental variability and larval demographics across water masses

To relate possible variation in ELHTs to environmental variability or differences in larval distributions, we compared temperature, fluorescence, plankton displacement volume, distance from shore, larval age and standard length, and larval abundance among water masses. Temperature and fluorescence were averaged across the water column at each sampling station, after spurious data from the first 2 m were removed. Plankton displacement volume was determined using standard techniques (Postel et al. 2000) for samples from the small-mesh nets (i.e., 150 μm) collected from the most shallow depth

bin (i.e., 0-20 m) at each station. Distance from shore was determined for each station using the 'haversine' function which calculates the shortest distance over the earth's surface (between each station and the closest point on land), taking into account the curvature of the earth. Temperature, fluorescence, plankton displacement volume, and distance from shore were compared among water masses using one-way ANOVAs and Tukey post-hoc pairwise comparisons. In addition to these environmental variables, standard length and age of larvae were compared among water masses separately for *S. partitus* and *C. roseus* using one-way ANOVAs and Tukey post-hoc pairwise comparisons. Finally, larval abundance was compared across water masses with Kruskal-Wallis tests as data did not conform to assumptions of parametric tests and sample sizes were small for some comparisons.

Data analysis

To insure that larvae belonged to a single cohort (i.e., hatched within a limited time window), hatch date was calculated for each individual by subtracting the collection date from age at collection. Then all hatch dates falling outside of a 26-d (*S. partitus*) or 30-d (*C. roseus*) hatch window were removed from further analysis (D'Alessandro et al. in review). Using a single cohort for each species, we examined otolith-derived patterns in ELHTs. As previous work has shown that the water mass in which larvae are entrained can significantly influence growth (see Chapter 3), we first compared larval growth (i.e., otolith increment width) and size-at-age (i.e., otolith radius) of the late-stage larvae collected in light traps (L_S, i.e., survivors: larvae that successfully reached the point of settlement) to pelagic larvae sampled from each water mass. In the analysis of *S. partitus*, we used larvae from two water masses defined in Chapter 3 as eddy (ED) and no eddy

(NE). The NE grouping corresponds to the FC stations in Chapter 2 that are located on the LK, MQ, and LC transects. For *C. roseus*, we used larvae from ED and NE water masses, and from two additional water masses delineated in Chapter 2 as nearshore/no eddy (NN) and eddy edge (EE). If no differences among water masses were detected, samples were combined for comparisons among age groups. In cases where growth differed significantly among water masses, we compared two age groups separately for each water mass (where sample sizes allowed). To compare ELHTs among age groups, larvae collected in ichthyoplankton tows were divided into young (i.e., L_Y) and old (i.e., L_O) age groups that maximized sample sizes in each group, and compared to the surviving late-stage larvae collected in light traps (i.e., L_S).

Growth and size were plotted for each day of pelagic life, but for analysis, we tested growth and size at only 2-3 points in larval life. To reduce noise in the data at those points, we averaged growth over 3-d intervals [*S. partitus*: 4-6 and 8-10 d post-hatch (dph); *C. roseus*: 4-6, 14-16, and 23-25 dph]. Size-at-age is a cumulative trait and thus was compared among groups at specific time points (*S. partitus*: 5 d and 9 dph; *C. roseus*: 5, 15, and 24 dph). All time points or intervals at which we compared ELHTs were chosen to maximize sample sizes yet maintain independence between comparisons. Data were log-transformed when necessary to conform to assumptions of normality and homoscedasticity. For cases in which transformation was ineffective and data remained non-normal or heteroscedastic, ANOVA has been shown to be robust to these deviations from assumptions when sample sizes are sufficiently large (i.e., > 6, Underwood 1997). As our sample sizes were quite large, ranging from 18 to 133, we proceeded with ANOVAs in spite of some variations from normality or homoscedasticity. Mean otolith

growth and size-at-age were compared among water mass and age group using one-way ANOVAs (SYSTAT 11). Significant results for an ANOVA were followed up with Tukey post-hoc pairwise comparisons.

Results

Environmental variability and larval demographics across water masses

Mean temperature was lowest in the ED water mass compared to all others, though this difference in temperature was not significant for the comparison between ED and NE (Table 4.1). Fluorescence was similar across water masses, though the ED water mass had a significantly higher mean than the NN water mass. Plankton displacement volume was low in the NE water mass compared to all others. Finally, the average distance from shore for NE stations was greatest, followed by ED, and then NN and EE stations.

Standard length and age of *S. partitus* larvae did not differ significantly among water masses (Figure 4.2a, Table 4.1). In contrast, characteristics of *C. roseus* larvae varied significantly among water masses. Mean standard length was highest in EE larvae (7.73 mm) compared to larvae from all other water masses (ED = 7.13 mm, NE = 6.79 mm, NN = 7.05 mm; Table 4.1), however, the pattern in age did not correspond to that observed for standard length. *Cryptotomus roseus* larvae were younger in ED and NN water masses relative to EE and NE water masses (Figure 4.2b, Table 4.1). Thus, larvae in the NE water tended to be relatively small and old, compared larvae from other water masses. Although NE larvae were older than EE larvae (27.1 versus 24.7 d), this difference was marginally non-significant (Tukey post hoc pairwise comparison: $p = 0.069$).

Larval abundance of *S. partitus* was significantly greater at NE than ED stations (Kruskal-Wallis, p = 0.043), with a mean (± SE) of 19.29 (± 5.76) and 7.83 (± 2.15) larvae per 100 m^2 at NE and ED stations, respectively (Figure 4.3a). The opposite trend was apparent for *C. roseus* with a mean (± SE) of 34.71 (± 7.08) larvae per 100 m^2 at ED stations and 13.40 (± 2.17) larvae per 100 m^2 at NE stations. However, there were no significant differences in abundance of *C. roseus* larvae across water masses (Kruskal Wallis, p = 0.929; Figure 4.3b).

Stegastes partitus

Residence of *S. partitus* larvae in different water masses did not influence their growth or survival. Specifically, larvae from ED and NE water masses did not differ from each other or from surviving, late-stage larvae in growth or size-at-age (Figure 4.4, Table 4.2). Although the slight increase in size-at-age at 5 dph of NE larvae compared to survivors was marginally significant, the same comparison was not significant in Tukey post-hoc tests. When we combined larvae from ED and NE water masses and compared ELHTs among age groups (i.e., L_Y, L_O, and L_S), mean growth at 4-6 dph was significantly slower in the old compared to the young age group, even while growth of larvae from young and old age groups did not differ significantly from survivors (Figure 4.5, Table 4.3). This growth difference was not maintained through time, as mean growth was the same in all age groups by 8-10 dph. However, the growth difference early in larval life (4-6 dph) did manifest into a smaller size-at-age for old compared to young larvae at 9 dph, suggesting the presence of weak selection for slow growth or small size-at-age for *S. partitus* during early larval life (i.e., 9 dph). However, the survivors were

larger-at-age than the old group indicating that the direction of selection for size-at-age may reverse as larvae continue through the pelagic stage to settlement.

The PLDs of *S. partitus* captured in light traps ranged from 26-34 d with a mean (±SE) of 28.98 (± 0.24) d and a coefficient of variation (standard deviation/mean) of 0.059 (Figure 4.6a).

Cryptotomus roseus

In contrast to *S. partitus*, mean growth and size-at-age of *C. roseus* larvae were significantly impacted by the water mass from which larvae were sampled. Specifically, NE larvae grew more slowly than larvae from all other water masses and from survivors during all time periods (i.e., 4-6, 14-16, and 23-25 dph; Figure 4.7, Table 4.4). In addition, survivors grew faster than ED and EE larvae at 23-25 dph. Growth differences led to a divergence in size-at-age between NE larvae and all other larvae (i.e., ED, EE, NN, and survivors), with significant differences in size-at-age detected at all time points examined (i.e., 5, 15, and 24 dph). The difference in growth at 23-25 dph between the survivors and ED/EE larvae did not translate into a difference in size-at-age.

Due to the significant effect of water mass on *C. roseus* larval growth and size-at-age, we compared age groups separately for ED, EE, and NE larvae. NN larvae sample sizes were small, precluding an analysis of age groups. Although larval growth and size-at-age were similar in ED and EE water masses, environmental variables (i.e., temperature and distance from shore) differed. Since samples sizes were sufficient, we kept ED and EE larvae separate in further analyses. When divided by water mass, there was evidence of selective mortality late in the larval period. Specifically, in both the ED and EE water masses, survivors were growing faster than old larvae at 23-25 dph (Figure

4.8, Table 4.5). However, earlier in the larval period (i.e., 4-6 and 14-16 dph), mean growth did not differ among young larvae, old larvae, or survivors. The growth difference late in the larval stage for *C. roseus* was not apparent in comparisons of size-at-age between old larvae and survivors (see right panels in Figure 4.8). In the NE water mass, young and old larvae grew consistently slower than survivors throughout the larval period. Because differences in growth were large and persistent, young and old larvae had smaller sizes-at-age than survivors at all time points examined. There were also some differences between young and old larvae early in the larval period. Specifically, young larvae had significantly larger sizes-at-age than old larvae at 5 dph. Young larvae were also growing slightly faster than old larvae at this time (i.e., 4-6 dph), but this difference was not significant nor was it maintained throughout the rest of the larval period.

The mean (±SE) PLD of *C. roseus* was 31.56 (± 0.41) d. PLDs of larvae captured in light traps ranged from 27-45 d with a coefficient of variation of 0.091 (Figure 4.6b).

Discussion

Variability in ELHTs across water masses

Otolith-derived ELHTs did not vary by water mass for *S. partitus* larvae. This is consistent with Chapter 3 findings showing that the high productivity of mesoscale eddies (i.e., the ED water mass) did not confer higher recent growth upon larvae of this species residing in eddies. In contrast to *S. partitus*, larval *C. roseus* exhibited significantly slower growth in the NE water mass compared to larvae sampled from ED, NN, and EE water masses. Because growth differences were substantial and consistent throughout the larval period, NE larvae were also smaller-at-age than all other larvae. These differences in ELHTs, particularly between ED and NE water masses, are comparable to the finding

that recent growth of *C. roseus* larvae was enhanced by residence in mesoscale eddies (see Chapter 3).

Temperature variation among water masses does not explain the observed growth differences for larval *C. roseus*. The ED water mass had the lowest mean temperature, yet growth of ED larvae was comparable to that of larvae in NN and EE water masses which were, on average, >1°C warmer. Warmer temperatures should lead to increased growth (Houde 1989); thus, the fast growth in ED larvae due to the high productivity associated with mesoscale eddies (Hitchcock et al. 2005) may have been moderated by relatively low temperatures, resulting in similar growth rates in ED, NN, and EE larvae. However, the NE water mass had temperatures similar to NN and EE stations yet larvae in this water mass had significantly slower growth, indicating that productivity and food availability are interacting with temperature to shape growth variability among water masses.

