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Early Life Dynamics in Tropical Western Atlantic and Caribbean Snappers (Lutjanidae) and Barracudas (Sphyraenidae)

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EARLY LIFE DYNAMICS IN TROPICAL WESTERN ATLANTIC AND CARIBBEAN SNAPPERS (LUTJANIDAE) AND BARRACUDAS (SPHYRANIDAE)

By

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Processes occurring during the early life of marine fishes encompassing the larval, settlement, and juvenile stages can have important impacts on recruitment and subsequent population dynamics. Yet these life stages remain poorly understood, especially in coral reef-associated species of commercial and recreational fisheries interest. Two years (2003-2004) of monthly sampling of 17 stations along a transect spanning the east-west axis of the Straits of Florida revealed consistent spatiotemporal patterns in larval abundance, growth, and mortality of several snapper and barracuda species. Much of the species-specific variability in these patterns tracked adult life history, and spatial (several snapper species) and temporal (*Sphyraena barracuda*) patterns in larval growth were related to larval food availability. While no patterns were identified in larval mortality rates, tethering experiments examining relative rates of predation on late-stage *Lutjanus griseus* larvae in surface waters of the lower Florida Keys revealed that relative predation rate and probability of predation in oceanic areas seaward of the reef was significantly greater than over reef or nearshore seagrass/hardbottom habitats. The combined effects of

mortality during these early stages in concert with variability in early life traits caused selective mortality to be pervasive throughout the early life stages of snappers and barracudas. Patterns in selective mortality were investigated by tracking and repeatedly sampling several cohorts of larvae in 2007 and 2008, and for the first time in tropical reef fishes, linking young pelagic larvae with settlement-stage fish and juveniles. In agreement with the growth-mortality hypothesis, large size-at-hatch and fast larval growth conveyed a survival advantage in most species examined, but several switches in the direction of selection with ontogeny and over time occurred, and were contrary to this hypothesis. Consistent patterns of trait-mediated selective mortality lower trait variability in the surviving population, while inconsistencies in these patterns may contribute to the high degree of variability that characterizes these early life stages. Results presented in this dissertation help fill knowledge gaps critical to the understanding and modeling of dispersal and connectivity in several economically valuable snapper and barracuda species. In addition, the identification of life history traits important to the survival of individuals through the larval and into the juvenile stage, has implications for future management of these ecologically and economically valuable species.

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Chapter 1: General Introduction

Background

Processes occurring in the early life stages of organisms with complex life cycles, such as insects, crustaceans, amphibians, and fishes, can have profound effects on subsequent population ecology (Houde 1987, Hellriegel 2000, Beckerman et al. 2002). Most marine organisms exhibit life cycles that include a pelagic larval stage that lasts from days to months. This pelagic larval stage is characterized by high egg and larval abundances and severe mortality, resulting in survival rates near zero (Bailey and Houde 1989, Leggett and Deblois 1994). For many decades, a lack of simple stock-recruitment relationships in fisheries led to extensive research on early life stages, with early work focusing on starvation and advection of larvae as the major causes of recruitment fluctuation (Hjort 1914, Cushing 1975, Lasker 1981, Sinclair 1988). Today, it is generally accepted that predation is likely the ultimate cause of most mortality during the early life stages, while other factors such as starvation and advection make larvae more or less susceptible to this endpoint (Bailey and Houde 1989).

Pelagic larvae are subject to a suite of physical and biological influences, such as water temperature and food availability, that can affect their survival, growth, and dispersal (Cushing 1990, Rutherford and Houde 1995, Meekan et al. 2003, Bergenius et al. 2005, Sponaugle et al. 2006). The planktonic larval stage is also the main mechanism of dispersal and determinant of population connectivity for most benthic marine fishes (Cowen et al. 2007, Cowen and Sponaugle 2009), including coral reef fishes, which are relatively site-attached as adults. In these fishes, the pelagic larval duration (PLD) can range from 9 to 100 d (Leis 1991), which allows for dispersal on the order of 10s to 100s

of km based on passive transport alone (e.g. Roberts 1997). While transport-related processes have been shown to directly influence population replenishment in reef fishes (Milicich and Doherty 1994, Thorrold et al. 1994, Sponaugle and Cowen 1996b, Sponaugle et al. 2005b, D'Alessandro et al. 2007), reef fish larvae are by no means passive particles (e.g., Fisher et al. 2000), and even early in ontogeny exhibit behaviors that can affect their overall dispersal (e.g., Cowen et al. 2000, Cowen 2002, e.g., Paris and Cowen 2004).

The pelagic environment is dynamic and patchy in space and time, contributing to a high degree of overall variability in larval traits ranging from size and growth rates, to genetic identity (Vigliola et al. 2007), to experience with predators (McCormick and Holmes 2006). In combination with high mortality rates, this variability often leads to selective mortality whereby individuals possessing certain traits preferentially survive. The growth-mortality hypothesis (Anderson 1988) has provided a conceptual framework to examine selective mortality in larval fish and contends that larvae that grow faster ("Growth Rate Hypothesis"; Ware 1975), complete the high mortality larval stage faster ("Stage Duration Hypothesis"; Houde 1987), or are larger at given ages ("Bigger-is-Better Hypothesis"; Miller et al. 1988) will preferentially survive. The growth-mortality hypothesis has been supported by numerous temperate (e.g., Hovenkamp 1992, Meekan and Fortier 1996, Hare and Cowen 1997) and tropical studies (Searcy and Sponaugle 2001, Vigliola and Meekan 2002, McCormick and Hoey 2004, Meekan et al. 2006), though some studies have identified advantages for smaller size or slower growth (Fuiman 1989, Litvak and Leggett 1992, Pepin et al. 1992), or no selective patterns (Bertram and Leggett 1994, Robert et al. 2010). Thus, even small changes in larval traits

such as growth, mortality, and stage duration may translate to large fluctuations in the trait composition and magnitude of recruitment, and affect juvenile and adult population dynamics (Houde 1989).

In many reef fishes, settlement (defined here as the act of leaving the pelagic environment to associate with benthic juvenile habitat) is characterized by particularly high mortality due to predation (Almany and Webster 2006) and may also dramatically alter patterns of recruitment and subsequent population dynamics (Steele and Forrester 2002, Doherty et al. 2004). In fact, that most settlement occurs at night (Dufour and Galzin 1993) and during dark phases of the lunar cycle may be adaptations to alleviate intense mortality caused by visual predators (Victor 1986b, 1991). Similar to the pelagic larval stage, trait variability is often high at the time of settlement and shortly thereafter (McCormick 1998), which results in a high probability that mortality at this time will be selective (Sogard 1997). Indeed, many recent studies of reef fishes have found that mortality at the time of settlement is selective in terms of condition, growth, and size (Searcy and Sponaugle 2001, Hoey and McCormick 2004, McCormick and Holmes 2006, Sponaugle and Grorud-Colvert 2006, Gagliano et al. 2007a, Vigliola et al. 2007), though after settlement, competitive, density, and habitat-related processes may become more important and facilitate or mask selective mortality (Brunton and Booth 2003, Holmes and McCormick 2006, McCormick and Meekan 2007, Samhouri et al. 2009). Strong selective mortality during the transition to juvenile life may continue patterns established in the plankton, but may also dampen or reverse them if selective pressures change (e.g., Gagliano et al. 2007a), further altering patterns of overall population replenishment.

While many cyclic and stochastic physical factors affect the delivery of late-stage larvae to settlement habitats (Milicich 1994, Thorrold et al. 1994, Sponaugle and Cowen 1996b, Kingsford and Finn 1997), settlement also typically involves substantial habitat selection behavior on the part of larvae (Booth 1992, Sponaugle and Cowen 1996a, Booth and Wellington 1998, Tolimieri 1998, Wilson 2001, Lecchini et al. 2005). Some species do not settle directly to the coral reef they occupy as adults, but instead bypass this environment to settle in shallow nearshore backreef habitats such as seagrass and algal beds, hardbottom, and mangroves (Cocheret de la Moriniere et al. 2002, Gratwicke et al. 2006, Pollux et al. 2007). These areas are often heralded as nursery habitat due to an abundance of food (Odum and Heald 1972) and/or reduced predation (Blaber and Blaber 1980, Parrish 1989, Cocheret de la Moriniere et al. 2004, Adams et al. 2006, Dahlgren et al. 2006), and mortality rates of juvenile reef fishes generally are lower in these habitats when compared to the reef (Chittaro et al. 2005). Many species settling to these areas are economically important, long-lived, large predatory reef fishes, such as snappers (Lutjanidae), groupers (Serranidae), barracudas (Sphyraenidae), and grunts (Haemulidae). These species, like most reef fishes, have lecithotrophic larvae that develop in oceanic waters and must reach nearshore environments to settle. Yet they face an additional leg in this journey as compared to reef-settling larvae, as the entire reef (and in some cases extensive expanses of shallow backreef habitat) must be traversed before settlement habitat is reached. The cost and nature of this additional journey is unknown, as is the general early life ecology of most of these important fishes. In fact, most information we know regarding the early life ecology of coral reef fishes is from small, highly abundant (and easily sampled and reared) species. This is due in part to the

difficulty in studying diffuse concentrations of larvae in a vast offshore environment, and identifying these larvae to the species level (Leis 1987). For long-lived predatory species, obtaining relatively rare young juveniles is similarly challenging (Sponaugle, unpubl. data). However, new techniques in depth-stratified ichthyoplankton sampling (Guigand et al. 2005), as well as high-throughput molecular larval identification (Richardson et al. 2007) hold promise in overcoming these obstacles.

Study Area

All sampling and experiments in this dissertation were carried out over the shallow nearshore habitats, fringing coral reefs, or in the deep oceanic waters offshore of the Florida Keys (FK) and Miami. The islands of the FK are an ancient calcium carbonate reef tract stretching 300 km from Key Largo in the north to the Dry Tortugas in the southwest. The prevailing flow seaward of the FK is greatly influenced by the interaction of the Florida Current (FC) with the westward curve of the continental shelf in the lower Keys (Big Pine Key to the Dry Tortugas) to a north-south orientation off the upper FK (Key Largo to Lower Matecumbe Key). To the north and west of the FK lies Florida Bay, a shallow sub-tropical lagoon. Shallow (< 3m) nearshore bathymetry south and east of the FK gradually gives way to Hawk Channel, which lies approximately 1 km offshore and may be as deep as 10 m. This natural feature is bordered on the seaward side (~ 5 km offshore) by numerous patch reefs and eventually the fringing reef (~ 7 km offshore). Beyond the fringing reef the continental shelf drops off quickly to a break at approximately 30 m, where a steep drop-off plummets hundreds of meters into the Straits of Florida (SOF; Lee and Williams 1999).

Current flow landward of the fringing reefs and along the entire FK is dominated by seasonally varying wind and tidal (predominantly alongshore and causing little net flow) cycles, while shelf waters seaward of the fringing reefs are dominated by the FC, a major western boundary current with flows as fast as 2 m s^{-1}. In the lower FK, nearshore flow is influenced mainly by dominant westward alongshore wind forcing and resultant cross-shelf Ekman transport, causing a net southwestward flow averaging 3.5 cm s^{-1} (Pitts 1997, 2002). This flow encompasses the nearshore component of the "coastal countercurrent" which normally extends from the middle FK to the Dry Tortugas, but may extend to Key Largo in the fall when winds become strong and to the southwest (Lee and Williams 1999). This seasonal shift in wind direction and intensity is also responsible for minimum flow in the FC during the fall-winter (Lee and Williams 1988). Offshore waters of the lower FK are dominated by the presence of Tortugas eddies, which have been associated with nearshore delivery of spiny lobster and penaeoid shrimp larvae (Criales and Lee 1995, Yeung and Lee 2002), and together with the "coastal countercurrent", make the lower FK an area of high probability for larval retention on the order of days to months (Lee and Williams 1999, Hare and Walsh 2007).

In the upper FK and offshore of Miami, the prevailing westerly winds are cross-shelf, resulting in a net northward flow in Hawk Channel and little onshore Ekman transport (Pitts 1994). Larval assemblages offshore and at the shelf break in this area are influenced by the prevailing north to northeast alongshore flow of the FC and its associated mesoscale (elongated and accelerated remnants of Tortugas eddies; Fratantoni et al. 1998) and sub-mesoscale meanders, frontal eddies (Lee et al. 1992, Limouzy-Paris

et al. 1997, Lee and Williams 1999, Sponaugle et al. 2005b, D'Alessandro et al. 2007), and internal tidal bores (Leichter et al. 1998).

Study Species

This dissertation focuses on two families of coral reef dwelling fishes: snappers in the family Lutjanidae, and barracudas in the family Sphyraenidae. Although seemingly disparate families, many of the species within them share two important characteristics: they are both economically important predatory components of coral reef fisheries in the southeast United States and Caribbean, and the larvae of many species of both settle to nearshore backreef habitats. Much is known about the adult biology and ecology of these families due to their importance to fisheries, and the following is not meant to be an exhaustive review of these topics. Instead, I focus on what is known regarding their early life history and reproduction as it applies to the primary chapters of this dissertation.

Sphyraenidae

There are 21 species of sphyraenids, or barracudas, in one genus, *Sphyraena*, which are all marine (sometimes estuarine) and found in tropical to sub-tropical seas (Nelson 2006). Only five species have been reported in the western central north Atlantic Ocean (Ditty et al. 2006). Four of these species are relatively common while the occurrence of one, *Sphyraena sphyraena*, is tenuous (de Sylva 1963), and it will not be mentioned further.

The great barracuda (*Sphyraena barracuda*) is perhaps the most well known of these fishes due to its circum-global distribution, large size (up to 2 m in length), importance as a food and light-tackle gamefish, reputation for attacking humans, and its curious and territorial nature in the presence of divers (de Sylva 1963). Larval *S.*

barracuda have been described by de Sylva (1963), though little is known of the larval ecology except that they are captured in offshore waters. While all post-larval stages of barracuda are almost exclusively piscivorous (de Sylva 1963, Schmidt 1989, Nagelkerken et al. 2001b), only six larval barracuda (5.5-12.1 mm SL) have ever been examined for stomach contents (de Sylva 1963). Each contained fish fragments and thus, despite the small sample size, it was presumed that larvae are also piscivorous. The mean pelagic larval duration (PLD) has been estimated as 17.6 d (range: 15-21) from ten late-stage larvae collected over the fringing reef in the FK during nearshore intrusion of a mesoscale eddy (Sponaugle et al. 2005b).

Barracuda appear to have a somewhat protracted spawning season with peak activity occurring in the summer months (June-September). Histological examination of female gonads by de Sylva (1963) suggested that each individual spawns several times each year. Spawning activity has never been observed. Peak catches of late-stage larvae captured in light traps over nearshore coral reefs in the FK occurred in summer months (June-August) between the third quarter and new moons (D'Alessandro et al. 2007). New recruits < 2.5 cm standard length (SL) are abundant in nearshore habitats of south Florida from April-November (de Sylva 1963, Kadison et al. 2010). Larvae settle mainly to nearshore seagrass and mangrove habitats (Nagelkerken et al. 2000a, Gratwicke et al. 2006) and individuals move progressively farther offshore as they grow, such that the largest individuals are found on fringing reefs, around wrecks and seamounts, or in open water (de Sylva 1963, Eggleston et al. 2004, Gratwicke et al. 2006).

Much less is known about the adult or larval forms of the guachanche (*Sphyraena guachancho*), southern sennet (*Sphyraena picudilla*), or northern sennet (*Sphyraena*

borealis), though the guachanche is a significant commercial species in the Greater Antilles and considered a delicacy in the West Indies (Russell 2002). Larval guachanche have been described from wild samples collected off of Brazil (Matsuura and Suzuki 1997) and larval northern sennets were reared and described from eggs collected offshore of Miami, Florida (Houde 1972). Larval southern sennet are poorly described and this species may be synonymous with the northern sennet (Russell 2002, Ditty et al. 2006). For these reasons, hereafter "sennets" will refer to both the northern and southern species.

Lutjanidae

The lutjanids consist of about 105 species and 17 genera broken into four sub-families (Nelson 2006). Only three sub-families (Apsilinae, Etelinae, and Lutjaninae), containing six genera (*Apsilus*, *Etelis*, *Lutjanus*, *Ocyurus*, *Pristipomoides*, and *Rhomboplites*) and 18 species, are found in the western central Atlantic Ocean (though *Lutjanus purpureus* may not be a unique species; Gomes et al. 2008). They are gonochoristic, long-lived, slow-growing fishes with relatively low rates of natural mortality and high vulnerability to overfishing (most fishing pressure is artisanal and recreational) due to their popularity as a food fish (though some have been associated with ciguatera poisonings; Anderson 2003). Despite their importance, very little early life history information exists for snappers. Relative rarity in ichthyoplankton samples and difficulty in identifying most to species has hampered research on larval snappers (reviewed in Leis 1987, Lindeman et al. 2006). In fact, of the 18 snapper species reported in the study area, early life stages of only eight (*Etelis oculatus*, *Lutjanus analis*, *Lutjanus campechanus*, *Lutjanus griseus*, *Lutjanus synagris*, *Ocyurus chrysurus*, *Pristipomoides aquilonaris*, and *Rhomboplites aurorubens*) have been formally described (though

descriptions and photographs of several more based on molecular identifications can now be found at http://www.coralreeffish.com/larvae.html). Because half of these descriptions rely largely on reared specimens, (*L. analis*, *L. synagris*, *L. griseus*, and *O. chrysurus*), wild larval specimens remain challenging if not impossible to identify morphologically, and few species level studies of larval snappers exist (but see Comyns et al. 2003). Several studies have sampled ichthyoplankton, including snapper larvae, in the western central north Atlantic (Powles 1977, Cha et al. 1994, Limouzy-Paris et al. 1994), but taxonomic and spatial resolution in these samples is limited.