Variation in fluorescence among water masses was not consistent with observed growth differences in *C. roseus*; however, the pattern in plankton displacement volume, with a significantly lower volume in the NE water mass, mirrored the pattern in larval growth. As plankton displacement volume (i.e., secondary production) is a more relevant measure of prey availability for larval fishes, these data suggest that ED, NN, and EE water masses which were all located closer to shore than the NE water mass, may provide better feeding habitats for *C. roseus* larvae. Nearshore environments have long been described as highly productive compared to their offshore counterpart (Sander and Steven 1973, Denman and Powell 1984), and in the SOF this productivity may be driven in large part by mesoscale and sub-mesoscale processes. The formation and propagation of eddies

along the front of the FC is well documented (Lee 1975, Lee et al. 1994, Fratantoni et al. 1998, Kourafalou and Kang 2012), and both primary and secondary production increase in response to the upwelling of nutrients at eddy cores (Lee et al. 1992, Lane et al. 2003, Hitchcock et al. 2005). The increased growth of ED and EE larvae can be explained by the high productivity associated with eddies, although the EE larvae should be regarded with caution. Identification of precise eddy boundaries is challenging and the EE water mass may contain some stations that fall outside of the eddy. Although we cannot determine the precise dispersal history of larvae sampled from each water mass, it is possible that NN larvae also spent a portion of the larval stage associated with an eddy. Alternatively, the high growth rates of NN larvae were simply sustained by high nearshore productivity. The nearshore waters of the upper Keys (i.e., the area between the reef tract and the FC) are periodically impacted by the passage of sub-mesoscale eddies (Sponaugle et al. 2005, D'Alessandro et al. 2007) and the increased productivity resulting from such events may have contributed to high growth in NN larvae.

Variable larval growth among water masses has also been identified in the Bay of Biscay where juvenile anchovy (*Engraulis encrasicolus*) residing over the shelf break grew faster than individuals in oceanic waters (Allain et al. 2003). This is consistent with the present study in that higher growth was associated with a position closer to shore. Hamilton et al. (2008) also observed faster growth for *T. bifasciatum* larvae developing in nearshore waters, although slow-growers returning from offshore compensated by growing faster late in the larval period as they moved onshore to settle. In contrast, the growth trajectories we observed for NE *C. roseu*s larvae never converged with those of nearshore larvae or survivors. If NE larvae were exhibiting compensatory growth prior to

settlement, we would have seen a signal of this in the growth trajectories of survivors. This was not the case, indicating that *C. roseus* individuals from offshore waters did not exhibit compensatory growth.

Regardless of the exact processes driving growth differences among water masses the presence of associated variation in ELHTs is significant. As differential growth and size-at-age during the larval stage can influence larval survival and success in subsequent stages (Searcy and Sponaugle 2001, Vigliola and Meekan 2002), these collective results suggest that residence in a water mass will be an important determinant of survival during and potentially after the larval stage.

Selective mortality

The signal of selective mortality across *S. partitus* larval stages was weak and inconsistent. Although there was some indication that slow-growing larvae may have survived preferentially during early larval life (i.e., 5 dph), larger size-at-age was associated with survivors by 9 dph, and in general there was little variation in ELHTs among individuals. Although the range in ages of larvae examined in our old and young groups was limited (i.e., all were < 14 d old), these results suggest that selective mortality is not a significant force shaping distributions of ELHTs in *S. partitus* in the plankton. Research focused on *S. partitus* late-stage larvae and juveniles revealed that the direction and strength of selective mortality during and immediately following settlement was strongly influenced by season and temperature (Rankin and Sponaugle 2011). In the winter and spring (i.e., cool temperatures) surviving juveniles had faster larval growth and shorter PLDs, while juvenile survivors in the summer (i.e., warm temperatures) had longer PLDs, slower growth early in the larval period, and faster growth later in the larval

period. Although the signal of selection was weak in the present study, it is consistent with the observation of Rankin and Sponaugle (2011) that summer survivors had slow growth early in the larval period.

In contrast to *S. partitus*, the pattern of selective mortality for *C. roseus* was clear and consistent. Although mortality was not selective with regard to growth or size-at-age for most of the larval period, at ~ 20 dph the growth curve of old larvae began to diverge from that of the survivors. This divergence was most apparent in the NE water mass, where growth of both old and young larvae was consistently slower than that of survivors. Young and old NE larvae were also consistently smaller-at-age than survivors, while for larvae in ED and EE water masses, growth divergences at 24 dph did not translate immediately into differences in size-at-age. This is likely due to the inherent delay between growth differences contributing to differences in cumulative size-at-age. However, if the lack of size-at-age differences is real, this would be consistent with the 'growth-rate' mechanism of the growth-mortality hypothesis whereby the slower growers are selectively removed. The absence of fast-growing larvae from the old age group at 24 dph could also be explained by net avoidance as these more highly developed larvae were presumably better swimmers. However, the fact that we observed the pattern consistently across water masses (i.e., ED, EE, and NE) while age, standard length, and growth varied among water masses, suggests this pattern is best explained by selective mortality in *C. roseus*.

Our finding of selective loss of slow growing *C. roseus* larvae is in contrast to another study in which older pelagic larvae of the bluehead wrasse, *Thalassoma bifasciatum*, in the northern SOF were found to have slower growth and smaller sizes-at-

age than younger larvae (Sponaugle et al. 2011). However, this latter study used a somewhat different approach in which larvae from multiple cohorts where combined in a cross-sectional analysis. In addition to the methodological, taxonomic, spatial, and temporal differences between the two studies, our contrasting findings may also be explained by predation, as several studies have shown that the pattern in selective mortality is determined by and varies with predator-type. Studies focusing on a variety of predators (e.g., large piscivores and jellies) have shown that prey selection is either not size- or growth-dependent or that predators remove larger, fast-growing individuals from the population (Litvak and Leggett 1992, Pepin et al. 1992, Takasuka et al. 2004, 2007). On the other hand, small pelagic predators and cannibalistic conspecifics have been shown to remove slow-growing larvae from the population as would be predicted by the growth-mortality hypothesis (Takasuka et al. 2004, 2007). Thus, the preferential survival of small, slow-growing *T. bifasciatum* and fast-growing *C. roseus* could be explained by differences in predator fields.

Comparison of life history strategies

The contrasting results we obtained for *S. partitus* and *C. roseus* mirror substantial species-specific differences in life histories and morphology. A major dichotomy in the early life history strategies of reef fishes is the production of demersal versus planktonic eggs (Cowen and Sponaugle 1997). Our study species encompass both modes of egg production, as *S. partitus* is a demersal spawner with nest-guarding by adult males and *C. roseus* is a pelagic spawner that releases eggs directly into the plankton. As maternal investment has been shown to be important to survival of larval and juvenile stages and can determine the direction of selection (Berkeley et al. 2004, Gagliano and

McCormick 2007), it is likely that mode of egg production influences patterns of selective mortality in the plankton. However, additional work with greater temporal coverage that focuses on more species with contrasting life histories is required to elucidate the relationship between mode of egg production and selective mortality.

The relatively short and less variable PLD (CV = 0.059) exhibited by *S. partitus* is accompanied by considerably less variation in ELHTs (e.g., mean growth and size-at-age) compared to *C. roseus*. It is possible that *S. partitus* ELHTs do not provide sufficient variation upon which selective processes can act. In contrast, *C. roseus* has a slightly longer and more variable PLD (CV = 0.091). Greater flexibility in the timing of settlement may lead to greater growth- and size-related differences by the end of the pelagic phase, paving the way for selective mortality.

Morphological differences between *S. partitus* and *C. roseus* may also underlie the contrasting results we obtained for these species. *Stegastes partitus* larvae are short and relatively deep-bodied compared to the long, slender *C. roseus* larvae, and such morphological differences likely influence swimming abilities and vulnerability to predation. Damselfish are known to be strong swimmers (Leis 2006) and wrasses and parrotfishes less so (Stobutski and Bellwood 1997), thus differential swimming ability may influence both encounter rates and predator avoidance capabilities. Although significant species-specific differences in early life history strategies, morphology, and behavior likely influence patterns of mortality in the plankton, the precise effects of such distinctions on mortality remain unclear.

Implications for population connectivity in the SOF

The variation we observed in ELHTs among water masses for *C. roseus*, and the presence of selective mortality acting upon that variation has significant implications for population connectivity. While slow-growers were selectively removed from the larval population in all water masses starting at approximately 20 dph, NE larvae were removed entirely from the population of survivors as a signal of the distinct growth trajectories of NE larvae was absent from the growth trajectories of survivors. Thus, larvae sampled from the NE water mass (i.e., the Loop Current) do not appear to contribute to the settlement occurring onto reefs of the lower Keys. It is possible that NE larvae settled to reefs farther downstream (i.e., UK), however, the extremely low catches of late-stage *C. roseus* larvae in light traps deployed in the upper Keys indicate that this is unlikely. Thus, our results suggest that *C. roseus* larvae from the NE water mass do not contribute to population replenishment in the Florida Keys. It is reasonable to assume that a significant proportion of larvae in the NE water mass originated from distant populations due to the upstream locations of the NE stations. This is also consistent with the observation of older ages in the NE water mass. Hamilton et al. (2008) similarly found slow growth in larval *T. bifasciatum* that were developing in offshore waters. However, they hypothesized that these larvae were able to compensate by growing rapidly late in the larval stage as they moved through nearshore waters towards settlement habitat. We did not observe an increase in growth for NE larvae as they apparently never entered nearshore waters. The slow-growing NE larvae with small sizes-at-age may have lacked the swimming capabilities required to enter nearshore waters or they could have been rapidly removed from the nearshore population by selective predation. D'Alessandro and

Sponaugle (2011) found high rates of predation mortality in waters just offshore of the reef tract in the lower Keys; however, this work was conducted in waters closer to shore than the ED, EE, and NN water masses in our study and, therefore, may not represent predation experienced by *C. roseus* moving inshore from the NE water mass.

Our examination of two reef fishes in the SOF highlights species-specific differences in patterns of selective mortality during the larval stage. The ELHTs of *S. partitus* did not differ between water masses nor did they exhibit a pattern of selective mortality. In contrast, *C. roseus* larvae in the NE water mass had slow growth and were smaller at age compared to larvae from all other water masses. In addition, slow-growing *C. roseus* larvae from all water masses were selectively removed from the population late in the larval stage, prior to settlement. Thus, selective mortality appears to be important in shaping *C. roseus* populations as they prepare to transition to a benthic existence. Importantly, NE larvae were not represented in the survivor group. As most larvae originating from distant sources would be found in the NE water mass, our results suggest larvae with long-distance dispersal trajectories do not contribute to the replenishment of reefs in the lower Keys.

Table 4.1. Comparison of environmental variables and larval demographics among water masses. Mean (±SE) values are shown for five environmental variables. In addition, mean (±SE) standard length and age in each water mass are provided for *Stegastes partitus* and *Cryptotomus roseus*. n = sample size. Significant p-values resulting from one-way ANOVAs are in bold and accompanied with results from Tukey pairwise comparisons. ED = eddy, EE = eddy edge, NE = no eddy, and NN = nearshore/no eddy. [#]water masses not shown were not involved in any signficant Tukey pairwise comparisons.

	Water mass					
	ED	NE	NN	EE	p-value	
Temperature (°C)	27.17 (0.17)	28.21 (0.09)	28.74 (0.37)	28.48 (0.51)	**< 0.001**	NN = EE > ED [#]
Fluorscence (volts)	0.119 (0.001)	0.112 (0.004)	0.109 (0.003)	0.120 (0.005)	**0.030**	ED > NN [#]
Plankton displacement volume ($mL \cdot L^{-1}$)	0.092 (0.005)	0.045 (0.005)	0.099 (0.010)	0.107 (0.007)	**< 0.001**	ED = NN = EE > NE
Distance from shore (km)	41.32 (6.25)	116.25 (10.59)	11.12 (0.94)	11.53 (1.00)	**< 0.001**	NE > ED > NN = EE
Stegastes partitus						
Standard length (mm)	3.51 (0.19)	3.26 (0.79)	-	-	0.369	
Age (d)	12.30 (0.57)	11.96 (0.35)	-	-	0.589	
n	56	67	-	-	-	
Cryptotomus roseus						
Standard length (mm)	7.13 (0.09)	6.79 (0.15)	7.05 (0.19)	7.73 (0.11)	**< 0.001**	EE > ED = NE = NN
Age (d)	21.87 (0.39)	27.11 (0.84)	21.62 (0.86)	24.73 (0.56)	**< 0.001**	NE = EE > NN = ED
n	133	38	26	49	-	

Table 4.2. Comparisons of *Stegastes partitus* early life history traits among water mass groups and a survivor group (ED, NE, and L_S). using one-way ANOVAs. Mean growth (otolith increment width) was compared over 4-6 dph and 8-10 dph and size-at-age (otolith radius) was compared at 5 dph and 9 dph. ED = eddy, NE = no eddy, and L_S = surviving late-stage larvae captured in light traps. [#]not significant in Tukey pairwise comparisons.

Trait	Days post-hatch	F	df	p
Mean growth	4 - 6	1.216	2, 170	0.299
(otolith increment width)	8 - 10	0.358	2,123	0.700
Size-at-age	5	3.114	2,170	0.047[#]
(otolith radius)	9	0.433	2,151	0.649

Table 4.3. Results of one-way ANOVA comparisons of *Stegastes partitus* mean otolith growth (otolith increment width, 4-6 dph and 8-10 dph) and size-at-age (otolith radius, 5 dph and 9 dph) among age groups (young, old, and surviving larvae). Significant values are in bold and accompanied with results from Tukey pairwise comparisons. L_Y = young larvae, L_O = old larvae L_S = surviving larvae captured in light traps. [#]age groups not shown were not involved in any signficant Tukey pairwise comparisons.

Trait	Days post-hatch	F	df	p	
Mean growth	4 - 6	4.330	2,182	**0.015**	$L_O < L_Y$ [#]
(otolith increment width)	8 - 10	2.105	2,134	0.126	
Size-at-age	5	1.034	2,182	0.358	
(otolith radius)	9	5.601	2,163	**0.004**	$L_O < L_Y = L_S$

Table 4.4. Comparisons of *Cryptotomus roseus* early life history traits among water mass groups and a survivor group. Results are from one-way ANOVAs comparing mean growth (otolith increment width) and size-at-age (otolith radius) among groups. Traits were compared separately at three time points: 5, 15, and 25 dph. Significant values are in bold and accompanied with results from Tukey pairwise comparisons. ED = eddy, EE = eddy edge, NN = nearshore/no eddy, NE = no eddy, and SUR = survivor. [#]water masses not shown were not involved in any signficant Tukey pairwise comparisons.

Trait	Days post-hatch	F	df	p	
Mean growth	4 - 6	6.265	4,291	**<0.001**	ED = EE = NN = L_S > NE
(otolith increment width)	14 - 16	6.219	4,274	**<0.001**	ED = EE = NN = L_S > NE
	23 - 25	13.933	3,118	**<0.001**	L_S > ED = EE > NE
Size-at-age	5	3.849	4,291	**0.005**	ED = NN > NE [#]
(otolith radius)	15	20.668	4,281	**<0.001**	ED = EE = NN = L_S > NE
	24	7.356	3,137	**<0.001**	ED = EE = L_S > NE

Table 4.5. Comparisons of *Cryptotomus roseus* early life history traits among age groups. One-way ANOVAs comparing mean growth (otolith increment width) and size-at-age (otolith radius) among age groups were conducted separately for each water mass. Traits were compared at three time points: 5, 15, and 25 dph. Significant values are in bold and accompanied with results from Tukey pairwise comparisons. ED = eddy, EE = eddy edge, NE = no eddy. Subscripts indicate age groups within a water mass: $_Y$ = young, $_O$ = old, and $_S$ = survivor. [#]age groups not shown were not involved in any signficant Tukey pairwise comparisons.

Trait	Water mass	Days post-hatch	F	df	p	
Mean growth	ED	4 - 6	0.285	2,180	0.753	
(otolith increment width)		14 - 16	0.088	2,168	0.916	
		23 - 25	8.825	1,71	**0.004**	$ED_O < L_S$ [#]
Size-at-age		5	1.504	2,180	0.225	
(otolith radius)		15	0.386	2,172	0.681	
		24	0.475	1,81	0.493	
Mean growth	EE	4 - 6	0.335	2,96	0.716	
(otolith increment width)		14 - 16	2.739	2,95	0.070	
		23 - 25	8.922	1,70	**0.004**	$EE_O < L_S$ [#]
Size-at-age		5	0.339	2,96	0.714	
(otolith radius)		15	0.044	2,95	0.957	
		24	0.091	1,77	0.913	
Mean growth	NE	4 - 6	8.177	2,85	**0.001**	$NE_O < L_S$ [#]
(otolith increment width)		14 - 16	5.933	2,83	**0.004**	$NE_Y < L_S$ [#]
		23 - 25	29.703	2,74	**< 0.001**	$NE_O < L_S$ [#]
Size-at-age		5	3.847	2,85	**0.025**	$NE_O < NE_Y = L_S$
(otolith radius)		15	19.600	2,84	**< 0.001**	$NE_Y = NE_O < L_S$
		24	26.819	2,75	**< 0.001**	$NE_O < L_S$

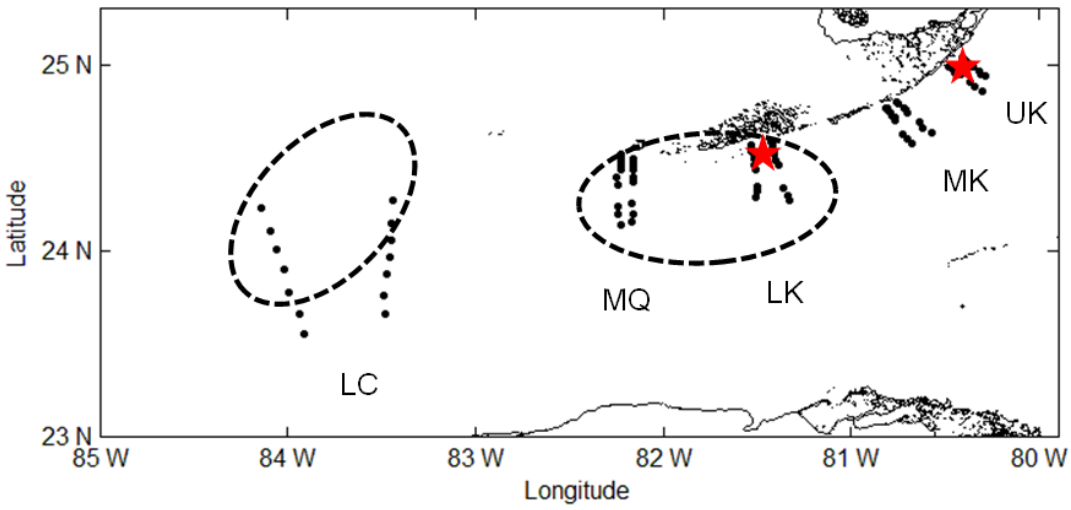


Figure 4.1. Map of study area showing sampling station locations (black points) during the August 2007 cruise and approximate locations of reef sites where late-stage larvae were collected with light-traps (red stars). Rough positions of mesoscale eddies at the time of the cruise are superimposed on the map with dotted lines.

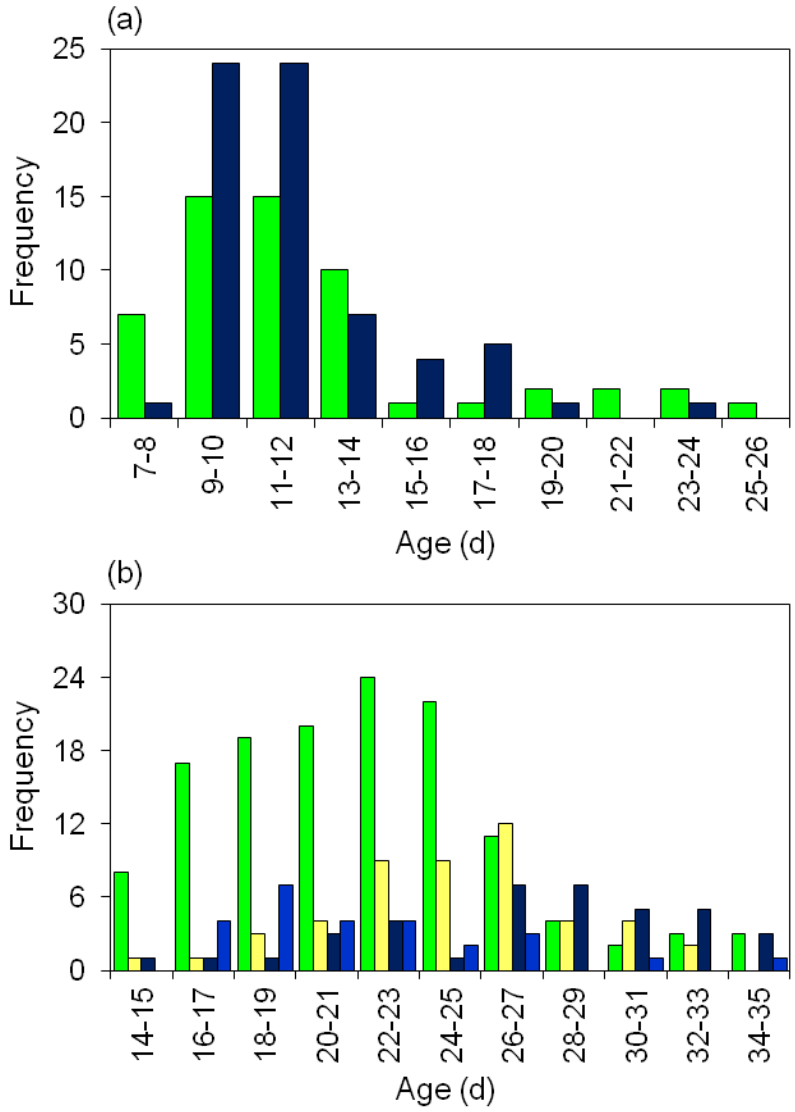


Figure 4.2. Age distributions of (a) *Stegastes partitus* and (b) *Cryptotomus roseus* larvae sampled from ED (green bars), NE (dark blue bars), NN (blue bars), and EE (yellow bars) water masses. ED = eddy, NE = no eddy, NN = nearshore/no eddy, and EE = eddy edge.