Most information on spawning and early life history has been gleaned from adult observations and otolith microstructure in late-stage larvae and juveniles. Daily increment formation has been validated in young juveniles of *L. apodus*, *L. griseus*, *O. chrysurus*, and *L. synagris* (Lindeman 1997, Allman 1999, Ahrenholz 2000, Allman and Grimes 2002, Mikulas and Rooker 2008). The PLDs of *L. apodus* (32 d), *L. griseus* (33 d), *L. synagris* (34 d), *L. analis* (31 d), *L. mahogoni* (42 d), and *O. chrysurus* (31 d) have also been estimated from otoliths of newly settled juveniles (Lindeman 1997). Two different spawning modes are thought to exist in lutjanids, whereby populations along continental shelves exhibit extended summer spawning, and insular populations reproduce throughout the year with peaks in spring and fall (Grimes 1987). Lunar periodicity is commonly observed in spawning (Grimes 1987), though the particular patterns are equivocal and likely vary by species. Several species (*L. analis*, *L. cyanopterus*, *L. jocu*) are known to migrate long distances to form annually consistent transient spawning aggregations (Domeier and Colin 1997), while *L. griseus* migrates from inshore to offshore areas to spawn (Domeier et al. 1996, Heyman and Kjerfve

2008). Spawning aggregations of *O. chrysurus* and *L. synagris* have also been observed, but likely have no migrations associated with them (Domeier and Colin 1997). Consistent spawning in one location or location type can have important implications for larval dispersal, retention, and resultant population connectivity. Two recent studies have investigated these aspects of snapper spawning aggregations in the FK and Cuba, and highlight the need for species-specific early life history information to parameterize models and calibrate theoretical studies (Domeier 2004, Paris et al. 2005).

Based on information gained from light-trapping and channel-netting late-stage larvae, settlement in the study area probably occurs between the third quarter and new moons in summer months (Halvorsen 1994, D'Alessandro et al. 2007). Although patterns are somewhat species-specific, most reef-associated snappers settle to shallow (< 10 m) nearshore seagrass and hardbottom habitats (Lindeman et al. 1998, Nagelkerken et al. 2000b, Watson et al. 2002, Bartels and Ferguson 2004) and migrate seaward with ontogeny to the coral reef (Cocheret de la Moriniere et al. 2002, Eggleston et al. 2004, Gratwicke et al. 2006).

Objectives

The overall goal of this dissertation was to investigate larval demographic patterns and determine the role of selective mortality in several long-lived, predatory, economically important reef fishes. The first objective was to investigate species-specific spatiotemporal patterns of growth, mortality, and abundance throughout the planktonic larval stage in both snappers and barracudas. Depth-stratified ichthyoplankton samples were taken at seventeen stations along a transect across the SOF, monthly for two years (2003-2004). Snapper and barracuda larvae from these samples were identified to species

level with the aid of molecular techniques, and early demographic information was obtained through examination of otolith microstructure (Chapters 1 & 2). The second objective was to determine if late-stage larvae settling to backreef nursery habitats (as opposed to the fringing reef) incur higher mortality during settlement. This objective involved an experimental test of whether relative rates of nocturnal predation differed in open water and over different shallow nearshore habitats, including an examination of whether mortality was size-selective. Late-stage *L. griseus* larvae were captured in light traps, measured, tethered live to a small raft, and drifted in open water and over different nearshore habitats for defined intervals to determine the relative number and composition of larvae lost to predation (Chapter 3). The third objective was to test for the presence of selective mortality throughout the early life history of several snapper and barracuda species. To accomplish this, several cohorts of *O. chrysurus*, *L. synagris*, *L. griseus*, and *S. barracuda* were tracked through time by sampling early pelagic larvae, late-stage larvae, and juveniles (Chapter 4). Otolith microstructure analysis was used to identify spawning dates, align cohorts, and determine the intensity and direction of size- and growth-selective mortality from hatching through the post-settlement juvenile stage. This is the first such multi-stage effort linking pelagic larvae with surviving juveniles in tropical reef fishes.

Chapter 2: Larval Ecology of a Suite of Snappers (Family: Lutjanidae) in the Straits of Florida

Background

The 106 species of snapper (family Lutjanidae) are economically important demersal predators found worldwide in tropical and sub-tropical waters (Nelson 2006, Moura and Lindeman 2007). Inhabiting diverse ecosystems ranging from shallow mangrove/seagrass systems and coral reefs to deep shelf edges, snappers are targets of subsistence, commercial, and recreational fisheries around the globe. The 18 lutjanids that occur in the western central North Atlantic (bounded by 35º N latitude, the equator, and 40º W longitude) are among the most economically important fishes in the region and are members of six genera divided among three sub-families: Lutjaninae (*Lutjanus*, *Ocyurus*, and *Rhomboplites*), Etelinae (*Pristipomoides* and *Etelis*), and Apsilinae (*Apsilus*; Lindeman et al. 2006). The 11 species in the genus *Lutjanus* and one species in the genus *Ocyurus* encompass all of the lutjanids that, as adults, inhabit nearshore coral reefs and shallow back-reef habitats. The three species in the genus *Pristipomoides* and one species in each of the genera *Apsilus*, *Etelis,* and *Rhomboplites* are all found as adults in deeper shelf waters, usually well below 50 m.

Lutjanids, like most marine fishes, have a pelagic egg/larval stage that lasts for several weeks during which time they are highly vulnerable to starvation, predation, and advection away from suitable juvenile habitat, and survival rates may be near zero (Houde 1987). Although adults undertake spawning migrations and ontogenetic movements of juveniles connect nearshore habitats, dispersal of the pelagic larval stage is believed to be the primary process determining connectivity between fragmented adult populations (Pineda et al. 2007, Cowen and Sponaugle 2009). Larval dispersal may be

influenced by a variety of factors in the pelagic environment (e.g., currents, larval behavior, vertical distribution, growth, and mortality). Understanding the impacts of these factors is critical in light of the importance of connectivity for establishing and implementing spatially-based fishery management (Fogarty and Botsford 2007).

Despite their economic importance, very little is known about the early life history (ELH) of lutjanids. Complete descriptions of larval ontogeny are available for only six of the 18 western Atlantic species, and the few studies on lutjanid larvae have been descriptive in nature and/or utilized captive-bred larvae (Riley et al. 1995, Clarke et al. 1997, Drass et al. 2000), or have examined otolith-based traits of late-stage larvae and juveniles to make inferences about pelagic larval life (Tzeng et al. 2003, Denit and Sponaugle 2004). Studies directly examining the ELH of wild-caught larvae beyond coarse distributions at the genus level are largely lacking (but see Powles 1977, Houde et al. 1979, Comyns et al. 2003), due in large part to the difficulties involved in adequately sampling diffuse populations of larvae in the open ocean, and in identifying them to the species level (Leis 1987, Lindeman et al. 2006). A recent 2-yr study collected monthly plankton samples across the Straits of Florida (SOF) and revealed consistent spatiotemporal patterns in abundance, distribution, and growth of several larval fish taxa; most notably higher larval growth on the western side of the SOF (Llopiz and Cowen 2009, Sponaugle et al. 2009, Richardson et al. 2010, Sponaugle et al. 2010). Using these same samples, the objectives of this study were to: (1) test for species-specific spatio-temporal patterns in larval snapper abundance and distribution, (2) estimate both seasonal and within-month (lunar) patterns of spawning, and (3) quantify larval growth and mortality and test whether these differed between eastern and western sides of the SOF.

Materials and Methods

Sample collection

Plankton samples were collected during daylight hours from January 2003 through December 2004 on 24 monthly cruises at 17 fixed stations along a transect in the SOF, from the east Florida shelf to the Great Bahama Bank (25.5º N; Fig. 2.1). Current flow in this area is dominated by the Florida Current (FC, a major western boundary current flowing north through the SOF at speeds of up to 2 m s^{-1}). Coastal upwelling and passage of numerous mesoscale and sub-mesoscale eddies make the western SOF adjacent to the Florida Keys (FK) higher in primary production than the eastern portion (Hitchcock et al. 2005). Stations were at least 2 km apart, were spaced closer together at the extremes of the transect, and were considered independent of each other. Inclement weather prevented complete sampling of this transect in December 2003, and January and November 2004. A shipboard acoustic Doppler current profiler (ADCP) recorded vertically discrete current speeds to 100 m depth while a multiple-opening-closing-net-and-environmental-sampling-system (MOCNESS) was used make oblique tows of 25 m depth bins from the surface to 100 m, and a neuston net sampled the top ~ 0.5 m of the water column. Both of these nets were towed at a speed of 1 m s^{-1} and were outfitted with continuously recording flow meters, depth and temperature sensors, and contained dual openings with 1-mm and 150-µm mesh nets (MOCNESS – 4 m^2 1 mm mesh and 1 m^2 150 µm mesh (Guigand et al. 2005); Neuston – 2 m^2 1 mm mesh and 0.5 m^2 150 µm mesh). Samples from the 150 µm mesh nets were not utilized in this study. Upon collection, samples were immediately fixed in 95% ETOH and later sorted to remove all larval fishes. All larval lutjanids were staged as pre-flexion (posterior notochord in line

with the plane of the body), flexion (posterior notochord turned upward but caudal peduncle not yet fully developed), or post-flexion (caudal peduncle fully developed) and their notochord lengths (NL; pre-flexion larvae) or standard lengths (SL; post-flexion larvae) were measured to the nearest 0.1 mm. *Rhomboplites aurorubens* and lutjanids in the sub-family Etelinae were identified to species level using a standard larval fish guide (Lindeman et al. 2006), and larvae in the genera *Lutjanus* and *Ocyurus* were identified using molecular techniques.

Molecular identification of snapper larvae

Isolation and purification of DNA, PCR, PCR purification, sequencing reaction, and sequence purification from snapper larvae in the genera *Lutjanus* and *Ocyurus* followed Richardson et al. (2007), utilizing the Genfind kit (Agencourt) for DNA isolation, and an Evolution P3 liquid-handling robot (Perkins Elmer) to minimize pipetting time and error. Primers used in the amplification of a 655 base pair (bp) region of the cytochrome c oxidase I (COI) gene were: FishF1, FishF2, FishR1, FishR2 (Ward et al. 2005), and an additional two snapper-specific primers designed for this study (FishF3: TTT GAG ACG ACC AGA TTT AT; FishR3: GAT TAG GAC GGC TCA RAC GAA). Combinations of these three forward and three reverse primers yielded a 366-655 bp region of the COI gene. Sequences with trace scores < 30 and read lengths < 100 were discarded and the entire molecular identification protocol was re-run on the corresponding larva. If two runs of this protocol failed to produce a sequence with an adequate trace score and read length, the specimen was not identified. Sequences that passed these criteria were entered into the Barcode of Life Data System's (BOLD) identification engine, producing both a neighbor joining tree highlighting the location of

the unknown sequence, as well as a list of the 100 closest reference sequence matches (Ratnasingham and Hebert 2007). If results were ambiguous or if the sequence was grouped at an equal distance with two or more species, the sequence was discarded and the specimen was re-run or left un-identified.

Abundance and distribution

To test for patterns in abundance across the SOF, the eight most abundant snapper species were examined, and stations 1-9 and 10-17 were grouped into western and eastern stations, respectively. Depth patterns were computed by converting larval catches to abundance by multiplying the density (number of larvae per m^3) of each oblique net tow by the vertical distance it covered, yielding the number of larvae under 1 m^2 of sea surface within a given depth bin. To examine seasonal and cross-SOF patterns, abundance was summed across depth bins to give the number of larvae under 1 m^2 of sea surface. It has been suggested that this measure of abundance more accurately reflects changes in abundance than mean density when larvae are not distributed equally throughout the water column (Lyczkowski-Shultz and Steen 1991, Comyns et al. 2003). Abundances were summed across stations (after being weighted to correct for unequal distances between sampling stations) to test for temporal (monthly) patterns, and across time (all 24 cruises over the 2 yrs) to identify spatial patterns. Total abundance from all stations and all cruises was separated into 1 mm SL size classes to construct length-frequency plots. The spatio-temporal abundance patterns of the eight most abundant taxa overall were individually examined. The low sample size of the remaining species (including unidentified larvae) prevented meaningful analysis. Even in the eight most abundant taxa, however, the abundance of zero values prevented standard statistical

analyses of species-specific abundances, thus we applied the delta approach *sensu* Serafy et al. (2007). Specifically, we analyzed patterns in larval frequency of occurrence (proportion positive) and larval concentration (density when present, ignoring zero values) separately. Species-specific patterns in frequency of occurrence were examined by month using Rayleigh tests (Zar 1999), and by depth and station using chi-square tests under the null hypothesis of uniform distributions. Where the Rayleigh test indicated a significant difference in monthly patterns of occurrence, the mean month about which the data were distributed was calculated. Patterns in concentration were examined by month, again using Rayleigh tests, and by depth and station using Kruskal Wallis tests (due to failure of these data to meet assumptions of parametric statistics).

Ontogenetic differences in vertical distributions of snapper larvae were investigated by utilizing stage-specific centers of mass (z_{cm}) of the eight most abundant taxa at each station as the statistical unit. Center of mass was calculated at each station as the mean depth each net sampled weighted by the proportion of the larvae sampled at that station and captured in those nets:

$$z_{cm} = \sum_i \frac{a_i}{\sum a_i} \; z_i$$

where z_i is the mean of the depth range sampled by net i (based on volume sampled at each depth within the depth range) and a_i is the abundance of larvae in net i. A mean center of mass and standard error was then calculated for each stage within a taxon and statistical differences were determined with Kruskal-Wallis tests.

Otolith analysis

Six species were selected for otolith analysis based on sample size, economic relevance, and cross-SOF distributions (Table 2.1). Individual larvae were randomly selected from all peak spawning months, eastern and western regions, and from 1 mm SL size bins to encompass the complete length distribution and spawning season in approximately even sample sizes from each portion of the SOF. One sagittal otolith was randomly selected per sampled individual and imbedded in crystal-bond thermoplastic glue on a glass microscope slide (Fig. 2.2). A transverse section of each otolith was obtained by polishing (with P2000 silicon-carbide abrasive paper [Nihonkenshi Co., Ltd.]) each side of the otolith to the core (Fig. 2.2). A digital image of each section was taken at 1000× using a Leica DMLB microscope equipped with a Dage MTI video camera and frame-grabber. Using Image Pro Plus 4.5 image analysis software (Media Cybernetics), increments were measured and enumerated along the broader, more rounded of the two longest axes from the otolith's core to its outer edge (Fig. 2.2). This process was repeated twice for each otolith by the same reader, and if counts differed by ≤ 5%, one count was randomly selected for analysis. If replicate counts differed by > 5%, the otolith was read a third time. If this third read differed by ≤ 5% of one of the other two reads, one of these was randomly chosen for analysis. Otherwise, the otolith was excluded from further analysis (e.g. Sponaugle 2009).

Daily otolith increment formation has been validated in *Lutjanus griseus, Lutjanus synagris, Lutjanus apodus,* and *Ocyurus chrysurus* (Lindeman 1997, Allman 1999, Ahrenholz 2000, Allman and Grimes 2002, Mikulas and Rooker 2008) and was assumed in *Lutjanus analis* and *Etelis oculatus*. Overall similarity in increment widths

and appearance between these species and those that have been validated were consistent with this assumption. The number of otolith increments plus a 2 d correction for the delay between hatching and exogenous feeding/increment formation (Lindeman 1997) provided post-hatch larval age in days, while the distance between each pair of increments provided a measure of daily growth for each larva. Because eggs of several western Atlantic snapper species are known to hatch within 24 h of fertilization in 27-28 ºC seawater (e.g., Watanabe et al. 1998, Turano et al. 2000), an additional day was added to post-hatch age to obtain an estimate of the spawning/fertilization day. To ensure that otolith deposition rates could be used as a proxy for somatic larval growth, standard least-squares regressions were performed for each species analyzed between SL and otolith radius as well as between residuals of an otolith radius-at-age regression and residuals of a SL-at-age regression (Hare and Cowen 1995).