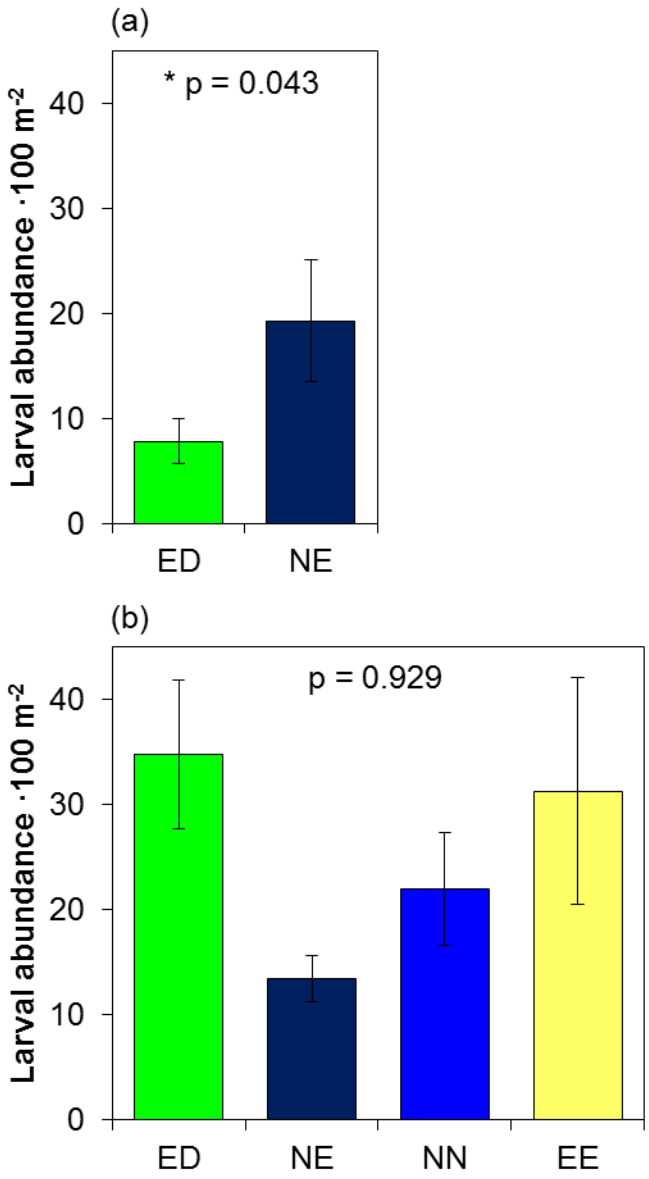


Figure 4.3. Comparison of larval abundance (±SE) among water masses for (a) *Stegastes partitus* and (b) *Cryptotomus roseus* larvae. P-values from Kruskal-Wallis tests are shown on each plot with significance denoted by an asterisk. ED = eddy, NE = no eddy, NN = nearshore/no eddy, and EE = eddy edge.

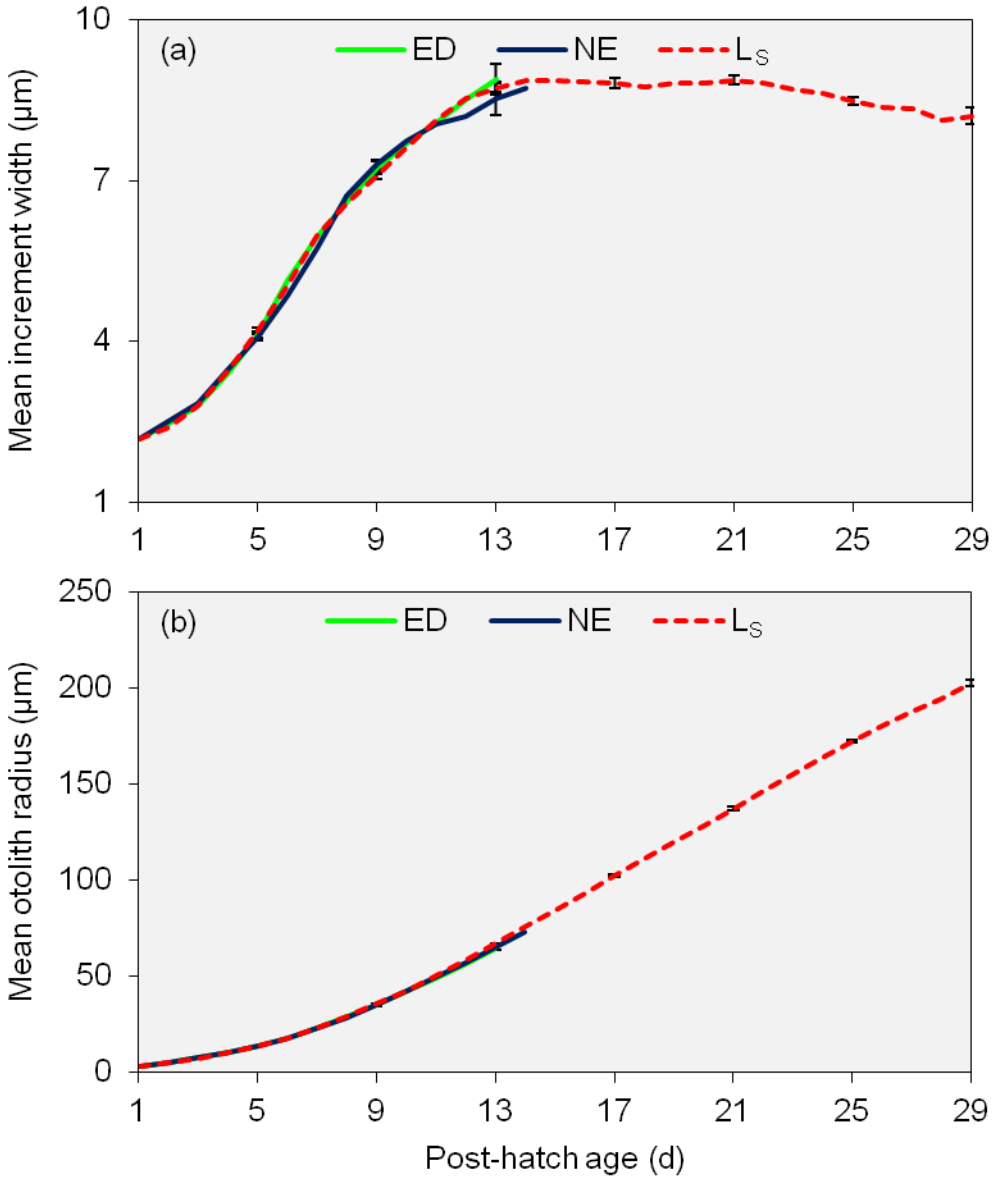


Figure 4.4. *Stegastes partitus* (a) mean daily growth (otolith increment width) and (b) size-at age (otolith radius at age) at each day of life for ED (green line) NE (blue line) and L_S larvae (orange dashed line). Error bars (±SE) are shown every four increments for reference. ED = eddy, NE = no eddy, and L_S = surviving late-stage larvae captured in light traps.

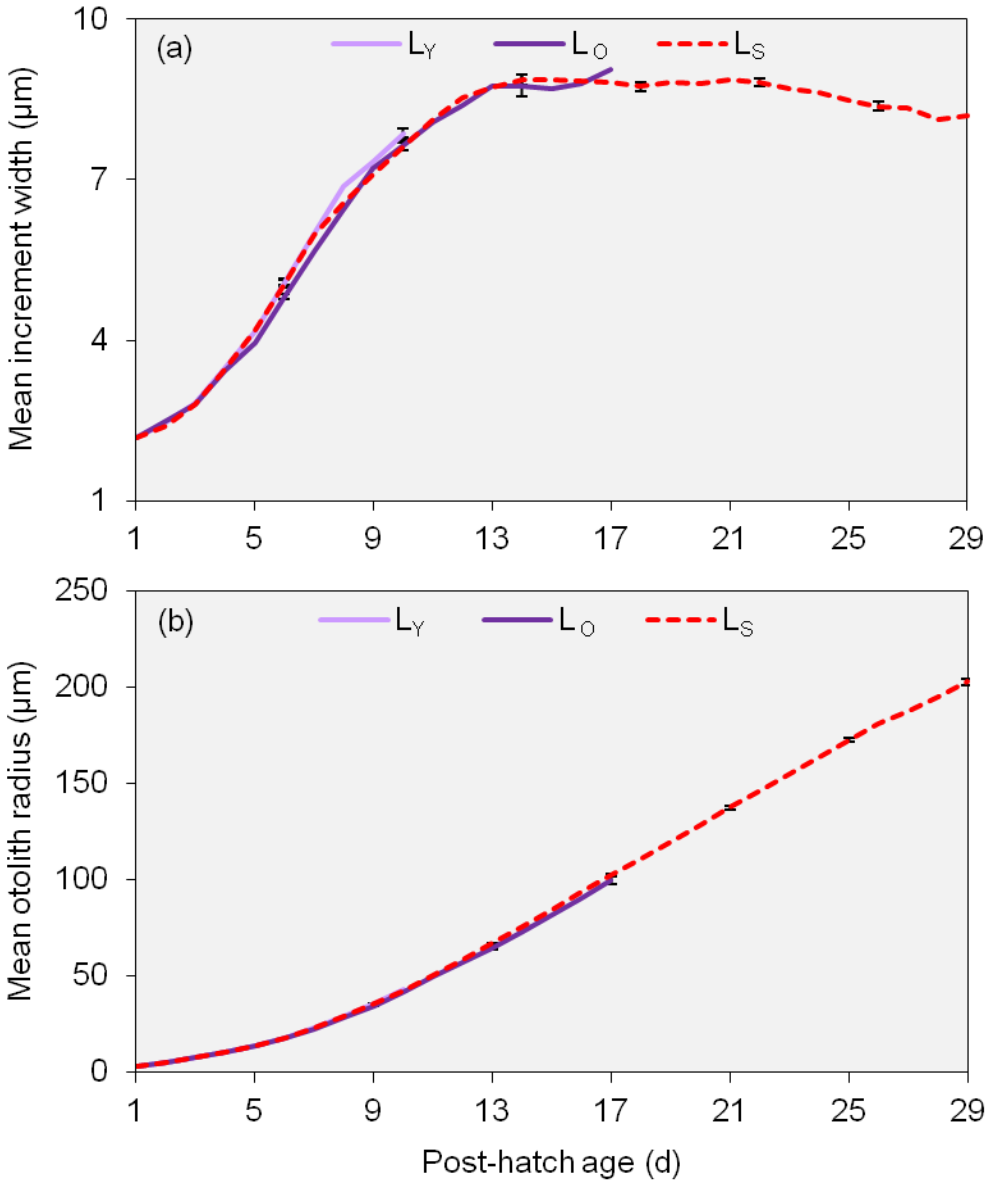


Figure 4.5. *Stegastes partitus* (a) mean daily growth (otolith increment width) and (b) size-at age (otolith radius at age) at each day of life for L_Y (light purple line) L_O (dark purple line) and L_S larvae (orange dashed line). Error bars (±SE) are shown every four increments for reference. Significant comparisons among groups are denoted with an asterisk. L_Y = young larvae, L_O = old larvae, and L_S = surviving late-stage larvae captured in light traps.