Otolith-based growth comparisons

Initial analyses were performed to determine whether larval growth differed between sampling depths for each species. Larval growth (mean width of increments 1-5, increments 5-10, and increments 10-15) was unrelated to depth of collection (ANOVA: $P > 0.05$), thus larvae were pooled across depth bins for further analysis. Differences in daily growth and SL-at-age of larval snappers between the eastern and western sides of the SOF were evaluated using individual otolith increment widths and otolith radii, respectively, at days 10 and 13 post-hatch. Statistical significance in these patterns was evaluated using standard analysis of covariance (ANCOVA) with temperature included in the model to account for its effect on growth. The strong uni-directional nature of the FC results in larvae of different ages captured along the transect at the same time potentially

having very different origins and early growth environments (older larvae may have originated farther upstream). To minimize this potentially confounding effect, a mean of the 3 d of growth prior to capture was calculated for each larva (excluding the marginal increment) and these data were tested for differences between eastern and western stations using ANCOVA with water temperature and larval age included as covariates to account for their effect on larval growth (Sponaugle et al. 2010).

Overall larval growth of the analyzed species was modeled using length-at-age data and the Laird-Gompertz growth equation (Nielsen and Munk 2004):

$$L_t = L_0 * e\ (g_0/\alpha) * (1-e^{-\alpha t})$$

where L_t is length at time t, L_0 is length at hatching, g_0 is specific growth rate at hatch, and α is the rate of exponential decay of the specific growth rate. Due to a lack of newly hatched (age-0 d) and very young larvae (ages 1-7 d) in the samples, size-at-age data were not used to calculate L_0. Following Serafy et al. (2003a), available species-specific mean size-at-hatch data from the literature were utilized to force the y-intercept through realistic values. For three species where no data were available, the mean of the values for those species with known lengths-at-hatch were used.

Separate growth models for the east and west sides of the SOF were created using a truncated age range such that both regions had representative data points throughout. These models were then tested with a likelihood ratio test (Kimura 1980) to determine if model fit was significantly improved by the addition of an east-west division of the sampling stations. If no significant difference was detected, the pooled model was reported and used in subsequent analyses. Also, the instantaneous growth rates, *K*, from a

simple exponential growth model ($L_t = L_0 e^{Kt}$) were calculated to simplify comparison between species and with other studies.

Mortality

Using the Laird-Gompertz models and SL data, an age was assigned to every snapper larva of the analyzed species. An apparent mortality rate, *Z*, was then determined from age-specific abundance data by fitting a line of the form:

$$\ln N_t = \ln N_0 - Z(t)$$

where N_t is the abundance of larvae at time t, N_0 is the abundance of larvae at hatching, and the slope of the line, *Z* is the apparent mortality rate (Houde et al. 1979). Because very young and old larvae were not sampled efficiently by the gear, the age range was truncated to minimize these biases (Richardson et al. 2009; *Etelis oculatus*: 20-35d; all others: 16-24 d). In addition, because larvae may be distributed differently in the vertically stratified flow of the FC with ontogeny, larval abundances were weighted by the mean current flow within depth bins before pooling abundances vertically. Mortality rates were tested for differences between east-west portions of the SOF using homogeneity of slope tests and were pooled across regions where no differences were found. Although mortality rates may have varied in time during this study, sampling was out of phase with larval production cycles and data were pooled over the entire study to satisfy the assumption of constant production (Morse 1989).

Spawning

To examine the timing of spawning relative to the lunar cycle, the lunar day on which each larva was spawned was obtained by first assigning a lunar day to each calendar day in 2003-2004 (new moon = 1, full moon = 15) and subtracting the post-

fertilization/spawning age from the capture date. For consistency with mortality calculations, a truncated age range was used, and larval abundances were weighted by mortality rates and sampling effort across the lunar cycle to yield relative spawning output. These data were then collapsed into a single lunar cycle. If the resulting lunar distribution was found to be significantly different from random using a Rayleigh test (Zar 1999), then the mean lunar day about which the data were distributed was calculated.

Results

Species and size distributions

In total, 1500 snapper larvae ranging from 2.7 to 24.0 mm SL were collected during the 2-yr study, representing at least 14 of the 18 species known to occur in the western Atlantic and Caribbean (Table 2.1). Of these, 96.3% were identified to species level, leaving only 55 larvae unidentified. Larvae in the genus *Pristipomoides* could not be identified to species level because the COI regions of the mitochondrial DNA of two of the three western Atlantic species in this genus have not been sequenced, nor have their larval stages been adequately described. Of the identified larvae, 651 were identified morphologically as *Rhomboplites aurorubens*, *Pristipomoides* spp., or *Etelis oculatus*, while the remaining 794 were identified molecularly. Catches were dominated by the deeper dwelling taxa *R. aurorubens* and *Pristipomoides* spp., which accounted for 35% of the total catch. The most abundant shallow water coral-reef associated snapper larvae were *Lutjanus apodus* and *Lutjanus synagris*, which together accounted for 23% of the total catch. The eight most abundant species which were further analyzed included three deeper dwelling species (that do not occur shallower than 20 m; *R. aurorubens*,

Pristipomoides spp., and *E. oculatus*), two shallow coral-reef associated species (that do not occur deeper than 80 m; *L. apodus*, *Lutjanus analis*), and three species that occupy both shallow and deeper habitats (*L. synagris*, *O. chrysurus*, and *L. griseus*; Anderson 2003, Lindeman et al. 2006; Table 2.1). For all species, flexion commenced between 4-5 mm SL and the caudal peduncle was fully developed by 5-7 mm SL (Table 2.1). Length-frequency distributions revealed that very few larvae < 3-4 mm SL or > 8-9 mm SL were captured. The only larger larvae captured were of the deeper dwelling taxa *R. aurorubens*, *Pristipomoides* spp., and *E. oculatus* (Table 2.1; Fig. 2.3).

Temporal patterns

Although snapper larvae were captured in 23 of 24 months sampled, significant temporal patterns were identified in the frequency of occurrence (hereafter referred to as "occurrence") and concentration (density when present) of the eight most abundant species (Table 2.2). Peaks in both of these metrics as well as total cross-SOF abundance occurred from July through September when mean water temperatures in the upper 50 m of the water column across the SOF were ≥ 28 ºC (Fig. 2.4). Temporal distributions of all other lutjanids (not shown) also followed these general patterns. The only exception was *Etelis oculatus*, whose occurrence peaked in late September, but whose concentrations peaked in April (Table 2.2). Peak abundances of *Pristipomoides* spp. and *Lutjanus analis* were more than three times greater in 2003 than in 2004 while *Lutjanus griseus* and *Lutjanus apodus* displayed the opposite trend (Fig. 2.4). Abundances of *Rhomboplites aurorubens*, *Lutjanus synagris*, *E. oculatus*, and *Ocyurus chrysurus* were relatively consistent between years.

Among the six species for which the timing of spawning was back-calculated, a common pattern of lunar periodicity was evident in plots of total larval abundance vs. lunar spawning day. Four of the six examined species displayed significant peaks in back-calculated spawning around the third quarter moon (lunar days 19.2-22.4; Fig. 2.5). Only *Lutjanus griseus* exhibited a significantly different lunar pattern, peaking just after the new moon (lunar day 1.6), and *Etelis oculatus* lacked any significant lunar pattern (Fig. 2.5).

Spatial patterns

Neuston net catches were not directly comparable to MOCNESS nets due to differences in sizes of the net openings and tow trajectories (oblique in MOCNESS nets and level in neuston nets). However, only nine (0.6% of the total catch) snapper larvae were captured in neuston nets during the entire study despite the disproportionately large amount of time these nets sampled top 0.5 m of the water column. Occurrences of the eight most abundant larval snapper species in the MOCNESS depth bins were all significantly non-uniform (Table 2.2) and similar among species: larvae were nearly absent from the surface, were most abundant in the upper 25 m of the water column, and decreased in abundance with depth (Fig. 2.3). Representative examples of this pattern were *Lutjanus apodus* and *Lutjanus griseus*, where > 80% of larvae caught were in the 0-25 m depth bin (Fig. 2.3). The only species which was most abundant deeper than 0-25 m (i.e. occurred in 25-50 m) and did not have a uniform concentration across depth bins was *Etelis oculatus* (Table 2.2). Post-flexion larvae of this species along with Pristipomoides spp. were found significantly deeper in the water column than pre-flexion larvae ($P < 0.05$; Fig. 2.6). *L. apodus*, which is associated with shallow coral reefs, displayed the

opposite trend, where pre-flexion larvae were distributed deeper than flexion or post-flexion larvae, although this depth difference was modest (~ 5 m). The remaining species displayed a large amount of overlap in depth distributions of these stages.

Larvae of the deeper dwelling species *Rhomboplites aurorubens*, *Pristipomoides* spp., and *Lutjanus synagris* occurred more frequently in the western SOF, but concentrations (densities when present) were equivalent (Table 2.2), resulting in greater total abundances in the west for these species (Fig. 2.7). Larvae of *Lutjanus analis* and *Lutjanus apodus*, which are associated with coral reefs, were both more abundant in the eastern SOF, but for different reasons. *Lutjanus analis* was more than twice as concentrated in the east, but its occurrence was even across the SOF, while *L. apodus* was even in larval concentration across the SOF but had higher occurrence values in the east. The remaining species were evenly distributed between east and west in both occurrence, concentration, and the resulting total abundance patterns (Table 2.2; Fig. 2.7).

Larval growth and mortality

The otoliths of 387 snapper larvae of the six species chosen for analysis were removed and processed (Table 2.1). Fifty of these were not included in analyses due largely to damage caused to the fragile transverse section during processing. Highly significant ($p < 0.01$) positive relationships between SL and otolith radius, as well as between residuals of an otolith radius at age regression and residuals of a SL-at-age regression, were identified for all species indicating that otolith increment data were appropriate to examine somatic larval growth.

Larval growth of *Ocyurus chrysurus* and *Lutjanus synagris* (otolith increment width) tended to be faster, resulting in larger sizes-at-age (otolith radius), on the western

side of the SOF (Fig. 2.8). This difference was significant in four of six statistical tests performed on these otolith-based traits for these two species. *Lutjanus analis* and *Etelis oculatus* also exhibited this trend (Fig. 2.8), which was significantly different between regions in one test of individual otolith increment width (*L. analis*), or size-at-age (*E. oculatus*; Table 2.3).

SL-at-age data fit with the Laird-Gomperz larval growth model revealed that overall growth curves of *Ocyurus chrysurus*, *Lutjanus synagris*, and *Lutjanus analis* were significantly different between east and west sides of the SOF (Table 2.3), with larvae in the west exhibiting a greater length-at-age than those from the east. Instantaneous growth rates (*K*) were similar among species and ranged from 0.039 to 0.048 (Table 2.4). Mortality rates (*Z*) ranged from -0.544 to -0.133 (Table 2.5), and were not significantly different between the east and west SOF for any species.

Discussion

All eight snapper species had significant spatiotemporal distribution patterns with most snapper larvae occurring from July - September when water temperatures were warmest. They were rarely collected in surface waters, and were most abundant in the upper 50 m towards the east or west sides of the SOF. Length and age ranges of snapper larvae were likely constrained by the sampling gear because smaller, younger larvae likely slipped through the nets and larger, older larvae are increasingly able to avoid capture. Although we collected larvae as large as 24 mm SL, all larger larvae (>13 mm SL) were Eteline species. Larvae of coral-reef associated Lutjanine snappers typically settle to nearshore backreef environments at 13-25 mm SL (Lindeman 1997, Watson et al. 2002), and no larvae of these species > 10 mm SL were collected, suggesting that such

larvae were able to avoid being captured or had already settled to juvenile habitat. In contrast, the presence of much larger Eteline snappers in the samples suggests that there are swimming/sensory capability differences between these two groups. Eteline snappers may also have longer pelagic larval durations than Lutjanine snappers (Leis 1987), and our results are consistent with this suggestion (*Etelis oculatus* larvae captured to age 36 d compared to 25 d in all other analyzed species). Thus, it is likely that the difference in age ranges between Lutjanine and Eteline larvae is the result of both settlement schedules and larval performance; though no performance or settlement data for Eteline snappers are currently available to support or refute this hypothesis.

Seasonal larval abundance was similar among species, and the onset of spawning is likely cued by water temperature (above ~ 27º C) and/or photoperiod (~ 13 h daylight), manipulations of which have been used successfully to initiate spawning of captive *Ocyurus chrysurus* (24 C and 15 h daylight; Turano et al. 2000). Despite between-year variability and presence of snapper larvae in most months, temporal distributions of larval abundance, occurrence, and concentration all point to peaks in spawning activity in July-September, consistent with existing literature and the subtropical area sampled (Thresher 1984, Grimes 1987, Leis 1987).

Of the six species for which the spawning date could be back-calculated, four exhibited peak spawning centered within a 4-d period around the third quarter moon (lunar days 19-22), similar to when spawning aggregations of several snapper species have been observed in Florida (Domeier and Colin 1997, Burton et al. 2005) and Belize (Heyman and Kjerfve 2008). Although slightly different, the new moon peak in *Lutjanus griseus* also agrees with previous studies of this species (Domeier et al. 1996, Tzeng et al.

2003, Denit and Sponaugle 2004). Most literature identifies some form of lunar periodicity in snapper spawning (but see Allman 1999), yet the specific patterns identified vary (reviewed in Thresher 1984, Grimes 1987, Tzeng et al. 2003, Denit and Sponaugle 2004). Direct observations of spawning are rare or absent for most snapper species (but see Carter and Perrine 1994, Heyman and Kjerfve 2008), thus most lunar patterns have been identified through back-calculation of spawning dates from otolith analysis of juveniles and larvae. Such data represent successful spawning, or spawning of individuals that have survived and grown to the ontogenetic stage sampled, and do not preclude the possibility of less successful spawning at other times of the lunar month. *Etelis oculatus* was unique in having no lunar spawning pattern, and along with *Pristipomoides* spp., possessing several other attributes different from Lutjanine snappers. These taxa are the only representatives of the Etelinae subfamily in the western central Atlantic and adults are among the deepest dwelling of all snappers. The deep adult distribution of *E. oculatus* may have contributed to the lack of a lunar cyclic spawning pattern in this species, as such environments may not be significantly affected by lunar or tidal cycles.

The vertical distribution of all snapper larvae (scarce at the surface and most abundant in the upper 50 m) is shared by many reef fish families (reviewed in Leis 1991, Cowen 2002) and likely reflects larval behavior in response to prey and predator distributions (reviewed in Cowen 2002). Despite the frequently observed pattern that pelagic larval reef fishes, including snappers, exhibit more structured vertical distributions during the day than at night (reviewed in Leis 1987, 1991), two other ichthyoplankton studies in the SOF found similar patterns to ours, with no difference in

the vertical distribution of lutjanids between night and day (Cha et al. 1994). The deeper dwelling taxa, *Rhomboplites aurorubens*, *Pristipomoides* spp., and *Etelis oculatus,* all exhibited somewhat deeper depth distributions (especially *E. oculatus*) and all moved deeper in the water column with development. These differences in depth distributions and changes with ontongeny are consistent with relative differences in depth distributions for adults of the species.

The sampling transect across the SOF spanned several different environments including continental shelf, shelf slope, and oceanic waters. The low larval abundance at middle stations (slope and oceanic waters) relative to those closer to Florida or the Great Bahama Bank (shelf waters) exhibited by most examined snapper species likely reflects the restriction of adults to shallower eastern and western sides of the SOF. Reduced cross-SOF mixing in the strong unidirectional FC would result in retention of eggs and larvae close to the side where they originated. In contrast, larvae of *Etelis oculatus,* although statistically evenly distributed across the SOF, tended to be more abundant at middle stations than those on the periphery of the SOF. Similar results have been found elsewhere for other Eteline snappers (Leis 1987), and likely reflect their deep adult distribution. Although species-specific variability in cross-SOF distributions of the seven remaining species could have been caused by spatial differences in growth and mortality rates, different patterns of abundance exhibited by closely related species make this explanation unlikely. More likely, these patterns are also reflective of upstream adult populations. Adult *Pristipomoides aquilonaris* are not reported in the areas upstream of the eastern SOF (northern coast of Cuba and Bahamas; Anderson 2003), while adults of the other two species in this genus (*Pristipomoides macrophthalmus* and *Pristipomoides*

freemani) are not reported in areas upstream of the western SOF (Florida Keys, Gulf of Mexico, and Yucatan Peninsula). Most of our *Pristipomoides* spp. larvae may therefore be *P. aquilonaris*, and reflect adult distributions. Adults of both *Rhomboplites aurorubens* and *Lutjanus synagris* inhabit the deep shelf (40-100 m), and the larvae of both were more abundant in the western SOF. In contrast, *Lutjanus apodus* and *Lutjanus analis* are restricted to nearshore backreef and shallow coral reef habitats (juveniles < 10 m; adults < 70 m), and their larvae were more abundant in the eastern SOF. Although regional adult stock assessments are not available, the areas upstream of the eastern side of the SOF (Yucatan peninsula, Cuba, Cay Sal Bank) contain ample shallow coral reefs. The Florida Keys and Dry Tortugas also contain numerous coral reefs, but areas farther upstream of the western side of the SOF (Florida's west shelf) are devoid of coral reefs and likely the fishes associated with them. Horizontal distributions of larvae reflecting adult distributions is not a novel idea for snappers and was suggested by Powles (1977). Our data are consistent with this concept, suggesting that larval distributions mirror adult distributions in both horizontal and vertical dimensions.

Instantaneous larval growth rates (K) were similar among species and regions in this study, but were markedly lower than larval growth rates of Atlantic blue marlin (*Makaira nigricans*; K=0.110; age range: 1-20d) and sailfish (*Istiophorus platypterus*; K=0.134; age range: 2-18d) from the same ichthyoplankton samples (Sponaugle et al. 2010), or *R. aurorubens* larvae (K range: 0.087-0.115; age range: 5-14d) collected in the GOM (Comyns et al. 2003). However, these differences are likely species-specific as growth rates presented here were more similar to larval growth rates of laboratory-reared larvae of *L. analis* (K=0.071; Clarke et al. 1997), *L. synagris* (K=0.064; Clarke et al.

1997), and *O. chrysurus* (K=0.036; Riley et al. 1995, K=0.0618; Clarke et al. 1997) that were held at temperatures (27.0º C – 28.5º C) similar to those our larvae experienced.

Despite differences in horizontal distribution, four of six examined snapper species exhibited a trend of enhanced larval growth on the western side of the SOF which was significant in at least one statistical test (of increment width, otolith radius, last 3 d growth prior to capture or SL-age growth curve). This pattern was significant in five statistical tests for *O. chrysurus* and *L. synagris*. Although spatial differences in growth such as these may be obscured by active or passive mixing of larvae between east and west SOF, significant differences in the 3 d of growth prior to capture in these three species coupled with the strong unidirectional flow of the FC reduce the likelihood of this scenario. Further, cross-SOF mixing of larvae would serve to homogenize growth rates, making our results conservative. The observed pattern may have been caused by differences in water temperature, food availability, intrinsic growth rates, selective mortality, or density-dependence. That species more abundant in the west (*L. synagris*), more abundant in the east (*L. analis*), and equally abundant between sides (*O. chrysurus*) all exhibited higher growth in the west, precludes density-dependent growth as a dominant causative factor. Further, it has been suggested that the diffuse concentrations of larval reef fish in this area are insufficient to deplete prey to an extent that density dependence could operate (J.K. Llopiz & R.K. Cowen, RSMAS, unpubl. data). The possibility that two distinct populations with intrinsically different growth rates are supplying eggs and larvae to the east and west SOF is unlikely because molecular evidence suggests substantial gene flow in pelagic spawning Caribbean fish populations with moderate pelagic larval durations (Purcell et al. 2006, Shulzitski et al. 2009).

Although temperature can affect larval growth rates, its effect on otolith growth rate and size-at-age were never significant in east-west comparisons. In addition, temperature variability in the upper 50 m of the water column between east and west SOF was low (~ 2 ºC) during the truncated spawning season of the study species and tended to be ~ 0.2 ºC lower in the west during the 2-yr study (west: 26.97 ± 0.08 ºC; east: 27.24 ± 0.08 ºC), a difference that would have caused reduced, rather than increased larval growth. Higher mortality rates in conjunction with selection for slow-growing larvae in the west may have contributed to faster growth rates, however, mortality rates were equivalent between regions, precluding this scenario.

Growth of larval bluehead wrasse (*Thalassoma bifasciatum*) and small (< 9 mm SL) zooplanktivorous *M. nigricans* larvae was also higher in the western SOF (Sponaugle et al. 2009, 2010). Faster growth was correlated with fuller guts and higher abundances of primary prey items (*Farranula*, harpacticoid, and *Oncaea* copepods) in the west SOF for *T. bifasciatum* (Sponaugle et al. 2009), and with a higher proportion of *Farranula* relative to *Evadne* copepods in *M. nigricans* (Sponaugle et al. 2010). Consistent with the spatial pattern of primary and secondary production reported for this area (Hitchcock et al. 2005, Llopiz 2008), appendicularians, the major prey of Lutjaninae snappers, also are more abundant in the western SOF (Llopiz et al. 2010). Thus, the most likely cause of the observed pattern of higher larval snapper growth in the western SOF is the higher western abundance of this major prey.

Larval mortality rates presented here were apparent rates biased by net avoidance and advection, but are well within the range found for many other species of marine fish larvae (Houde 1989, Morse 1989). Although the larval mortality rate of *E. oculatus* was

lower than the other snapper species examined, it was similar to that of another deeper dwelling species, *R. aurorubens*, reported from the GOM (Z range: 0.18-0.29; Comyns et al. 2003). Alternatively, the lower larval mortality rate in this species may have resulted from the older age range (20-35 d) used to calculate Z in this species, as larval mortality is thought to decline with age and size (Houde 2002). Also consistent with a decline in mortality with ontogeny, larval mortality rates from the present study were higher than juvenile mortality rates of *L. synagris* (Z range: 0.097-0.165; Mikulas and Rooker 2008), *L. griseus* (Z range: 0.14-0.43; Allman and Grimes 2002), and *O. chrysurus* (Watson et al. 2002).

This study represents the first detailed early life-history information for several ecologically and economically important snapper species. Consistent spatial differences in larval growth rates such as those identified here may have important implications for larval survival, recruitment, and ultimately adult populations of reef fishes. Not only does larval growth influence survivorship of larvae and subsequent recruitment magnitude (reviewed in Houde 2002), but its effects can carry over and influence juvenile survival (e.g., Gagliano et al. 2007a) and effective population connectivity. Dispersal kernels, which define the probability that a larva will arrive at settlement habitat over a certain distance, are a function of larval transport, survival, and time spent in the plankton (Pineda et al. 2007, Cowen and Sponaugle 2009). The consistent spatial differences in larval growth rates shown here could alter dispersal kernels of the same species sourced from different areas, with larvae on the west side of the SOF reaching competency to settle sooner and thus having a smaller overall dispersal kernels. Understanding population connectivity (dispersal kernels) of ecologically and economically important

fishes like snappers is essential to effective spatial management (Fogarty and Botsford 2007). Thus, the species-specific spatio-temporal patterns of larval abundance as well as consistent growth patterns described in this study are directly applicable to management of snapper species, are key elements in parameterizing complex biophysical models, refining our understanding of population connectivity, and ensuring sustainability of marine resources in the future (Cowen and Sponaugle 2009). In addition, this study has provided the first glimpse into the larval life of snappers on a species by species basis. This resolution in conjunction with the consistent sampling design, provide insights into relative abundances of upstream adult populations that are difficult to survey.

Table 2.1. Taxon-specific adult depth ranges (ADR), sample sizes, overall standard length (SL) ranges, size ranges pre-flexion (PRF) at flexion (F) and post-flexion (PTF), and otolith sample sizes (D = otoliths discarded; R = otoliths retained) for lutjanid larvae caught in the Straits of Florida from 2003-2004. SCR indicates that a specific depth range was not available but the species is commonly associated with shallow coral reefs. *Lutjanus* spp. indicates snapper larvae in the genus *Lutjanus* that could not be identified molecularly. Bold text indicates that otolith-based age and growth analyses were conducted for the selected species.

Taxa	ADR	n	Standard length ranges (mm)				Otoliths	
	(m)		Overall	PRF	F	PTF	D	R
Rhomboplites aurorubens	25-?	275	2.9-12.2	2.9-4.7	4.0-6.2	5.8-12.2	0	0
Pristipomoides spp.	24-488	250	3.4-24.0	3.4-4.4	4.1-5.8	5.4-24.0	0	0
Lutjanus apodus	**0-50**	**196**	**3.1-9.4**	**3.1-4.8**	**4.4-6.3**	**6.3-9.4**	**8**	**75**
Lutjanus synagris	**0-400**	**153**	**2.8-8.9**	**2.8-4.6**	**3.9-5.7**	**5.6-8.9**	**10**	**45**
Etelis oculatus	**135-450**	**126**	**3.2-15.7**	**3.2-4.3**	**4.3-7.1**	**5.0-15.7**	**6**	**69**
Ocyurus chrysurus	**1-165**	**118**	**2.9-9.0**	**2.9-4.6**	**4.3-7.1**	**7.5-9.0**	**8**	**58**
Lutjanus analis	**0-80**	**114**	**2.7-8.8**	**2.7-4.3**	**4.1-6.3**	**6.8-8.8**	**8**	**44**
Lutjanus griseus	**0-180**	**95**	**2.7-9.5**	**2.7-4.4**	**4.3-7.0**	**6.6-9.5**	**10**	**54**
Lutjanus jocu	SCR	55	3.0-7.7	3.0-4.4	4.5-6.0	5.7-7.7	0	0
Lutjanus spp.	N/A	55	2.8-8.8	2.8-4.7	4.4-6.7	4.3-8.8	0	0
Lutjanus buccanella	60-230	18	3.0-7.2	3.0-4.5	4.8-6.6	6.1-7.2	0	0
Lutjanus mahogoni	SCR	18	3.4-7.2	3.4-4.2	4.3-6.0	5.5-7.2	0	0
Lutjanus cyanopterus	0-40	13	3.9-5.7	3.9-4.9	4.4-5.4	5.7	0	0
Lutjanus vivanus	90-240	12	3.3-8.3	3.3-3.8	4.8-5.8	5.6-8.3	0	0
Lutjanus campechanus	10-190	2	3.7-4.2	N/A	N/A	N/A	0	0
Total		1500	2.7-24.0	2.7-4.9	3.9-7.1	4.3-24.0	50	345

Table 2.2. P-values from Rayleigh tests on monthly probability (P) and concentration (C) distributions as well as Chi square tests on the vertical and cross-Straits of Florida (SOF) probability distributions (P; under the null hypothesis of uniform distributions), and Kruskal-Wallis and Mann-Whitney U tests of the vertical and cross-SOF concentration distributions (C) of the eight most abundant larval snapper species. Where monthly distributions were found to be significantly non-uniform, the mean month about which the data were distributed is given in parentheses (January = 1 and December = 12). Where cross-SOF distributions were found to be significantly different from uniform, the direction of this difference is given in parentheses.

Taxa	Temporal		Vertical		Cross-SOF	
	P	C	P	C	P	C
Rhomboplites aurorubens	**< 0.001**	**< 0.001**	**< 0.001**	0.752	**< 0.001**	0.189
	(8.3)	(7.6)			(W>E)	
Pristipomoides spp.	**< 0.001**	**< 0.001**	**< 0.001**	0.638	**< 0.001**	0.342
	(8.8)	(8.6)			(W>E)	
Lutjanus apodus	**< 0.001**	**< 0.001**	**< 0.001**	0.541	**0.030**	0.749
	(8.8)	(7.5)			(W<E)	
Lutjanus synagris	**< 0.001**	**< 0.001**	**< 0.001**	0.850	0.050	0.064
	(7.5)	(6.5)			(W>E)	
Etelis oculatus	**< 0.001**	**< 0.001**	**< 0.001**	**0.026**	0.864	0.570
	(9.7)	(4.3)			(W=E)	
Ocyurus chrysurus	**< 0.001**	**< 0.001**	**< 0.001**	0.916	0.751	0.487
	(8.5)	(6.6)			(W=E)	
Lutjanus analis	**< 0.001**	**< 0.001**	**< 0.001**	0.199	0.172	**< 0.001**
	(8.6)	(7.6)			(W=E)	(W<E)
Lutjanus griseus	**< 0.001**	**< 0.001**	**< 0.001**	0.355	0.251	0.379
	(9.0)	(9.3)			(W=E)	

Table 2.3. Probability values of statistical tests of larval growth (otolith increment width and SL-age curves) and size-at-age (otolith radius) between east and west sides of the Straits of Florida. ANCOVAs were used to test for differences between mean otolith increment widths, otolith radii at days 10 and 13, and mean width and radius of the three most recent increments (last 3). Likelihood ratio tests were used to test for differences in SL-age curves. Significant values ($p < 0.05$) are indicated by bold font. All significant test results indicated west growth > east growth.

Species	Growth (otolith increment width in μm) at increment			Size (otolith radius in μm) at increment			SL-age curve
	10	13	last 3	10	13	last 3	
Lutjanus synagris	**0.030**	**0.012**	**< 0.001**	0.072	0.150	**< 0.001**	**0.032**
Lutjanus griseus	0.532	0.072	0.084	0.465	0.361	0.357	0.127
Lutjanus analis	0.214	0.390	**< 0.001**	0.703	0.853	0.143	**0.010**
Lutjanus apodus	0.812	0.635	0.136	0.551	0.440	0.225	0.566
Ocyurus chrysurus	**< 0.001**	0.071	**< 0.001**	**0.014**	0.176	**0.041**	**0.001**
Etelis oculatus	0.588	0.415	0.425	0.929	**0.025**	0.436	0.113

Table 2.4. Parameters of the Laird-Gompertz growth curves fit to the analyzed snapper species age-SL data. Separate east (E) and west (W) SOF curves were calculated where log-likelihood tests indicated significant differences between these regions. L_0 source is the literature origin of the size-at-hatch parameter. "Average" indicates that size-at-hatch data were not available and the average of the values identified for the other studied species was used. "LRL" indicates that values were obtained from laboratory reared larvae. The instantaneous growth rate *K* from a simple exponential growth curve $L_t = L_0e^{KX}$ is also given (± SE) to simplify comparison among species and with other studies.

Species	g_0	L_0	alpha	r^2	*K*	L_0 source
Lutjanus apodus	0.032	2.26	-0.037	0.82	0.047 ± 0.004	average
Lutjanus synagris W	0.028	2.10	-0.053	0.75	0.047 ± 0.008	LRL; Clarke *et al*. 1997
Lutjanus synagris E	0.040	2.10	-0.007	0.66	0.042 ± 0.008	LRL; Clarke *et al*. 1997
Etelis oculatus	0.025	2.26	-0.029	0.91	0.040 ± 0.003	average
Ocyurus chrysurus W	0.044	2.23	-0.010	0.64	0.048 ± 0.007	LRL; Clarke *et al*. 1997, Riley *et al*. 1995
Ocyurus chrysurus E	0.025	2.23	-0.052	0.72	0.041 ± 0.009	LRL; Clarke *et al*. 1997, Riley *et al*. 1995
Lutjanus analis W	0.026	2.35	-0.057	0.71	0.044 ± 0.013	LRL; Clarke *et al*. 1997
Lutjanus analis E	0.017	2.35	-0.079	0.74	0.039 ± 0.012	LRL; Clarke *et al*. 1997
Lutjanus griseus	0.027	2.26	-0.049	0.80	0.047 ± 0.006	average

Table 2.5. Mortality rates (Z) of larval lutjanids captured in the Straits of Florida from 2003-2004. r^2 values are from the linear regressions fit to the descending half of the log-transformed age-frequency histogram. Rates were not significantly different between east and west portions of the Straits of Florida, so the data were pooled.

Species	Z (±standard error)	r^2
Lutjanus apodus	-0.512 (±0.099)	0.82
Lutjanus synagris	-0.429 (±0.053)	0.93
Etelis oculatus	-0.133 (±0.023)	0.65
Ocyurus chrysurus	-0.319 (±0.091)	0.64
Lutjanus analis	-0.544 (±0.084)	0.91
Lutjanus griseus	-0.508 (±0.075)	0.92

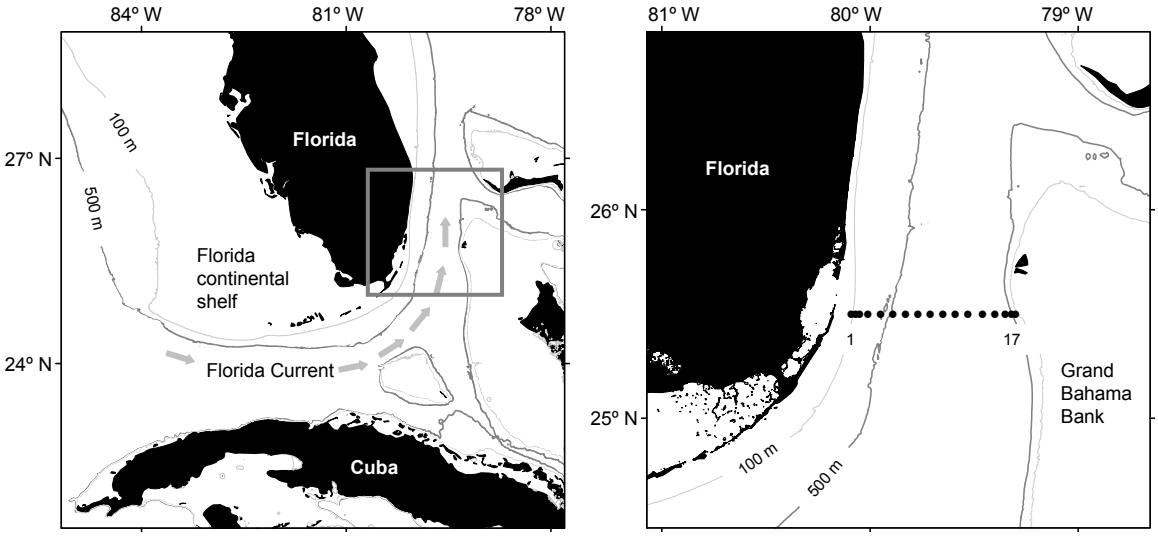


Figure 2.1. Left panel: map of the study area showing the 100 and 500 m isobaths, east and west Florida shelf, Cuba, the Grand Bahama Bank, the Florida Current; Right panel: blowup of the study area showing the 17 stations across the Straits of Florida sampled monthly from 2003-2004 (solid circles).