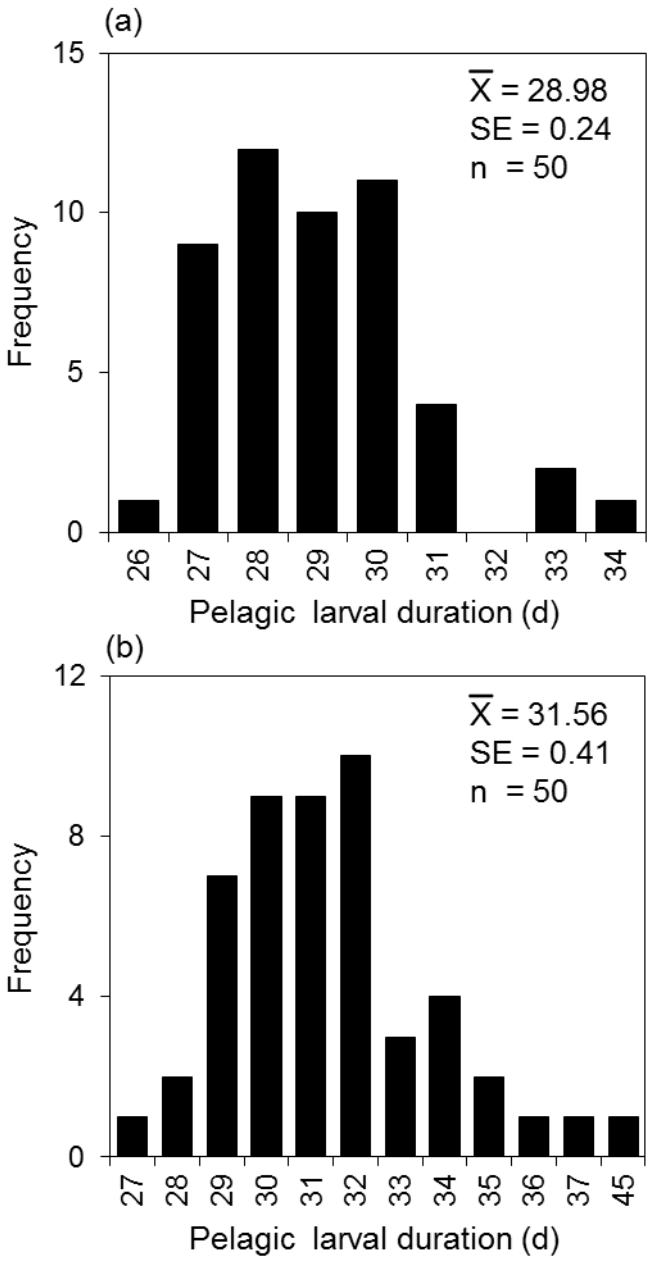


Figure 4.6. Distributions of pelagic larval duration (PLD) for (a) *Stegastes partitus* and (b) *Cryptotomus roseus* settlement-stage larvae captured in light traps. Mean PLD with standard error and sample size are included for each species.

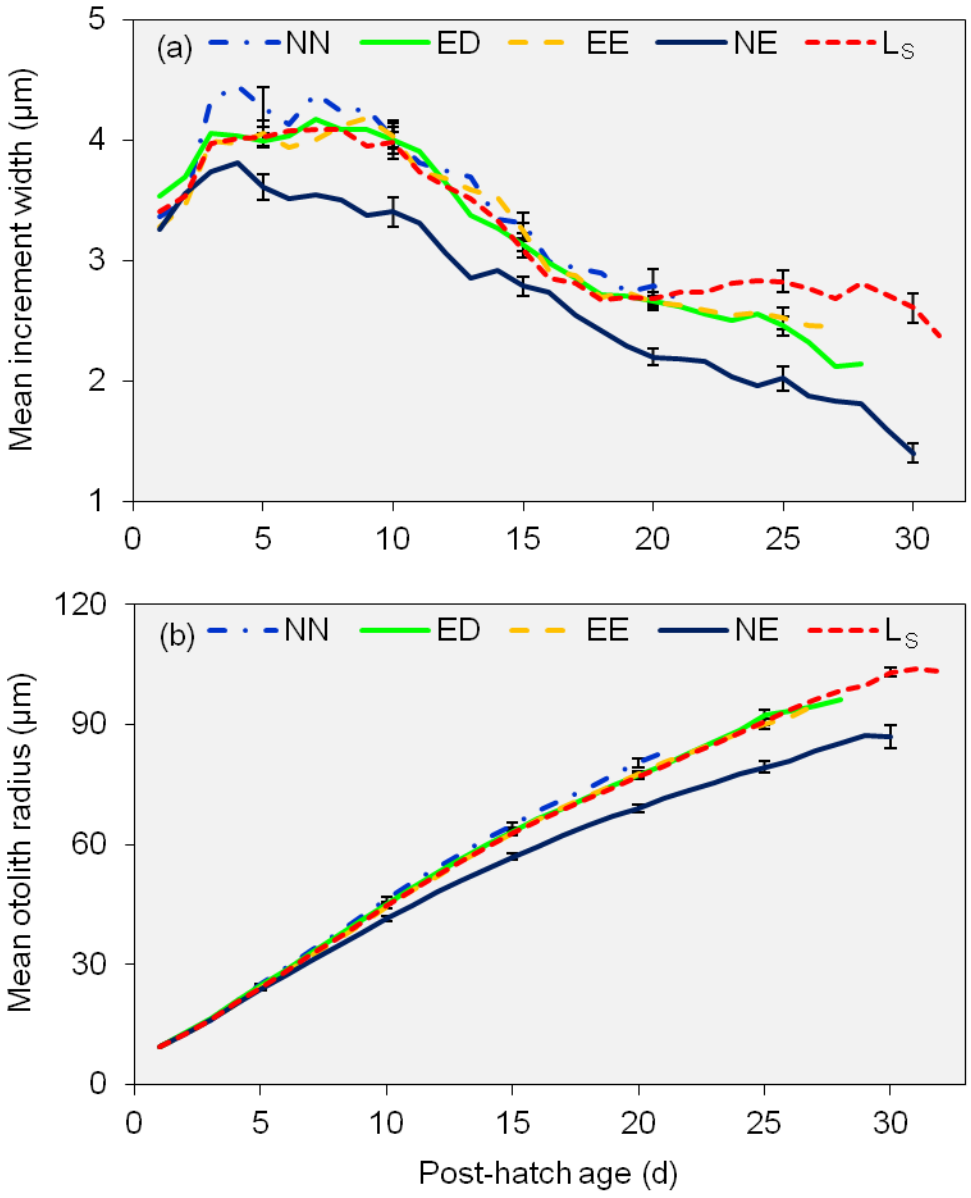


Figure 4.7. *Cryptotomus roseus* (a) mean daily growth (otolith increment width) and (b) size-at age (otolith radius at age) at each day of life for NN (blue dashed line), ED (green line), EE (yellow line), NE (dark blue line) and L_S larvae (orange dashed line). Error bars (±SE) are shown every five increments for reference. NN = nearshore/no eddy, ED = eddy, EE = eddy edge, NE = no eddy, and L_S = surviving late-stage larvae captured in light traps.

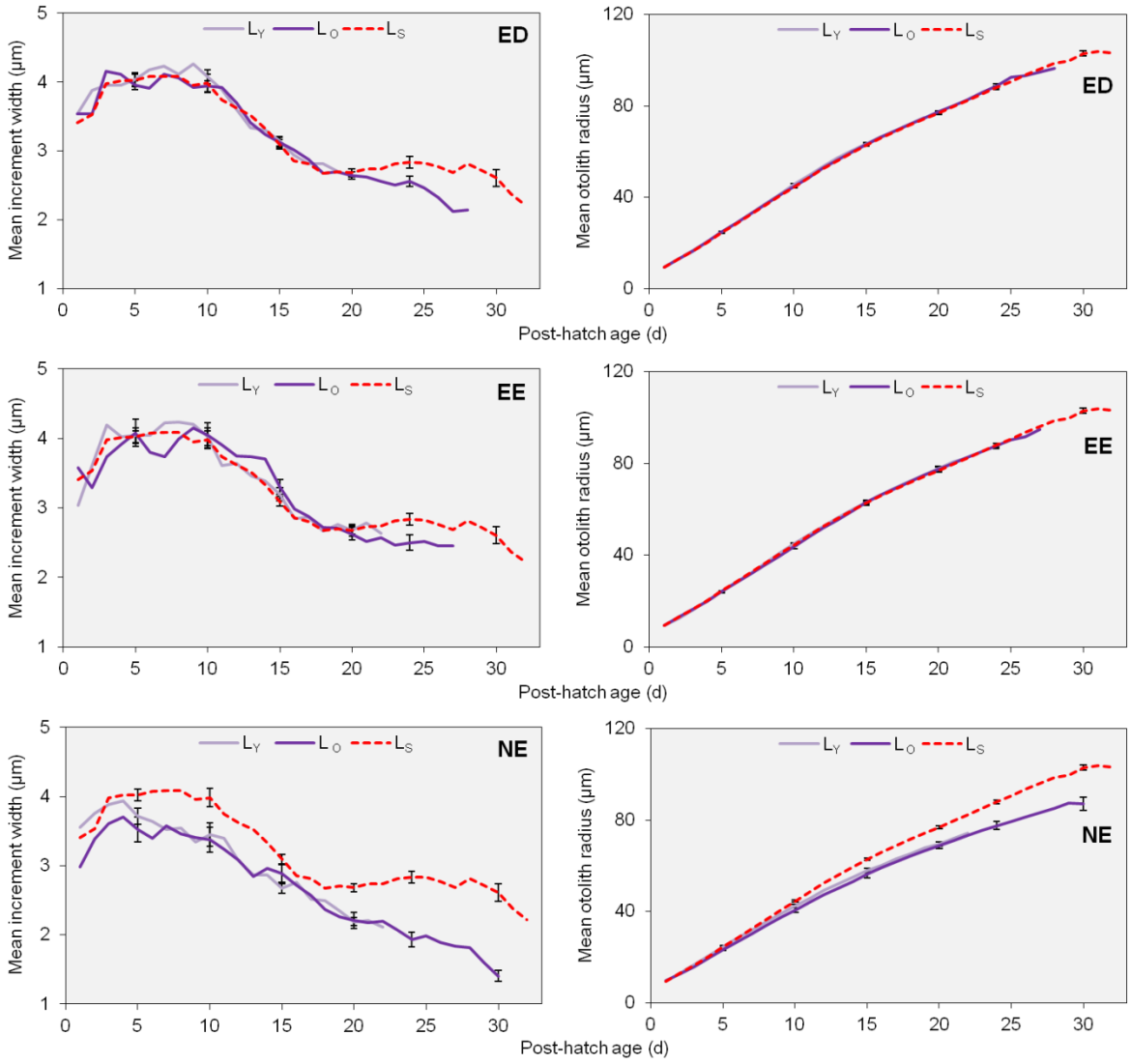


Figure 4.8. *Cryptotomus roseus* (left panels) mean daily growth (otolith increment width) and (right panels) size-at age (otolith radius at age) at each day of life for L_Y (light purple line) L_O (dark purple line) and L_S larvae (orange dashed line) separated by water mass. Error bars (±SE) are shown every five increments for reference. NN (nearshore/no eddy) did not have sufficient sample sizes for age group comparisons. ED = eddy, EE = eddy edge, NE = no eddy, L_Y = young larvae, L_O = old larvae, and L_S = surviving late-stage larvae captured in light traps.

Chapter 5. Conclusions

Overall, this dissertation contributes to our understanding of larval distributions, growth, and mortality, all of which collectively act to shape patterns of population connectivity. We extend evidence for the importance of self-recruitment in benthic marine populations to a dynamic system along a contiguous continental coastline. Specifically we found that environmental variation across the water column was most important in structuring larval assemblages in the Straits of Florida (SOF) and that horizontal variation in oceanographic features (i.e., mesoscale eddies, MEs, versus Florida Current, FC) significantly influenced growth-related processes. Specifically, larvae in eddy waters grew faster than those in non eddy waters (NE) located upstream and offshore. Selection for fast-growing larvae was evident during the late larval stage. In addition, slow-growing larvae from offshore waters did not contribute to the surviving population of settlement-stage larvae. Finally, several lines of evidence, including temporal changes in larval assemblages and patterns of larval abundance and age across water masses, are consistent with the existence of nearshore retention of locally-spawned larvae in the SOF.