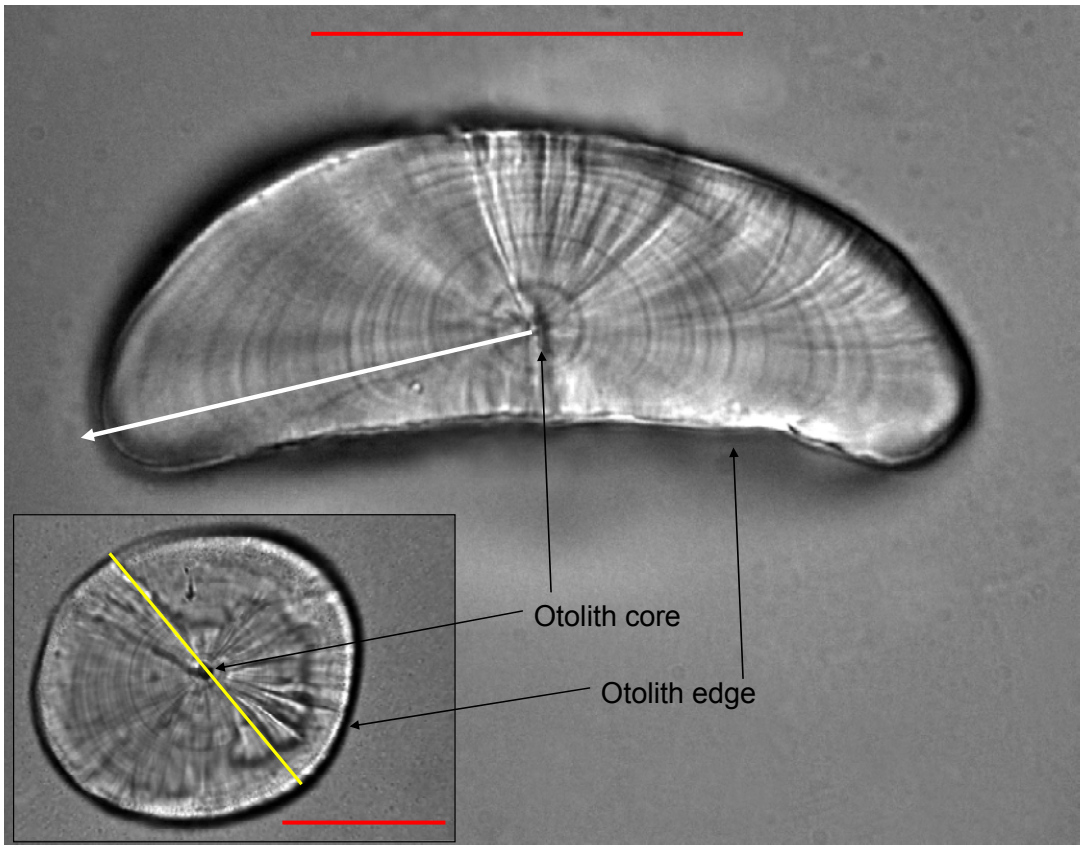


Figure 2.2. Whole sagittal otolith of an *Ocyurus chrysurus* larva laid flat (inset image) and after polishing (large image). Red lines represent 50 µm scale bars, the yellow line in the inset image represents the transverse section of the otolith shown in the larger image, and the white arrow represents a typical reading axis along which increments were measured and enumerated from the otolith core to the otolith edge.

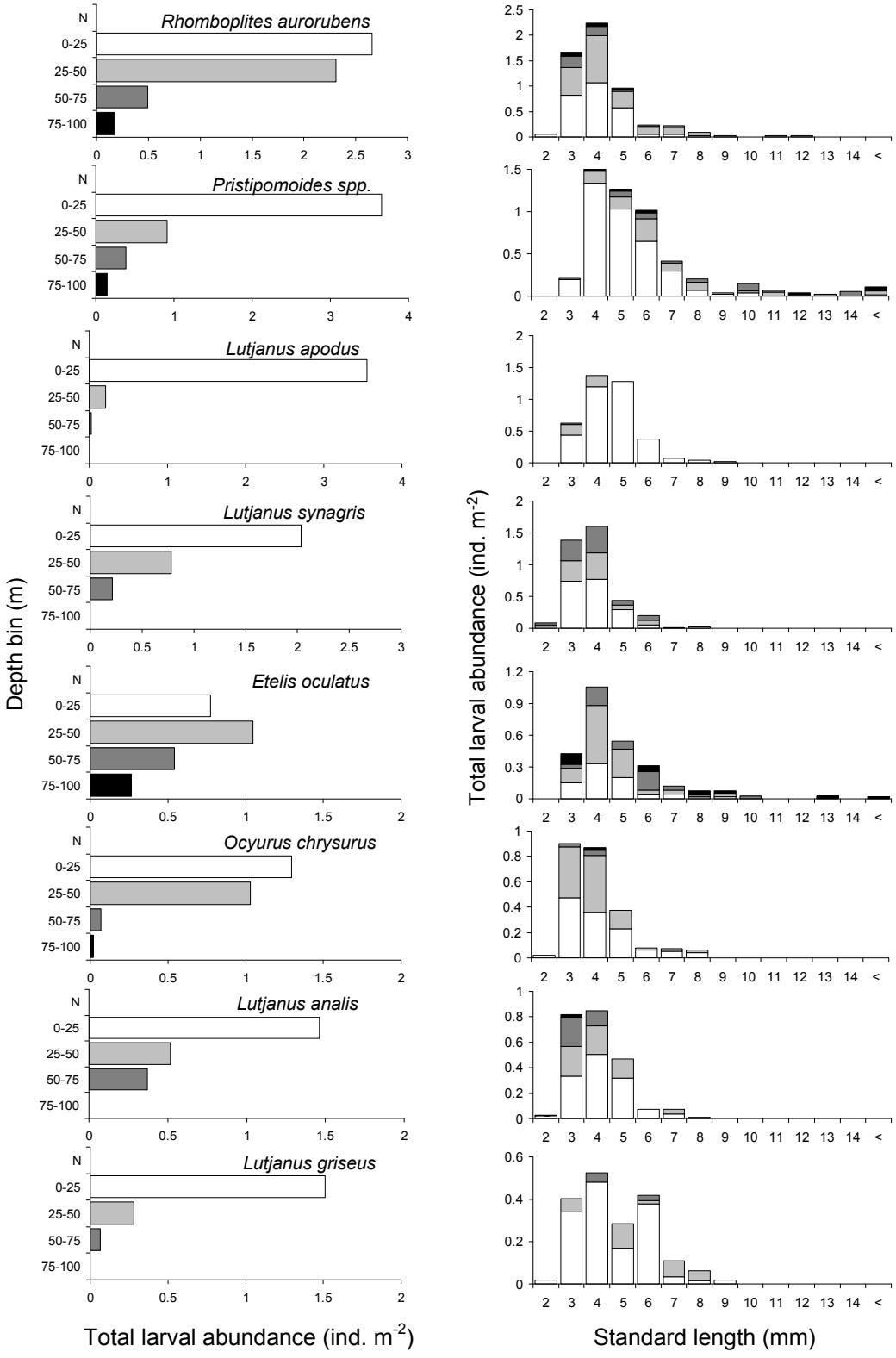


Figure 2.3. Depth distributions (left) and length frequency distributions (right) of the larvae of the eight most abundant lutjanid species captured in the Straits of Florida, expressed as total abundance summed across all stations and months.

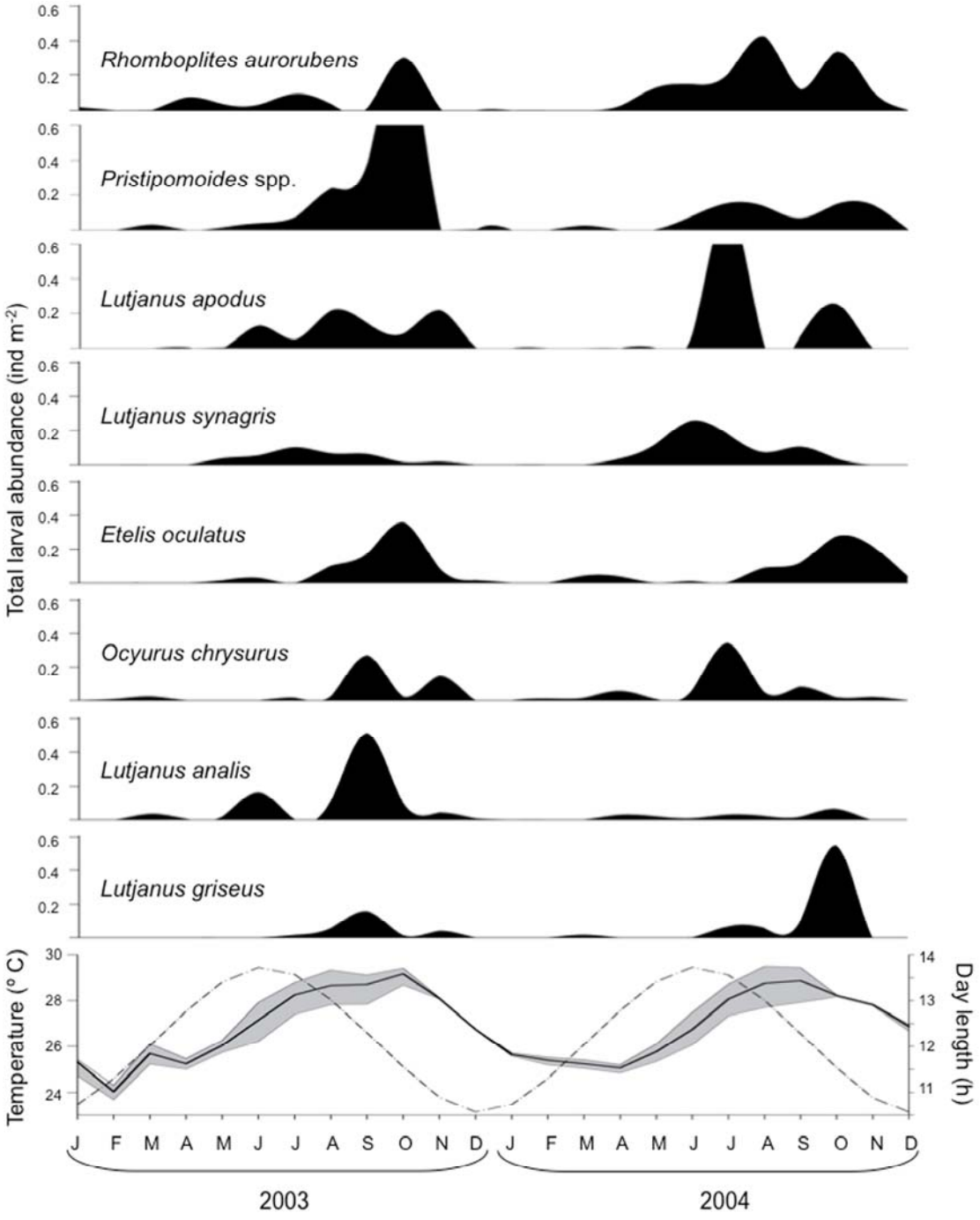


Figure 2.4. Spline-smoothed curves of abundance over time for the eight most abundant snapper species captured during the 2-yr study, mean water temperature (bottom panel, left axis) across the Straits of Florida in the upper 50 m of the water column (dark line = mean temperature; shaded area = temperature range), and day length (bottom panel, dotted line, right axis) across the sampling transect over time.

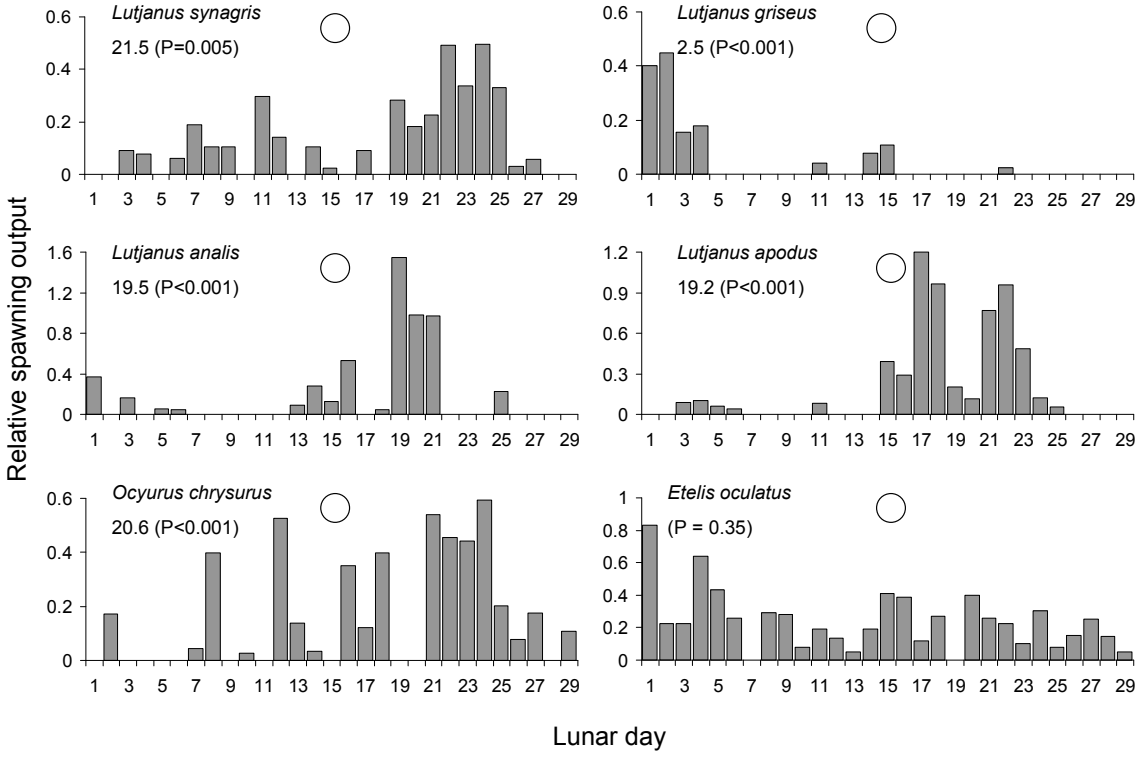


Figure 2.5. Back-calculated successful spawning output by lunar day for six lutjanid species. Lunar day 1 corresponds to the new moon and day 15 to the full moon. Open circles indicate full moons. Results of Rayleigh tests are given in parentheses and when significant, the lunar day about which the data were distributed is given.

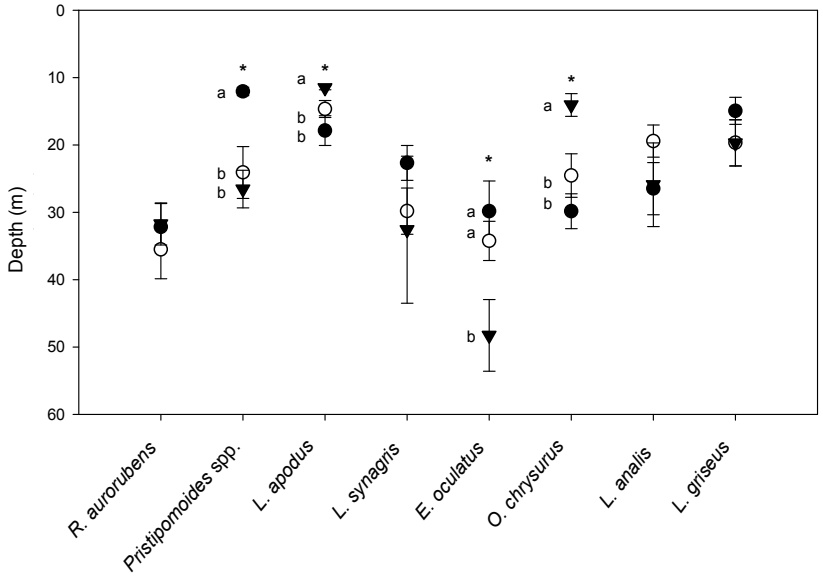


Figure 2.6. The center of mass of pre-flexion (black circles), flexion (open circles), and post-flexion (black triangles) larvae of the eight most abundant lutjanid taxa captured across the sampling transect in 2003-2004. Error bars represent standard error of the mean and asterix indicate statistically significant differences. Different letters indicate significant differences among stages.

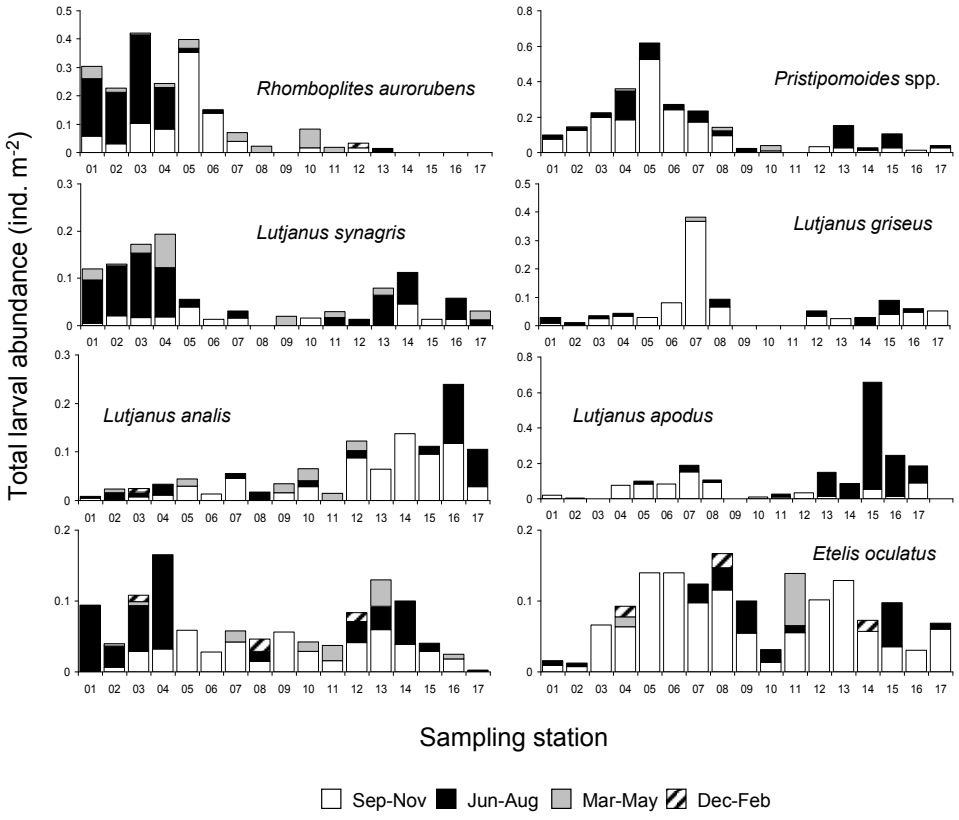
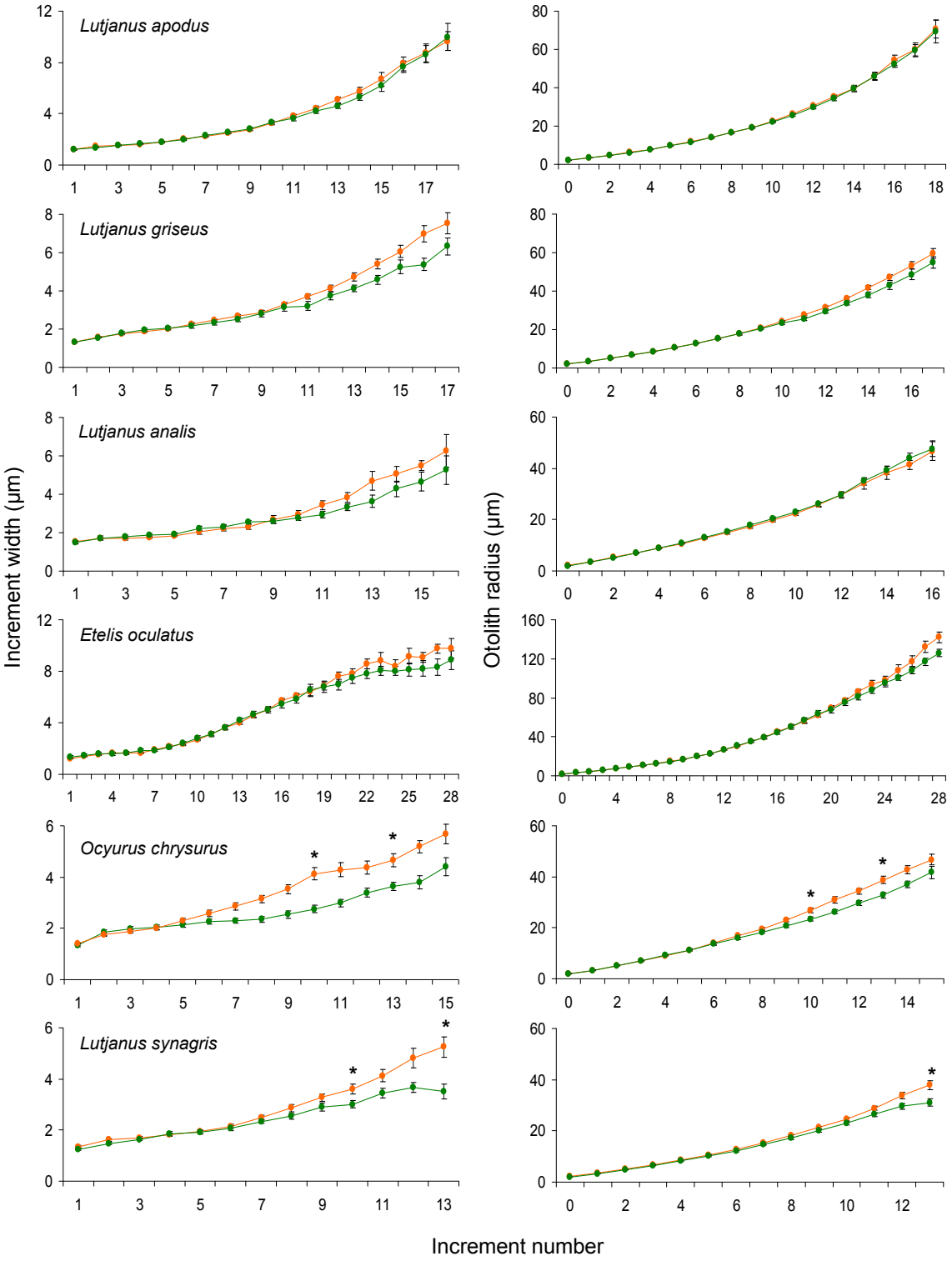


Figure 2.7. Total larval abundance of the eight most abundant lutjanid species collected from 17 stations across the Straits of Florida. Abundances were summed across years and broken into tri-monthly seasonal periods to simplify illustration.

Figure 2.8. Mean larval otolith trajectories of six lutjanid species in terms of growth (individual otolith increment widths; left) and size-at-age (otolith radius at increment; right). Growth and size trajectories of larvae captured on the western side of the SOF are represented by orange circles and those captured on the eastern side are represented by green circles. Error bars are standard error of the mean and asterix indicate statistically significant differences ($p < 0.05$).


Lutjanus apodus
Lutjanus griseus
Lutjanus analis
Etelis oculatus
Ocyurus chrysurus
Lutjanus synagris
Increment width (µm)
Otolith radius (µm)
Increment number

Chapter 3: Larval Ecology of the Great Barracuda, *Sphyraena barracuda*, and Other Sphyraenids in the Straits of Florida

Background

The larval stage of most marine fishes occurs in a diffuse and patchy open ocean environment. Many fishes have evolved the strategy, especially in lower latitudes, of producing many planktonic eggs over a protracted spawning season (Houde 1989, Robertson 1991) possibly to increase chances that larvae will encounter favorable conditions for survival. Despite this adaptation, mortality rates of fish larvae in the plankton are extremely high, and small fluctuations in survivorship and transport can have dramatic effects on subsequent recruitment and adult population abundance (Houde 1987). In addition to determining recruitment magnitude, high mortality coupled with high variability in larval traits can result in selective loss of particular individuals. Variation in larval traits resulting in selective loss of individuals can be caused by environmental factors such as food availability and temperature (Sponaugle and Grorud-Colvert 2006, Sponaugle et al. 2006), but may also stem from maternal identity and be evident at hatching or even in eggs. Advantages conveyed by this early variation influence not only survival in the pelagic larval stage, but may carry over and affect recruitment to and survival in subsequent juvenile and adult stages (Vigliola and Meekan 2002, Raventos and Macpherson 2005, Meekan et al. 2006). Understanding the inherent variability in recruitment of recreationally and commercially important species is one of the major goals of fishery science, which underscores the importance of basic early life history data for such fishes.

The great barracuda (*Sphyraena barracuda*) is a popular game fish in the United States, and despite its reputation for causing ciguatera poisonings in humans (de Sylva 1963, Review et al. 1984), it is an important food fish in many other areas of the world. Of the 21 or so species of barracuda in the family Sphyraenidae and the single genus *Sphyraena* (Nelson 2006), the great barracuda is the most widespread, largest, and well known species. It is found in all tropical and sub-tropical waters (except the eastern Pacific), ranges from Cape Cod, Massachusetts to southeastern Brazil in the Atlantic, and can reach 2 m in length and 45 kg in weight. *Sphyraena barracuda* occupies a diversity of habitats throughout ontogeny, preferring shallow seagrass beds and mangrove habitats as small juveniles, and coral reefs and other deeper habitats farther offshore as adults (Springer and McErlean 1961, de Sylva 1963, Blaber 1982). Large individuals share the highest trophic levels on the reef and in pelagic environments with sharks, jacks, snappers, dolphinfish, sailfish, tunas, and groupers (de Sylva 1963). Their widespread range, the diversity of habitats they occupy, and their role as apex predators highlight the ecological importance of *S. barracuda* to marine ecosystems.

Four other species of sphyraenids have been reported in the western central north Atlantic Ocean (bounded by 35º N latitude to the north, the equator to the south, and 40º W longitude to the east). Three of these species, the guachanche (*Sphyraena guachancho*) and the northern (*Sphyraena borealis*) and southern (*Sphyraena picudilla*) sennets are relatively common while the fourth, *Sphyraena sphyraena,* is thought to be rare in this area, if it occurs at all (de Sylva 1963). In addition, the validity of *S. picudilla* as a unique species is somewhat tenuous as it has been suggested that the larvae may be synonymous with *Sphyraena tome*, a southwestern Atlantic species, and the adults synonymous with *S.*

borealis (Ditty et al. 2006). Due to this ambiguity (and the results presented here), this complex hereafter is referred to as "sennets". Of the five sphyraenid species in the western central north Atlantic, only *S. barracuda* has been studied in detail (de Sylva 1963, Blaber 1982, Schmidt 1989, Kadison et al. 2010). Two recent stock assessments in adjacent areas off the southeast Florida coast reported conflicting results for *S. barracuda*, one identifying explosive growth of the population (Ault et al. 1998) and the other classifying it as overfished according to federal standards (Ault et al. 2001).

Despite its ecological importance and tenuous fishery status, little is known about the larval stage of *S. barracuda* (though some cursory notes are included in de Sylva 1963). Therefore, the overall objective of this study was to describe the ecology of the pelagic larval stage of *S. barracuda* and other sphyraenids using data on spatio-temporal patterns of abundance, larval diet, and larval growth from samples collected during an unprecedented 2 yr sampling effort in the Straits of Florida (SOF). Specifically, we examined (1) patterns in vertical, horizontal, and seasonal abundance among all sphyraenids. (2) Larval diets in the two most abundant taxa, and (3) spatial and temporal patterns in larval growth and mortality of *S. barracuda*.

Materials and Methods

Sample Collection

Plankton samples were collected during daylight hours from January 2003 through December 2004 on 24 monthly cruises at 17 fixed stations along a transect across the SOF, from the east Florida shelf to the Great Bahama Bank (25.5º N; Fig. 3.1). Current flow in this area is dominated by the Florida Current (FC), a major western boundary current flowing north through the SOF at speeds of up to 2 m s^{-1}. Coastal

upwelling and the passage of numerous mesoscale and sub-mesoscale eddies make the western SOF adjacent to the Florida Keys (FK) higher in primary production than the eastern portion (Hitchcock et al. 2005). Stations were at least 2 km apart, were spaced closer together at the extremes of the transect, and were considered independent of each other. Inclement weather prevented complete sampling of this transect in December 2003, and January and November 2004. A shipboard acoustic Doppler current profiler (ADCP) recorded vertically discrete current speeds to 100 m depth. A multiple opening/closing net and environmental sensing system (MOCNESS) was used make oblique tows from 100 m to the surface with 25 m depth bins, and a neuston net sampled the top ~ 0.5 m of the water column. Both of these nets were towed at a speed of 1 m s^{-1} and were outfitted with continuously recording flow meters, depth and temperature sensors, and contained paired asymmetrical nets with 1-mm and 150-µm mesh (MOCNESS – 4 m^2 1 mm mesh and 1 m^2 150 µm mesh (Guigand et al. 2005); Neuston – 2 m^2 1 mm mesh and 0.5 m^2 150 µm mesh). Samples from the 150 µm mesh MOCNESS were not utilized in this study.

Upon collection, samples were immediately fixed in 95% ETOH and later sorted to remove all larval fish. All larval sphyraenids were removed and staged as pre-flexion (posterior tip of notochord in line with the plane of the body), flexion (notochord turned upward but caudal fin rays not yet fully developed), or post-flexion (caudal fin rays fully developed) and their notochord lengths (NL; pre-flexion larvae) or standard lengths (SL; post-flexion larvae) were measured to the nearest 0.1 mm. They were then all identified to species using a combination of morphological characteristics (Richards 2006) or molecularly following the protocols of D'Alessandro *et al.* (2010).

Abundance and distribution

To examine distribution patterns of larvae, abundance was calculated by multiplying the larval density (ind. m^{-3}) of each net tow by the vertical distance covered, and summing across all depth bins, yielding the number of larvae per m^2 of sea surface (e.g., Comyns et al. 2003). Abundances were summed across stations to illustrate temporal (monthly) patterns, and across time (all 24 cruises over the 2 yrs) to identify horizontal patterns (after being weighted to correct for unequal distances between sampling stations and incomplete sampling of the transect in three months). To test for patterns in abundance across the SOF, stations 1-5, 6-12, and 13-17 were grouped into western, central, and eastern stations, respectively (Sponaugle et al. 2009). Individual larvae from all stations and all cruises were separated into 1 mm SL size classes to construct length-frequency plots. The low sample size of the species *S. guachancho* prevented meaningful analysis, but even for the more abundant species the prominence of zero values prevented standard statistical analyses of species-specific abundances. We therefore applied the delta approach (*sensu* Serafy et al. 2007) where patterns in larval occurrence (proportion positive) and larval concentration (average density when present, ignoring zero values) were analyzed separately (D'Alessandro et al. 2010). Species-specific patterns in frequency of occurrence were examined by month using Rayleigh tests (Zar 1999), and by station using chi-square tests under the null hypothesis of uniform distributions. Where Rayleigh tests were significant, the mean month about which the data were distributed was calculated. Patterns in average concentration were examined by month, again using Rayleigh tests, and by station using Kruskal Wallis tests (due to failure of these data to meet assumptions of parametric statistics).

Depth distributions, however, could not be examined using larval abundance calculations due to differences between neuston nets (towed level along the surface) and MOCNESS (towed obliquely). To facilitate comparison between these nets, density (ind. m^{-3}) proportions at depth were calculated. For each cruise during the main spawning season (June - October for *S. barracuda* and November – June for sennets), numbers of larvae at the surface and each 25 m depth interval were summed across all stations and converted to density. Each depth specific density was then expressed as a proportion of the total density for each cruise. Thus the entire transect acted as the sampling unit and allowed for differences in acrsine transformed proportions at depth to be tested with ANOVA and Tukey's honestly significant difference test for pair-wise comparisons (e.g. Llopiz et al. 2010).

Ontogenetic differences in vertical distributions of sphyraenid larvae were investigated by utilizing stage-specific centers of mass (z_{cm}) at each station as the statistical unit. Larvae from the 150 μm mesh neuston net were omitted from this and the above proportional density at depth analysis because samples from 150 μm mesh nets in other depth bins (MOCNESS) were not available for analysis in this study. Center of mass (z_{cm}) was calculated at each station as the mean depth each net sampled, weighted by the proportion of the larvae sampled at that station, and captured in those nets:

$$z_{cm} = \sum_i \frac{a_i}{\sum a_i} \; z_i$$

where z_i is the mean of the depth range sampled by net *i* (based on volume sampled at each depth within the depth range) and a_i is the abundance of larvae in net *i* (Ropke et al. 1993, Irisson et al. 2010). A mean center of mass and standard error was then calculated

for each stage within a taxon and statistical differences among centers were determined with Kruskal-Wallis tests.