Larval assemblages in the SOF

By resolving associations between larval fish assemblages and the oceanographic environment we can move towards a more mechanistic understanding of larval distributions and subsequent impacts on transport processes. In the SOF, larval assemblages were significantly more distinct vertically across the water column (separated by 10s of m) than they were horizontally across water masses (separated by 10s to 100s of km; Chapter 2). While the variation in larval assemblages among stations

was highly correlated with temperature, temperature co-varies with many other factors and, therefore, correlation in this case does not signal causation. Interestingly, temperature is strongly related to depth and associated pressure differences which have previously been identified as important in determining larval distributions of reef fishes in the SOF (Huebert 2008, Huebert et al. 2010). While the precise variables driving vertical structure in larval assemblages remain unclear, these results emphasize that examination of depth-related variation in distributions may be more productive than focusing on differences across water masses.

Although horizontal structure of larval assemblages was relatively weak compared to vertical patterns, we did observe that the larval assemblages found in MEs were consistently different from FC and NE water masses (Chapters 2 and 3). In addition, larval assemblages associated with the same ME were shown to be temporally variable, changing substantially over a two-month period (Chapter 3). Thus, while water mass may not be the primary driver shaping patterns of larval assemblages, our results indicate that MEs do alter the biological environment with which they interact. The degree to which these alterations affect population replenishment and connectivity patterns remains unknown and thus warrants future research as MEs are dominant features in the SOF (Lee et al. 1994, Kourafalou and Kang 2012) and elsewhere (e.g., Nakata et al. 2000, Atwood et al. 2010, Govoni et al. 2010, Holliday et al. 2011, Contreras-Catala et al. 2012).

MEs as "ocean triads" in the SOF

Our study strongly supports the role of MEs as 'ocean triads' (sensu Bakun 1996) in the SOF. Specifically, these oceanographic features enhance the survival of fish larvae

and subsequent recruitment success by augmenting production through nutrient enrichment, concentrating prey fields in zones of convergence, and retaining larvae near suitable settlement habitat (Bakun 1996). Although we did not observe consistently high levels of fluorescence or plankton displacement volumes at stations located in MEs (Chapter 3), this may have been due to a mismatch between the complex trophic dynamics occurring in eddies and sampling of the environment (Govoni et al. 2010). Alternatively, it is possible that the signal of productivity associated with MEs was simply not located in the eddy (ED) stations (i.e., at the eddy core), as such productivity may be concentrated in convergence zones located in the eddy periphery. However, in comparisons of environmental variables across water masses conducted specifically for the August 2007 sampling period, eddy edge (EE) stations did not exhibit high levels of fluorescence or plankton displacement volume (Chapter 4). Similarly, a key component of an 'ocean triad' is the concentration of prey fields. Thus by averaging our measures of productivity across the water column and stations, we may have obscured important fine-scale variations in prey fields between ED and NE water masses (Chapter 3). Finally, the measure of plankton displacement volume does not take into account species-specific diets of reef fish larvae (Llopiz and Cowen 2009), resulting in a coarse measure of feeding environment that does not represent a biologically-realistic scenario.

Regardless of the similarities in measured productivity between ED and NE stations, we found a strong pattern of enhanced recent growth for larval reef fishes in MEs (Chapter 3). This increase in growth was observed across four species from three different families, and it was temporally consistent among sampling periods. The main exception was a similarity in growth of *S. partitus* larvae from ED and NE stations.

Perhaps the preferred prey items of this species were not abundant in the ED stations. The diet of *Stegastes* spp. in general includes a variety of organisms, but *Farranula* spp. and *Onacaea* spp. are particularly important for smaller larval size classes with a transition to more calanoid copepods as larvae grow (Llopiz and Cowen 2009). There is also evidence that cool temperatures experienced by larvae in ED stations may have moderated the enhanced growth resulting from increased productivity. Growth trajectories of *C. roseus* larvae were similar in NN, EE, and ED water masses during the August 2007 sampling period, yet the mean temperature of ED stations was > 1°C cooler than mean temperatures of NN and EE stations (Chapter 4). Thus, decreased temperatures in ED stations may have limited the growth experienced by ED larvae. However, this explanation implies that *S. partitus* larvae are particularly sensitive to temperature variations relative to other species as we observed faster recent growth in eddies for larvae of four other species. Overall, the consistent pattern of enhanced growth in MEs indicates that these oceanographic features fulfill the requirements of an 'ocean triad' for nutrient enrichment and concentration of prey.

In addition, age distributions of larvae sampled from MEs are consistent with the idea that these features can retain locally-spawned individuals (i.e., young ages) and that those individuals can survive the duration of the larval period inside the eddy (i.e., old ages; Chapter 2). Temporal differences in the larval assemblages of Eddy 2 as it moved from an upstream position at the entrance of the SOF to a location offshore of the lower Keys also provide evidence for local retention (Chapter 3). These temporal differences were driven primarily by increases in abundance of a number of larval reef fishes, with the input of additional larvae into the eddy likely resulting from spawning events along

the FK reef tract coinciding with the propagation of Eddy 2. In fact, age distributions of *T. bifasciatum* in Eddy 2 show that the change in larval abundance for this species between the June and August 2007 sampling periods was mainly due to the addition of young larvae prior to August. As *T. bifasciatum* spawns daily on coral reefs, these larvae likely originated in the SOF. In contrast, Eddy 2 contained young *X. novacula* larvae in June 2007 and a range of ages in August 2007. While temporal patterns of spawning of *X. novacula* are unknown, *X. novacula* adults spawn over sandy areas that are likely extensive along the west Florida shelf, so the *X. novacula* larvae in Eddy 2 may have been entrained prior to its propagation farther east into the SOF. However, the range in ages in August 2007 is again consistent with larval retention. The differential pattern of larval retention by eddies observed for *T. bifasciatum* and *X. novacula* may be related to distinctions in adult spawning habitat as well as possibly spawning periodicity. Thus, the degree to which self-recruitment contributes to fish populations in the SOF may be mediated by the distribution of adult habitat and spawning activity.

In summary, our collective evidence supports the role of MEs as 'ocean triads' and thus emphasizes the importance of these oceanographic features as larval habitat in the SOF. While the importance of eddies in enhancing primary productivity is well-recognized (McGillicuddy et al. 1998, Hitchcock et al. 2005, Moore et al. 2007), and recent evidence suggests that eddies serve as important feeding habitats for organisms across a spectrum of trophic levels (Cotte et al. 2007, Sabarros et al. 2009, Kai and Marsac 2010), this is the first study to date illustrating that residence in MEs leads to increases in growth rates for a diverse array of larval reef fishes.

Patterns of selective mortality in the plankton

We found no evidence of selective mortality in our examination of a single cohort of *S. partitus* larvae (Chapter 4). In contrast, slow-growing *C. roseus* larvae were selectively removed from the population beginning at approximately 20 days post-hatch (dph). This positive selection for fast-growing larvae is consistent with the growth-mortality hypothesis, and the timing of such selection marks the importance of the settlement event, the transition between pelagic and benthic stages, in the life cycle of reef fishes (McCormick and Makey 1997, Doherty et al. 2004). The lack of selective mortality during the first 10-20 dph observed for both *S. partitus* and *C. roseus* suggests that selective processes are not significantly shaping ELHTs throughout a large portion of larval life. While these results represent only one cohort for each species, size-selective processes may be more likely to occur during the juvenile stage and may be easier to detect as the amount of variability in ELHTs increases over time (Sogard 1997). The results of our study indicate that mortality acting upon the earliest larval stages (~ 5-20 dph) is either random in relation to size and growth, or it is so complex that the signal of selective processes cannot be identified.

Yet our results for larvae of *C. roseus* indicate that near the end of the larval stage, fast growth may be critical for survival and the successful transition to the benthic juvenile stage. Fast growth may be beneficial if it confers the ability to avoid predators or reach suitable settlement habitat by swimming. Alternatively, fast growth may be an indication of high condition and, thus, larvae of high condition may be better equipped to divert resources to the process of metamorphosis (Searcy and Sponaugle 2001, McCormick et al. 2002). As many larval reef fishes undergo extensive developmental and

morphological changes during the transition from a pelagic to a benthic existence and mortality during this transition can be high (Doherty et al. 2004), it is likely that the examination of additional species with greater temporal coverage will also reveal selective processes acting near the end of the larval stage prior to settlement.

Population connectivity in the SOF

The SOF is located downstream of the Caribbean Sea and its network of reef systems, with the Loop Current (LC) serving as a potential conduit delivering larvae from the greater Caribbean to the FK reef tract. Thus, reef fish populations in the SOF have the potential to be strongly connected to upstream sources. On the other hand, locally spawned larvae originating from the FK reef tract may be retained subsequent to spawning events in nearshore current regimes, particularly the complex flow fields of mesoscale eddies forming and propagating along the front of the FC. Larvae embedded in the body of the FC may be more likely to be advected downstream out of the SOF.

Our results suggest that larvae transported to the SOF from upstream sources may not contribute substantially to population replenishment as we found that slow-growing *C. roseus* larvae from the NE water mass were not represented in the growth trajectories of surviving larvae captured by light traps as they settled onto reefs in the lower Keys (Chapter 4). It was not possible to assess the origin of surviving *S. partitus* larvae as growth trajectories did not vary between water masses. Thus, we cannot determine if the failure of larvae from distant sources (i.e., larvae from the NE water mass) to settle to reefs is a species-specific phenomenon (*C. roseus* versus *S. partitus*) or possibly a temporally variable pattern because only one cohort of each species was examined. However, the complete absence of NE larvae from the survivor population of *C. roseus* is

compelling and suggests that at least for some species and settlements events, distant populations of the Caribbean are not well-connected to reefs in the SOF. This finding echoes recent modeling results that show, even for *S. partitus*, replenishment of Florida Keys populations is largely from local sources (Sponaugle et al. 2012).

Evidence from larval abundances and age distributions collectively show that locally-spawned larvae can be retained in nearshore waters of the SOF. Specifically, larval abundances were highest in nearshore/no eddy (NN), EE, and ED water masses, particularly for reef fishes (Chapter 2). In fact, NN stations exhibited the highest larval abundances in spite of the potential for high predation rates in these waters (D'Alessandro and Sponaugle 2011). However, comparisons of larval abundances between ED and NE water masses (Chapter 3) demonstrated that abundance patterns are both species-specific and temporally variable. The presence of both young and old larvae in MEs indicates that recently-spawned (i.e., locally-produced) larvae can be entrained in eddies and subsequently survive in this water mass (Chapter 2). Retention of locally-spawned larvae is a prerequisite for self-recruitment, however, for larvae to contribute to local populations they must survive the larval stage and settle to the reef. As such, larval *C. roseus* from nearshore waters (i.e., ED, EE, and NN water masses) had growth trajectories similar to survivors (settlement stage larvae) indicating that these larvae were settling to reefs in the lower Keys and thus contributing to population replenishment and self-recruitment in the SOF (Chapter 4).

Self-recruitment along a continental coast

A variety of biophysical mechanisms have been advanced to explain the occurrence of, or potential for, nearshore retention and cross-shelf transport along

continental coastlines, some of which are similar in island environments. Storm-related wind events may be important in delivering larvae to shore in episodic pulses (Shenker et al. 1993, Milicich 1994); in addition, fish larvae can move onshore during periods of relaxation following wind-driven upwelling (Shanks et al. 2000). Internal waves and associated tidal bores have been implicated in the delivery of large nutrient pulses and invertebrate larvae to nearshore environments (Shanks 1983, Pineda 1991, Leichter et al. 1996, 1998). The coupling of simple larval behaviors (i.e., vertical movements) with vertically stratified flows can lead to cross-shelf transport for larvae positioned in the water column at depths of onshore flow (Hare and Cowen 1991, Cowen et al. 1993, Cowen and Castro 1994, Paris and Cowen 2004). Finally, mesoscale eddies have been hypothesized to be important to retention and transport of larval fishes residing along continental coastlines (Lee et al. 1994, Sponaugle et al. 2005).

As technological advancements have improved our ability to identify, track, and model MEs, it has become apparent that these features are more ubiquitous and complex than previously considered (Chen et al. 2011, Kourafalou and Kang 2012). This realization, in combination with the results of the current study, suggest that MEs play an essential role in larval retention and transport, particularly those eddies associated with major current systems. Retention and subsequent enhancement of larval condition have been shown for anchovy in a ME associated with the Kuroshio Current (Nakata et al. 2000). Unique larval fish assemblages have been identified and cross-shelf transport demonstrated in MEs propagating along current fronts in the northeast Pacific (Mackas and Coyle 2005, Atwood et al. 2010) and off of southwestern Australia (Condie et al. 2011, Holliday et al. 2011). The results of the present study enhance this body of

evidence supporting the role of MEs in replenishing fish populations along continental coastlines. Specifically, we provide evidence for retention of reef fish larvae in MEs propagating along the front of a major western boundary current (Chapters 2 and 3). Additionally, in a novel contribution, growth was shown to be enhanced by residence in MEs for a diverse array of reef fish larvae across multiple sampling periods and years (Chapter 3). Importantly, this growth was associated with increased survivorship to the point of settlement (Chapter 4). As MEs not only have the potential to retain larvae and facilitate transport to suitable settlement habitats, but also to provide enhanced feeding environments and increased survivorship, their role in the replenishment of fish populations is likely significant and warrants further investigation.

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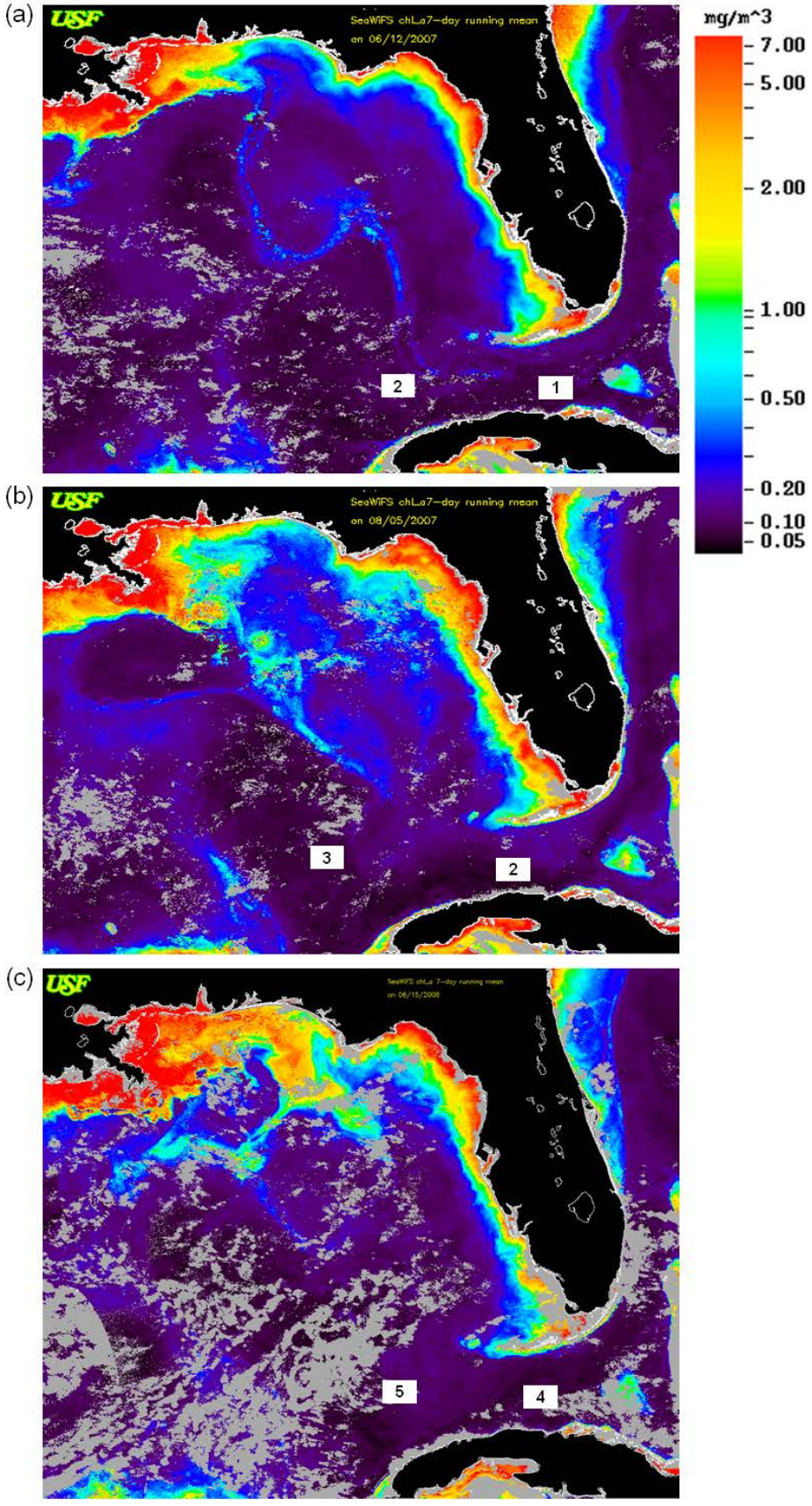
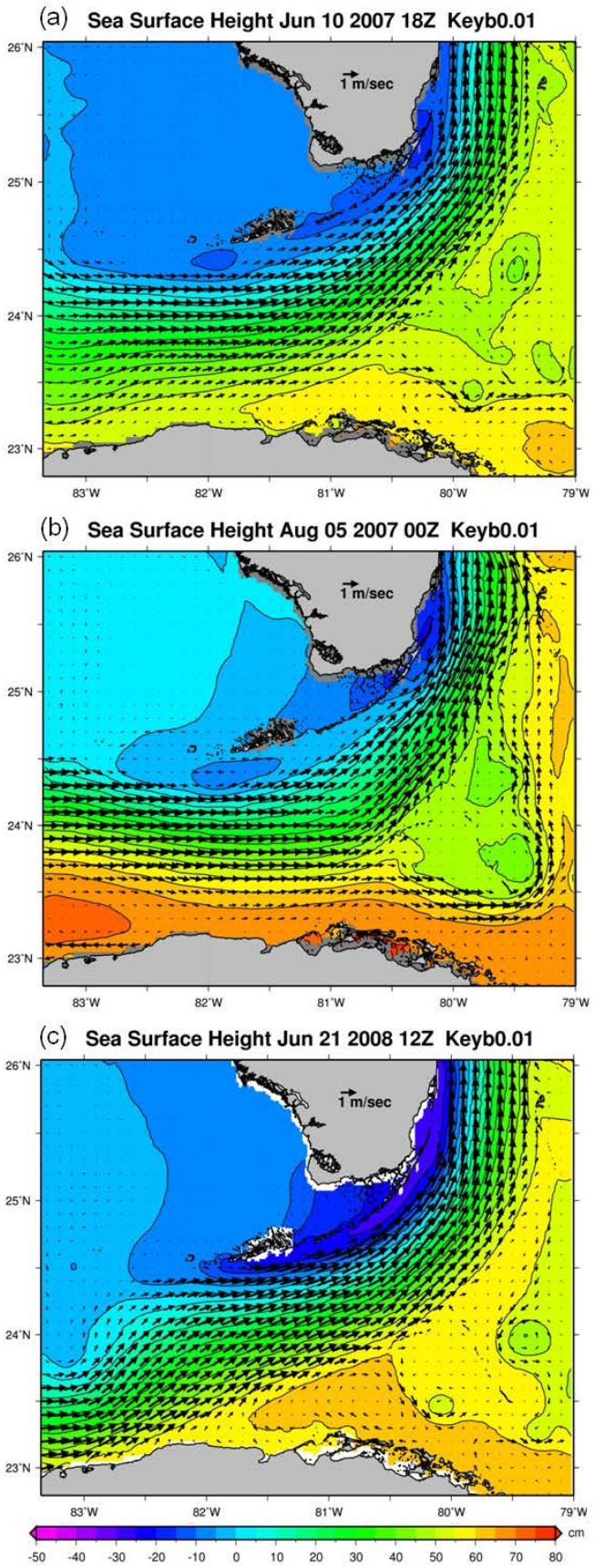
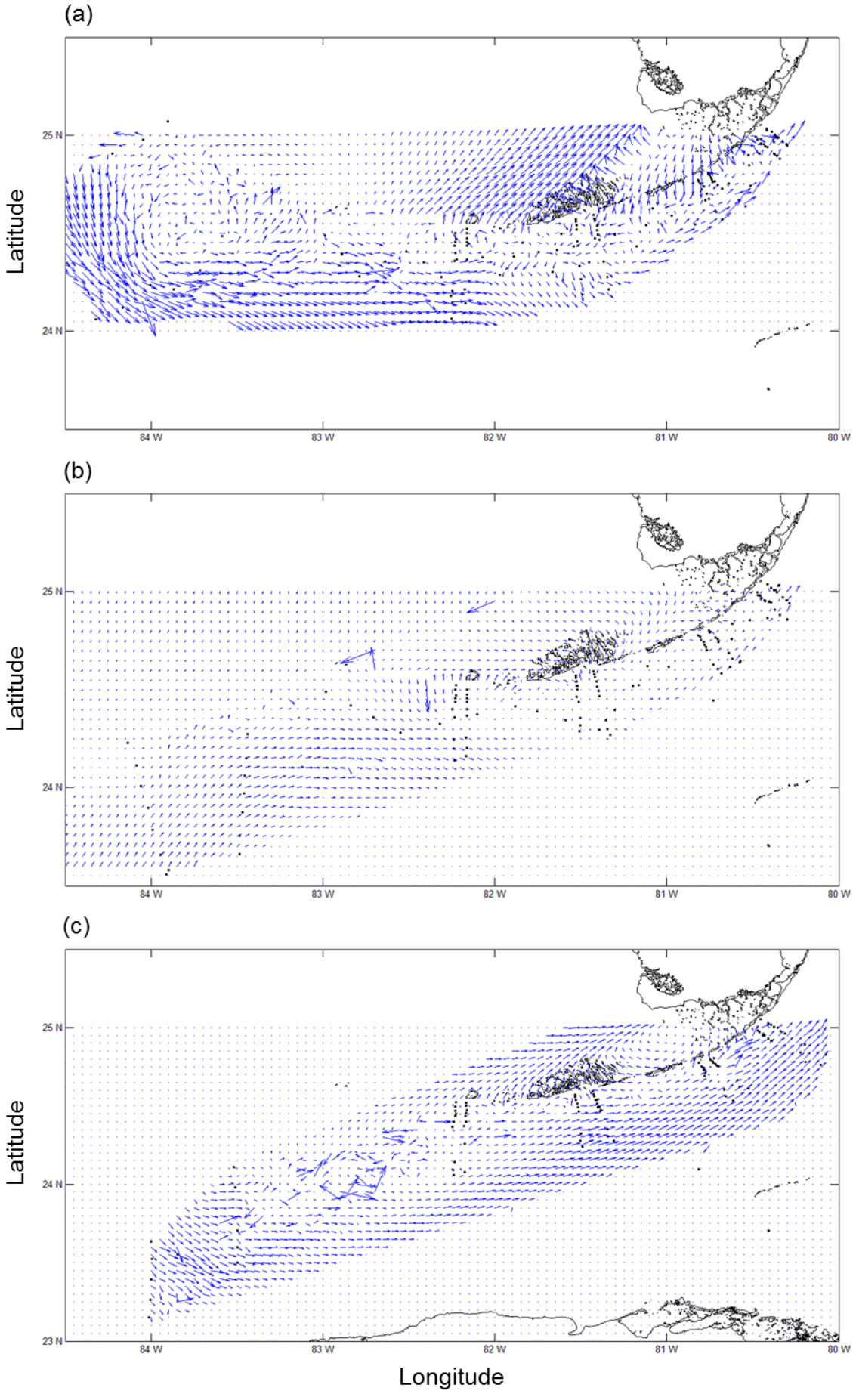
Appendix 1. SeaWIFS satellite images of 7-day running mean of chlorophyll *a*. Images were chosen to minimize cloud cover and represent general locations of mesoscale eddies during sampling periods in (a) June 2007, (b) August 2007, and (c) June 2008. Mesoscale eddies denoted on each image by numbers that correspond to those in the text (i.e., Eddies 1 - 5).