Diet

Sub-samples for diet analysis comprising a total of of 62 larval *S. barracuda* and 16 larval sennets were taken from monthly 1 mm SL size bins to encompass the full size and temporal range. The entire alimentary canal of each larva was excised, and prey items were teased out with minutien pins, identified, and enumerated. Feeding was described as feeding incidence (% of larvae with food present in the gut) and prey composition was examined by plotting prey type numerical percentages within larval SL and age bins to identify ontogenetic diet shifts in prey preference (as we did not formally test for selectivity).

Otolith Analysis

Daily otolith increment formation was validated in *S. barracuda* using eight newly settled individuals captured among mangroves surrounding Rodriugez Key, Florida (Fig. 3.1). Individuals were held in an 80-l flow-through aquarium and fed small live mosquitofish (*Gambusia* sp.) to satiation once daily for 1 wk. Fish were then transferred to an adjacent 80-l aquarium filled with a buffered (pH 7.8) 300 mg l^{-1} solution of Alizaren S and seawater where they were held for 24 h before being transferred back to the seawater aquarium and fed as before for up to 1 wk (2 fish died four days later). At the end of this week the remaining fish were euthanized and otoliths were removed and examined under transmitted fluorescent light. Submersion in the Alizaren S solution produced a clear fluorescent band on the otoliths comparable to the size of other juvenile increments. There were six increments present between this mark

and the otolith edge in the six fish that survived six days post-staining, and three increments in the two fish that survived three days post-staining, indicating that increments on the otoliths of juvenile and presumably larval *S. barracuda* are formed daily (Fig. 3.2).

To examine larval growth, a sub-sample of *S. barracuda* larvae were randomly selected from monthly 1 mm SL size bins to encompass the full size range and environmental variability experienced. One randomly chosen lapillus was removed from each selected larva, mounted flat on a glass microscope slide using crystal-bond thermoplastic glue, and polished down to the primordium (core; using P2000 silicon-carbide abrasive paper, Nihonkenshi) on one side (Fig. 3.2). A 1000x digital image of each lapillus was captured using a Leica DMLB microscope equipped with an Infinity 2 digital camera. Otolith increments were enumerated and measured along the longest axis from the core to the outer edge using Image Pro 7.0 software (Media Cybernetics). This process was repeated twice for each lapillus by the same person, and if counts differed by ≤ 5%, one count was randomly selected for analysis. If replicate counts differed by > 5%, the otolith was read a third time. If this third read differed by ≤ 5% from one of the other two reads, one of these was randomly chosen for analysis. Otherwise, the otolith was excluded from further analysis.

Post-hatch age in days (d post hatch; dph) was obtained from the number of otolith increments, while the distance between each pair of increments provided a measure of daily growth. In a captive rearing study of *S. borealis,* eggs hatched within 20 h of collection in 24º C water off Miami, so 1 d was added to dph age to obtain an estimate of spawning/fertilization day. To ensure that otolith deposition rates could be

used as a proxy for somatic larval growth, standard least-squares regressions were performed for each species analyzed between SL and otolith radius as well as between residuals of an otolith radius-at-age regression and residuals of a SL-at-age regression (Hare and Cowen 1995).

Otolith-based growth, mortality, and spawning periodicity

To describe larval growth in *S. barracuda*, overall larval growth curves were fit to age and SL data. Growth was modeled in two ways. First using the Laird-Gompertz growth equation (Nielsen and Munk 2004):

$$L_t = L_0 * e^{(g_0/\alpha)*(1-e^{-\alpha t})}$$

and second, the simple exponential growth equation:

$$L_t = L_0 * e^{Kt}$$

where L_t is length at time t, L_0 is length at hatching, g_0 is specific growth rate at hatch, α is the rate of exponential decay of the specific growth rate, and K is the instantaneous growth rate. Because very young larvae (< 3 dph) were not effectively sampled in this study, the hatch length (L_0) of *S. barracuda* was constrained to the range of known size-at-hatch of other sphyraenids (S. borealis: 2.6 mm NL, Houde 1972; Sphyraena ensis: 1.6 mm NL, Sandknop and Watson 1996). Differences in growth rates among east, central, and west portions of the SOF and between wet (June-October) and dry (November-May) seasons were evaluated using likelihood ratio tests (Laird-Gompertz curves; Kimura 1980), and homogeneity of slopes tests (log-transformed exponential growth curves). If growth differed significantly among east, central, and west SOF or between seasons, the data set was split and separate curves were reported.

To identify spatial and temporal differences in past growth of *S. barracuda* at specific points during larval life, individual growth trajectories re-constructed from otolith increment widths (daily growth) and otolith radii (size-at-age) were examined. These trajectories were evaluated in terms of growth among eastern, central, and western SOF, between wet and dry seasons, and between small and large size-at-hatch (otolith core radius; large ≥ 2 μm, small ≤ 1.75 μm). In addition, to test if differences in growth rate and size-at-age had an effect on larval survival, trajectories were broken into young (initial; < 8 mm SL) and old (survivor; > 8 mm SL) larvae, respectively. Although this cross-sectional method of examining selectivity during the larval duration is not as robust as longitudinally tracking the same cohort through time, multiple cohorts spanning the entire study were included in each comparison, likely averaging out among-cohort variability. Initial analyses were performed to determine whether larval growth differed among sampling depths for each species. Larval growth (mean width of increments 1-5, increments 5-10, and increments 10-15) was unrelated to depth of collection (ANOVA: $P > 0.05$), thus larvae were pooled across depth bins for further analysis. Differences in growth and size-at-age were tested using standard analysis of co-variance (ANCOVA) at increments 5, 10, and 15 (13 in size-at-hatch trajectories due to low sample sizes at higher increments) with water temperature and age included in the model to account for their effect on larval growth. These covariates were dropped from the final analysis when non-significant. Data were log-transformed where necessary to achieve normality and homogeneity of variances, and were excluded when tests for homogeneity of slopes failed. The strong uni-directional nature of the FC results in larvae of different ages captured along the transect at the same time potentially having different origins and

experiencing different early growth environments (older larvae may have originated farther upstream in different vertical and horizontal locations) than where they were captured. To minimize this potentially confounding effect, we examined recent growth by calculating a mean of the 3 d of growth prior to capture (last 3 d; excluding marginal increment) for each larva. Spatial, temporal, and hatch size differences in recent growth were examined using ANCOVA with water temperature and larval age included as covariates to account for their relationship with larval growth (Sponaugle et al. 2010).

Apparent larval mortality was calculated by assigning an expected age to every larval *S. barracuda* using the Laird-Gompertz growth models (r^2 values of these models were higher than exponential models; see Results) and fitting the resulting abundance-at-age data with a line of the form:

$$\ln N_t = \ln N_0 - Z(t)$$

where N_t is the abundance of larvae at time t, N_0 is the abundance of larvae at hatching, and the slope of the line, Z, is the apparent instantaneous mortality rate (Houde et al. 1979). Abundance data were scaled by depth to account for depth-related differences in dispersion within the vertically stratified flow of the FC (D'Alessandro et al. 2010), and the age range was truncated (to 13-26 dph) to minimize bias due to ineffective sampling of younger and older stages (Richardson et al. 2009). Instantaneous mortality rates were tested for differences among east, central, and west portions of the SOF and between seasons (size-at-hatch not tested as this trait could not be assigned to un-aged larvae) using homogeneity of slope tests, and were pooled where no differences were found.

The estimated age-at-capture of each *S. barracuda* larva was used to back-calculate the spawning date. To examine temporal patterns of spawning within the lunar

cycle, a lunar day was assigned to each back-calculated spawning date in 2003-2004 so that all dates could be collapsed into a single lunar cycle (new moon = 1, full moon = 15). The abundance of larvae spawned at each lunar day was scaled by sampling effort within the lunar cycle as well as mortality to yield relative spawning output. To remain consistent with mortality calculations, the same truncated age range was utilized. These data were then tested for cyclic patterns using a Rayleigh test (Zar 1999).

Results

In total 1,335 larval sphyraenids were collected across the SOF in the two year period. The two species of larval sennets reported in the study area (*S. picudilla* and *S. borealis*) could not be differentiated morphologically. Approximately 30% of captured sennets (27/88 larvae) were identified molecularly as *S. borealis*, and these larvae did not differ significantly in spatial or temporal distributions from the remaining sennet larvae. Considering these identifications and the questionable validity of *S. picudilla* as a unique species, it is likely that all sennet larvae captured in the SOF during this study were *S. borealis*. However, because the possibility still exists that *S. picudilla* larvae were collected, they are together referred to herein as "sennets". Collected larval sphyraenids consisted of 92.8% *S. barracuda*, 6.6% sennets, and 0.6% *S. guachancho* (Table 3.1), representing at least three of five species known to occur in the western central north Atlantic. *Sphyraena barracuda* ranged in size from 2.2 mm NL to 18.7 mm SL and reached flexion between 4 and 6 mm SL. Sennets and *S. guachancho* ranged in size from 3.6 mm NL to 34 mm SL and 5.0 to 9.9 mm SL, respectively, and sennets reached flexion between 4 and 8 mm SL (Fig. 3.3).

Sphyraenids were captured in every month of the year, but temporal distributions varied among species. *Sphyraena barracuda* larvae appeared in the samples mainly from June through November when water temperatures were near maximum (Fig. 3.4), peaking in both occurrence and concentration in August (Table 3.1). Although sample sizes of *S. guachancho* larvae were too small to show statistically significant temporal patterns in concentration or occurrence, they were also present only during the months with the warmest water temperatures (July-October; Fig. 3.4, Table 3.1). In contrast, sennet larvae were present mainly from November through June when water temperatures were below 27º C, peaking in occurrence between January and February (Fig. 3.4, Table 3.1).

Nearly all larval sphyraenids (99%) were collected in the upper 50 m of the water column, and 93% were from the upper 25 m. Proportional densities at depth peaked significantly in the upper 25 m of the water column for both *S. barracuda* and sennets, but relatively large proportions were also captured in the neuston (Table 3.1; Fig. 3.5). *Sphyraena guachancho* were only collected in the upper 50 m of the water column (Fig. 3.5), and there were no significant differences in density within this layer (Table 3.1). These patterns were consistent regardless of ontogeny as no statistically significant differences were found among the mean stage-specific centers of mass in *S. barracuda* ($p = 0.519$) or sennets ($p = 0.053$). For *S. guachancho*, the small sample size precluded this analysis.

The occurrence of *Sphyraena barracuda* was even across portions of the SOF, however, concentration when present was significantly greater in the central portion (Table 3.1), resulting in peak overall abundance values in this region as well (Fig. 3.6). In

contrast, sennet larvae occurred significantly more frequently on the western side of the SOF, and concentrations when present were significantly lower in the central portion of the SOF (Table 3.1), resulting in peak abundances in the western and eastern portions of the SOF (Fig. 3.6). *Sphyraena guachancho* larvae showed no significant differences in either occurrence or concentration across the transect, likely due to small sample sizes (Table 3.1).

Feeding incidences (food present in the gut) of sennet larvae (94%) as well as larval *S. barracuda* from the wet (85%) and dry (100%) seasons were all very high. Gut contents revealed that copepods (63%) and copepod nauplii (29%) dominate the diet of larval sphyraenids < 10 mm SL (Fig. 3.7). Copepods were dominated by calanoids (94%) but also included cyclopoid copepods of the genera *Farranula* and *Oncaea*. Fish larvae began to appear in the guts of both *S. barracuda* and sennets at 8 mm SL and *S. barracuda* from the wet season were exclusively piscivorous by 12 mm SL. However, calanoid copepods remained an important component of the larval diet of sennets, wet season barracuda 10-12 mm SL, and dry season *S. barracuda* of all sizes. Interestingly, and in contrast to wet season larvae, *S. barracuda* from the dry season displayed no piscivory (Fig. 3.7). However, this result does not preclude a later shift to piscivory in these larvae as no *S. barracuda* larvae > 14 mm SL were collected in the dry season. Minor components of the larval diets classified as “other” in Figure 6 included unidentified crustaceans, pteropods, tintinnids, and fish eggs in larval sennets, and unknown crustaceans, copepods of the genus *Oncaea*, and bivalve larvae in larval *S. barracuda*.

Otoliths of 67 *S. barracuda* were dissected from larvae and read, 58 of which (87%) were retained for analysis. Highly significant ($p < 0.01$) positive relationships between SL and otolith radius, as well as between residuals of an otolith radius-at-age regression, were identified for *S. barracuda*, indicating that otolith increment data were appropriate for examining somatic larval growth. *Sphyraena barracuda* lapilli were characterized by increasing increment widths during the first 3 dph (first three increments) and then a decrease in widths until 7-8 dph (increments 7-8). At this point the increment width increased steadily up to the otolith edge (Fig. 3.8).

Analysis of both Laird-Gompertz and exponential growth curves of *S. barracuda* revealed that growth was not significantly different among the eastern, central, and western portions of the SOF (likelihood ratio test: $p = 0.589$ and homogeneity of slopes test: $p = 0.679$, respectively), but was significantly higher in the wet season (likelihood ratio test: $p = 0.002$ and homogeneity of slopes test: $p = 0.021$, respectively), thus parameters of separate growth curves are given for each season (Table 3.2). Wet season growth was equivalent to approximately 0.675 mm d^{-1} and dry season growth to 0.423 mm d^{-1}.

Similarly, otolith growth trajectories revealed that although no significant difference in larval growth or size-at-age was identified in *S. barracuda* larvae from the eastern, central, and western portions of the SOF, in the wet season larval growth was significantly faster than in the dry season, resulting in larger larval sizes-at-age (Fig. 3.8, Table 3.3). In addition, these trajectories revealed that larvae that hatched at larger sizes (larger primordium radius) maintained higher growth and larger sizes-at-age throughout the first 2 wks of life (Fig. 3.8), and larger (older) larvae (> 8 mm SL) tended to be those

that grew faster and had larger sizes-at-age throughout most of the first 2 wks of life (Fig. 3.8, Table 3.3).

In contrast to larval growth, mortality rates of larval *S. barracuda* were not significantly different among the eastern, central, and western portions of the SOF ($p = 0.349$), or between wet and dry seasons ($p = 0.060$), and the data were pooled for a single instantaneous larval mortality estimate of 0.214 d^{-1} (± 0.030 SE). The relative spawning output back-calculated with this mortality rate revealed no significant lunar or semi-lunar patterns in spawning ($p = 0.246$; Fig. 3.9).

Discussion

Catches of larval sphyraenids in the SOF during 2003-2004 were overwhelmingly dominated by *S. barracuda* with only 7.2% of the overall catch consisting of other sphyraenid species. If this is due to the relative abundance of adults in coastal areas upstream of the sampling transect such as off the Florida Keys, Dry Tortugas, Cay Sal Bank, Cuba, and the Yucatan Peninsula, it suggests that adults of sphyraenids other than *S. barracuda* are relatively rare in these areas. In the Florida Keys, adult *S. barracuda* are highly abundant (Ault et al. 1998), but there are few published data on the other sphyraenid species from Florida or other upstream areas. Alternatively, the larvae of sennets and *S. guachancho* may be more abundant in shallow coastal waters that were not sampled in this study.

Although length-frequency distributions of the larvae we collected were likely biased by the collecting gear (very small larvae slip through the nets while large larvae are increasingly able to avoid being captured), the samples likely cover a near complete spectrum of larval sizes in the two most abundant taxa (*S. barracuda* and sennets). For *S.*

barracuda, this is supported by the underdeveloped state of the smallest larvae captured and the smallest size recorded for a newly settled post-larval juvenile in the study area (12.77 mm SL; D'Alessandro & Sponaugle unpubl. data). The smallest sennet captured (3.6 mm SL) was close to the reported hatch length of *S. borealis* (2.6 mm NL; Houde 1972). Little is known about settlement in sennets, but young-of-the-year *S. borealis* have been captured in coastal waters of New Jersey in June as small as 56 mm TL, which is larger than, but comparable to the largest sennet larvae captured here (34 mm SL).

While the sample size of *S. guachancho* was too small to reveal any significant spatial or temporal patterns, distributions of *S. barracuda* and sennet larvae revealed very different taxon-specific patterns. Larvae of all sphyraenids were largely constrained to the upper 50 m of the water column, a pattern common for the larvae of many reef fishes (reviewed in Leis 1991, Cha et al. 1994), but were also somewhat neustonic. It has been suggested that in the study area, food availability may play an important role in the evolution of discrete vertical distributions of fish larvae (Cha et al. 1994, Llopiz et al. 2010). However, settled plankton volume of samples from the present study and copepod nauplii, a major dietary component for young sphyraenids, both peak deeper than 25 m (Llopiz 2008). Alternatively, remaining near the surface may be an adaptation to keep *S. barracuda* larvae in close proximity to cover and prey provided by flotsam communities, and surface currents generated by prevailing winds. This may be particularly important for the larvae of piscivorous reef species like *S. barracuda,* which are distributed towards the center of the SOF, far from settlement habitat.