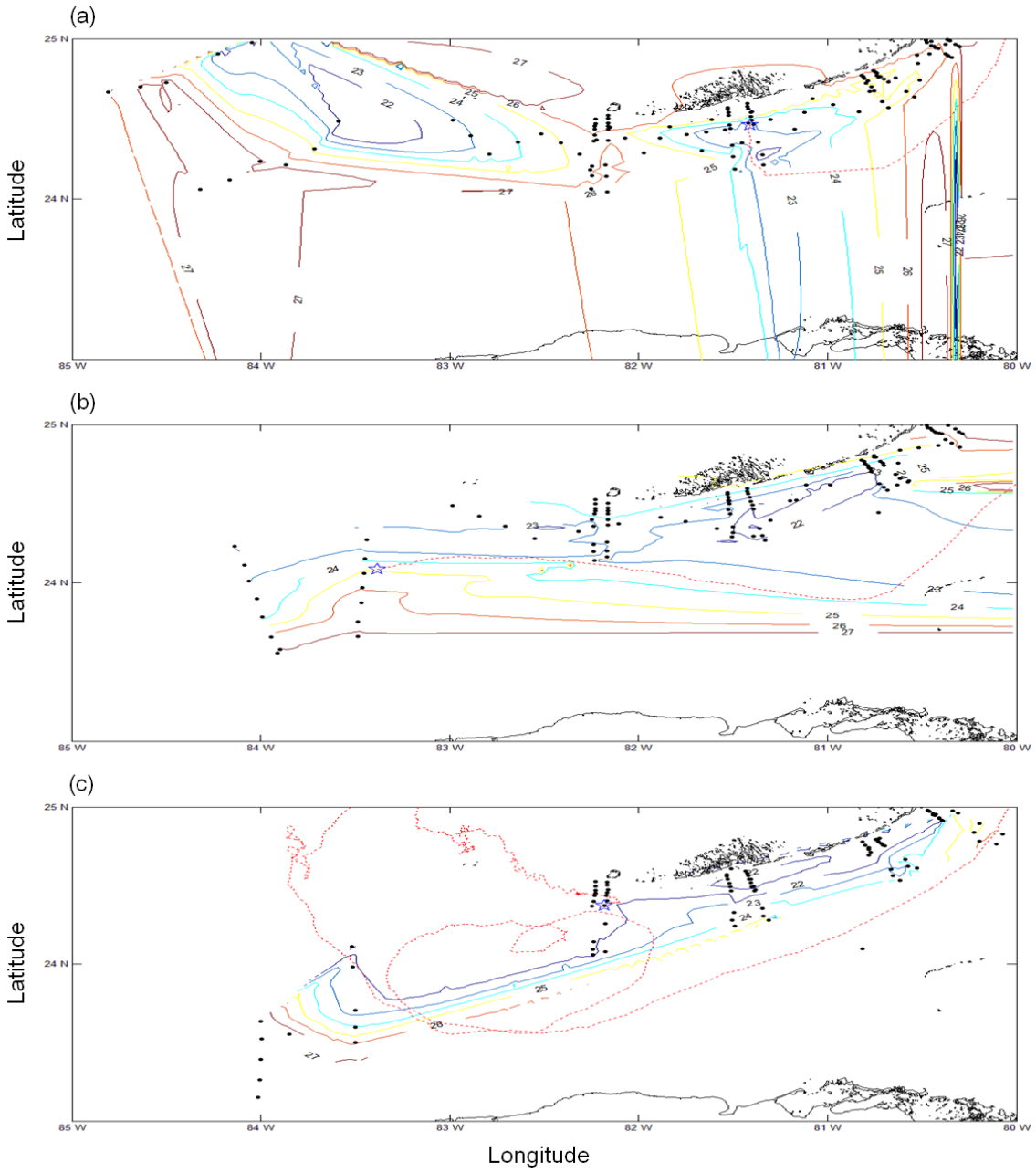

(a)
USF
SeaWiFS chLa 7-day running mean
on 06/12/2007
2
1
mg/m^3
7.00
5.00
2.00
1.00
0.50
0.20
0.10
0.05
(b)
USF
SeaWiFS chLa 7-day running mean
on 08/05/2007
3
2
(c)
USF
5
4

Appendix 2. Outputs from the Florida Keys Simulation model showing current fields (arrows) and sea surface height (colors) representative of the oceanographic environment during sampling periods in (a) June 2007, (b) August 2007, and (c) June 2008. Model outputs courtesy of V. Kourafalou and H. Kang.

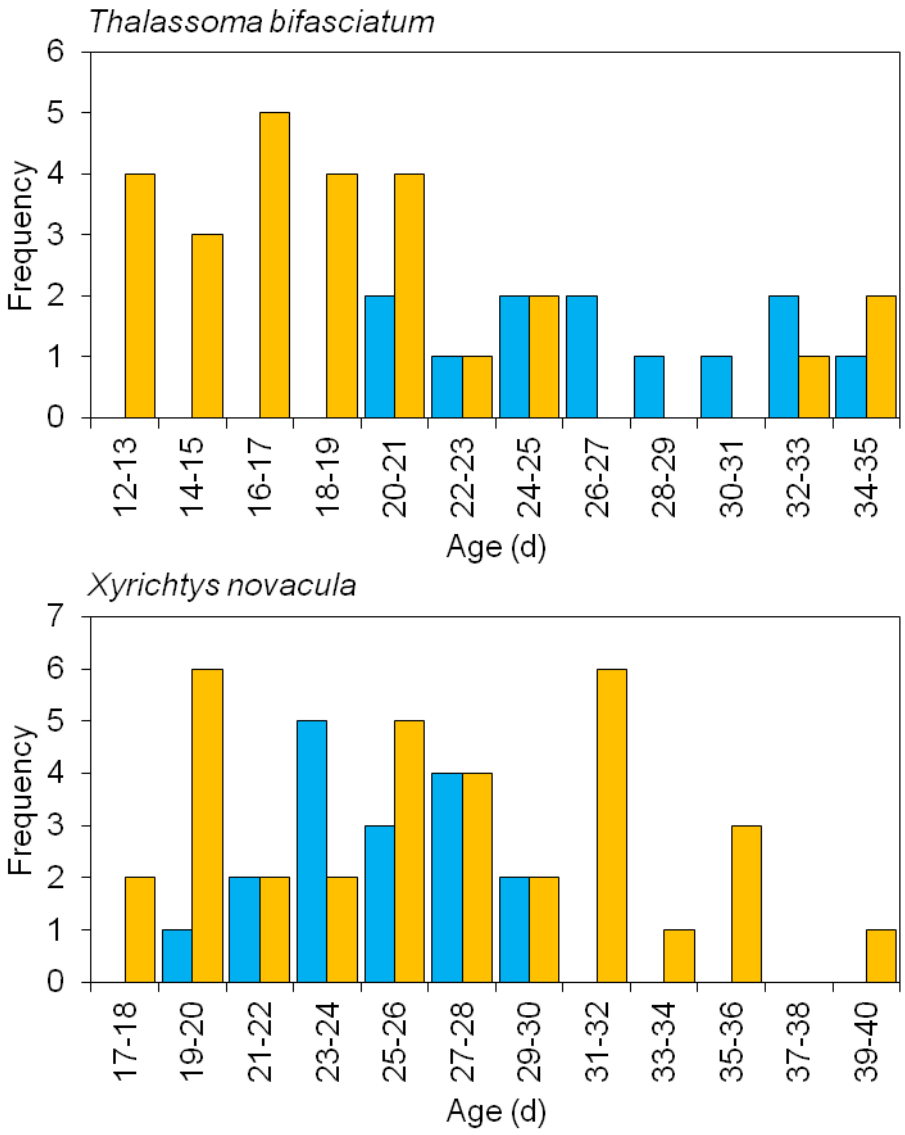

(a) Sea Surface Height Jun 10 2007 18Z Keyb0.01
1 m/sec
26°N
25°N
24°N
23°N
83°W
82°W
81°W
80°W
79°W
(b) Sea Surface Height Aug 05 2007 00Z Keyb0.01
1 m/sec
26°N
25°N
24°N
23°N
83°W
82°W
81°W
80°W
79°W
(c) Sea Surface Height Jun 21 2008 12Z Keyb0.01
1 m/sec
26°N
25°N
24°N
23°N
83°W
82°W
81°W
80°W
79°W
cm
-50 -40 -30 -20 -10 0 10 20 30 40 50 60 70 80

Appendix 3. Current fields interpolated from ADCP data collected in the shallowest depth bin (i.e., 16 - 24 m), with station locations (black dots) overlaid for sampling periods in (a) June 2007, (b) August 2007, and (c) June 2008.


(a)
25 N
24 N
Latitude
84 W
83 W
82 W
81 W
80 W
(b)
25 N
24 N
Latitude
84 W
83 W
82 W
81 W
80 W
(c)
25 N
24 N
23 N
Latitude
84 W
83 W
82 W
81 W
80 W
Longitude



Appendix 4. Locations of eddy cold-cores during sampling periods in (a) June 2007, (b) August 2007, and (c) June 2008. Temperature contours (solid lines) were interpolated from data at 50 m depth in June 2007 and 70 m in August 2007 and June 2008. Drifter tracks (dashed line) and station locations (black dots) are overlaid onto temperature contours. Star denotes release location for drifter.



Appendix 5. Age distributions of *Thalassoma bifasciatum* (top) and *Xyrichtys novacula* (bottom) in Eddy 2 during the June 2007 (blue) and August 2007 (orange) sampling periods.