The opposite patterns in cross-SOF and seasonal abundances of *S. barracuda* and sennets likely stems from the adult ecology of these two taxa. Adult sennets inhabit

coastal waters of depths of between 10 and 65 m (Russell 2002) and their larvae were more abundant in eastern and western sampling stations, closer to these habitats. Adult *S. barracuda* are commonly found much farther offshore in the deep waters of the SOF (de Sylva 1963), and greater abundances of larval *S. barracuda* were found at central stations across the transect. High larval abundances in the middle of the SOF also suggests that some *S. barracuda* may make an offshore migration to spawn. Seasonal patterns in larval abundance reflect the spawning patterns of adults. Peak wet season (August) abundance of *S. barracuda* larvae is consistent with previous studies examining gonadosomatic indices and histological preparations of gonads (de Sylva 1963, Kadison et al. 2010), as well as the occurrence of late-stage larvae in light traps (D'Alessandro et al. 2007) and observations of young-of-the-year in nearshore environments (Kadison et al. 2010). Comparatively little is known about the spawning of sennets, but peak larval abundance in the dry season (January) is consistent with a study that collected eggs and reared larvae of *S. borealis* near Miami in December, 1969 (Houde 1972).

The proximate cue for reproductive activity in these species is unknown, but de Sylva (1963) suggested that spawning in *S. barracuda* is cued by water temperatures rising above 23º C. Although water temperature never dropped below 23º C in the upper 50 m of the SOF in 2003 and 2004 (Fig. 3.4), temperature often fluctuates more widely in the shallow coastal waters many adult barracuda inhabit. If water temperature is in fact the cue for spawning in sphyraenids, then sennets appear to prefer water temperatures below 27º C. Both the seasonal and cross-SOF patterns (and to a lesser extent vertical distribution) of larval abundance suggest that *S. barracuda* and sennet larvae rarely co-occur in the SOF (*S. guachancho*, although very scarce in the samples, resembled *S.*

barracuda in spatiotemporal distribution). Such niche separation between these two groups was suggested previously by de Sylva (1963) who noted that the adult sphyraenids in the western north Atlantic do not occur in the same habitats, replacing each other in the food chain.

A high degree of niche separation has also been identified in the trophic roles of larval billfishes (Llopiz and Cowen 2008), tunas (Llopiz et al. 2010), and reef fishes (Llopiz and Cowen 2009) in the SOF. Despite the patchy and oligotrophic nature of lower latitude oceans (e.g. Longhurst and Pauly 1987), larval fishes in the SOF are highly successful feeders and exhibit a high degree of taxon-specific selectivity in their diets. Larval sphyraenids are consistent with these findings as feeding incidences were high in both *S. barracuda* and sennet larvae, and the dominance of calanoid copepods and copepod nauplii (and larval fish later in ontogeny) suggests a high degree of selectivity (though suitable data on prey availability were unavailable for selectivity analysis).

Sphyraenids are part of the suborder Scombroidei along with six other families including the relatively well studied mackerels and tunas (Scombridae), swordfishes (Xiphiidae), and billfishes (Istiophoridae). Like sphyraenids, the adults of all of these fishes are voracious piscivores, and the larvae are known to have some of the highest rates of growth (*Xiphias gladius*: 5.6 mm d^{-1} for larvae > 11 mm SL; Govoni et al. 2003) and mortality (*Thunnus orientalis*: 2.75 d^{-1}; Satoh et al. 2008) of any marine fish larvae studied. Their fast growth is fueled by a high degree of digestive system development and inclusion of larval fishes in their diet from an early age, as larval fishes are of much higher energy content and nutritional value than crustaceans (reviewed in Tanaka et al. 1996, Govoni et al. 2003, Sponaugle et al. 2010). *Sphyraena barracuda* caught in the wet

season included larval fishes in their diets beginning at 8 mm SL, and were exclusively piscivorous by 12 mm SL. As a result, larval *S. barracuda* growth in the wet season was rapid, nearing that of larval blue marlin (*Makaira nigricans*) and sailfish (*Istiophorus platypterus*) in the SOF (Sponaugle et al. 2005a, Sponaugle et al. 2010) which begin feeding on larval fishes at smaller sizes (5 mm SL; Llopiz and Cowen 2008). In contrast, dry season larval growth in *S. barracuda* was slower and similar to many marine fish larvae including tunas in the genus *Thunnus* that, like young *S. barracuda* larvae, feed largely on copepods and copepod nauplii (Tanaka et al. 1996). Because this difference in growth rate between the wet and dry season was evident even when the effect of temperature on larval growth was removed, the absence of larval fishes in the diets of dry season *S. barracuda* likely underlies these low growth rates. The lack of larval fishes in the guts of dry season larvae is probably related to an overall reduction in larval fish abundance across the entire SOF in the dry season (Llopiz & Cowen unpubl. data). Although seasonal differences in temperature even in the subtropics can strongly influence larval growth (Meekan et al. 2003, Sponaugle et al. 2006), variation in food availability and composition can also create significant spatial patterns in larval growth (Sponaugle et al. 2009, Sponaugle et al. 2010), and as demonstrated here, can influence seasonal growth patterns.

That larvae with larger sizes-at-hatch maintained higher growth for at least two weeks post hatch and had larger sizes-at-age suggests that maternal contributions may have an important influence on larval growth in *S. barracuda*. Size-at-hatching is inversely proportional to water temperature in Atlantic mackerel (Mendiola et al. 2007), but temperature seems an unlikely explanation in this study considering it was not a

significant covariate in a test of size-at-hatch between dry (cooler water temperatures) and wet (warmer water temperatures) seasons. Size-at-hatch was more likely affected by energy provisions within eggs (Gagliano and McCormick 2007) and egg size (Chambers 1997), which themselves are primarily determined by maternal identity (Marteinsdottir and Steinarsson 1998, McCormick 1999). That larger (older) larvae had significantly higher growth rates and sizes-at-age than smaller (younger) larvae suggests that higher larval growth conveyed in part by maternal input and piscivory during the wet season also enhances larval survival. The mechanisms by which survival advantages are conveyed by larger sizes-at-age and faster larval growth are described by the growth-mortality hypothesis (Anderson 1988). Such patterns are frequently found for both temperate (e.g., Meekan and Fortier 1996, Hare and Cowen 1997) and tropical (e.g.,Meekan et al. 2006, e.g.,Gagliano et al. 2007a) marine fish larvae, and can carry over to affect juvenile and adult survival (Searcy and Sponaugle 2001, Vigliola and Meekan 2002, McCormick and Hoey 2004, Raventos and Macpherson 2005, Sponaugle and Grorud-Colvert 2006).

Larval growth is inherently linked to mortality (Houde 1997), and rapidly growing larval fish such as members of the Scombroidei must feed frequently to fuel growth. Such larvae are therefore highly vulnerable to starvation, and often have high mortality rates. The instantaneous mortality rate for larval *S. barracuda* (0.214 d^{-1} ± 0.030) was comparable to the mortality rate for larvae of many other marine species such as American shad (*Alosa sapidissima* 0.210 d^{-1}; Houde 1989) and Gulf Stream flounder (*Citharichthys arctifrons* 0.215 d^{-1}; Morse 1989), but was markedly lower than that of many species of Scombroidei larvae such as Atlantic mackerel (*Scomber scombrus* 0.520

d^{-1}; Houde 1989) and Japanese Spanish mackerel (*Scomberomorus niphonius* 0.784 - 0.625 d^{-1}; Shoji et al. 2005). Though these differences in mortality rates may have been caused in part by differences in swimming ability (and thus net avoidance capability) among species, coupled with a very high feeding incidence, the low mortality rate suggests that larval *S. barracuda* are very successful larval predators.

Lunar cyclic spawning is common among reef fishes, and the proposed reason for this behavior is usually related to the transport of eggs by tidal flushing, predation on eggs (reviewed in Johannes 1978, Thresher 1984), or the reduction of predation risk to adults during spawning (Robertson et al. 1990). Although spawning has never been observed in any western Atlantic sphyraenid species, their offshore larval distributions suggest that they spawn near the juncture between coastal and oceanic circulation (de Sylva 1963). If this presumption is correct, then tidal flushing is of little benefit to larval transport. Further, as top predators, risk to spawning adults may be minimal. Either situation may underlie the lack of lunar cyclic patterns in back-calculated spawning output.

In summary, results of our 2-yr monthly sampling effort illustrate consistent spatiotemporal patterns in abundance of larval sphyraenids and distinct seasonal differences in larval growth of *S. barracuda*. The season, availability and composition of prey, maternal input as measured by size-at-hatch, and size (age) of larvae influence larval growth, providing the first evidence of selective mortality during the larval life of a large piscivorous coral reef predator. These data represent the first comprehensive examination of the larval life of sphyraenids, are applicable to management of sphyraenid species, contribute to our understanding of population connectivity (Cowen and

Sponaugle 2009), and may be of use in future assessments of the ecologically and socioeconomically important apex reef predator, *S. barracuda*.

Table 3.1. Sample sizes and p-values from Rayleigh, chi-square, and Kruskal-Wallis tests on occurrence (O) and concentration (C) distributions and ANOVA tests on arcsine transformed proportional densities at depth of larval sphyraenid species in the Straits of Florida (SOF). Rayleigh tests – temporal (monthly) O and C distributions; chi-square tests (null hypothesis: uniform distributions) – cross-SOF O distributions; Kruskal-Wallis tests – cross-SOF C distributions. Where monthly distributions were found to be significantly non-uniform, the mean month about which the data were distributed is given in parentheses (i.e. 1 is January, 12 is December). Where cross-SOF distributions were found to be significantly different from uniform, the direction of this difference is given in parentheses. W: west, C: central, E: east

Species	*n*	Type	Temporal	Cross-SOF	Vertical
Sphyraena barracuda	1,239	O	< **0.001** (8.2)	0.096	**< 0.001**
		C	< **0.001** (8.1)	**0.002** (C > E,W)	
Sphyraena borealis/picudilla	88	O	**0.013** (1.7)	**< 0.001** (W > C,E)	**< 0.001**
		C	0.684	**0.037** (W,E > C)	
Sphyraena guachancho	8	O	0.111	0.544	0.439
		C	0.078	0.698	

Table 3.2. Parameters of the Laird-Gompertz and exponential growth curves fit to *Sphyraena barracuda* age-SL data. Statistical differences were found for both curves between wet and dry seasons, thus parameters for each season are given separately.

	Laird-Gompertz				Exponential		
Species	L_0	α	g_0	r^2	L_0	K	r^2
Sphyraena barracuda (wet)	1.96	-0.040	0.061	0.90	1.600	0.096	0.74
Sphyraena barracuda (dry)	2.60	0.009	0.071	0.98	2.600	0.065	0.61

Table 3.3. Probability values of ANCOVA tests of larval growth (otolith increment width; IW) and size at age (otolith radius; R) between wet season (June-October) and dry season (November-May; Wet/Dry), east, central, and west portions of the Straits of Florida (E/C/W), small and large larval hatch size (Small/large), and larvae less than and greater than 7 mm SL (Initial/survivor) at increments 5, 10, and 15, and mean width and radius of the three most recent increments prior to capture (Recent). When significant, the p-value of temperature as a covariate is given in parentheses. Differences between small and large hatch size could be tested only to day 13 due to sample size limitations and is indicated by "Inc 15 (13)". Bold: significant ($p < 0.05$); all significant comparison p values indicated wet season growth > dry season growth, large hatch size growth > small hatch size growth, and larvae > 8 mm SL (survivor) greater than < 8 mm SL (initial) growth.

Comparison	Inc 5		Inc 10		Inc 15		Recent	
	IW	R	IW	R	IW	R	IW	R
Wet/Dry	0.788	0.431	**0.012**	0.057	**0.017**	**0.009**	**0.021**	**0.003**
E/C/W	0.544	0.083	0.974	0.715	0.451 **(0.006)**	0.998 **(0.042)**	0.731	0.772 (**0.047**)
Hatch size	0.457	**0.029**	**0.049**	0.066	**0.033**	**0.050**	0.097	**0.011**
Initial/ Survivor	0.788	**0.011**	**0.012**	**0.002**	**0.002**	**0.002 (0.005)**	**0.000 (0.011)**	**0.000 (0.011)**

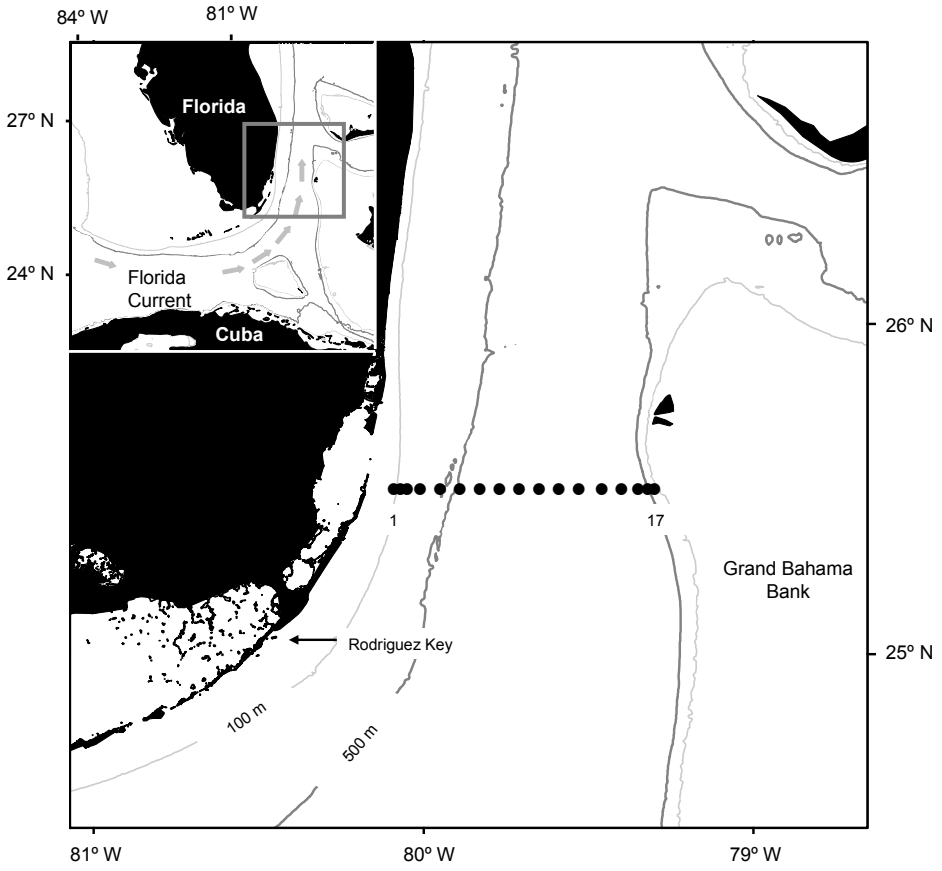


Fig. 3.1. Study area. (•) The 17 stations across the Straits of Florida, sampled monthly from 2003 to 2004.

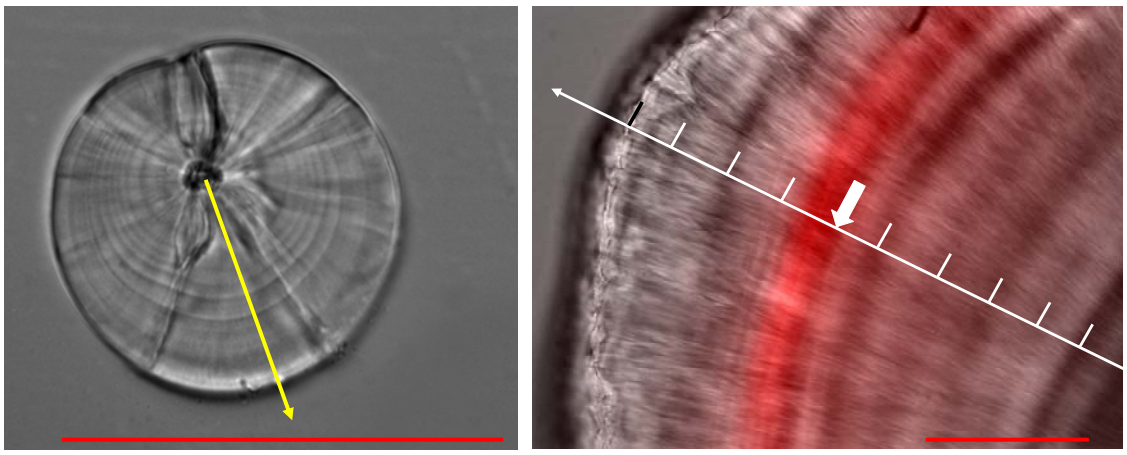


Fig. 3.2. Left picture: Lapillus of a larval *Sphyraena barracuda* (1000X) polished to the core from the top only. The red line indicates 50 µm and the yellow arrow indicates a reading axis along which daily increments were measured and enumerated from the core to the otolith edge. Right picture: Lapillus of a juvenile *Sphyraena barracuda* (1000X) that survived 3-4 d post staining, showing the reading axis (long white line), daily growth increments (short white lines), otolith edge (short black line) and the location of the fluorescent daily increment produced by alizarin staining (white arrow). The red line indicates 50 µm.

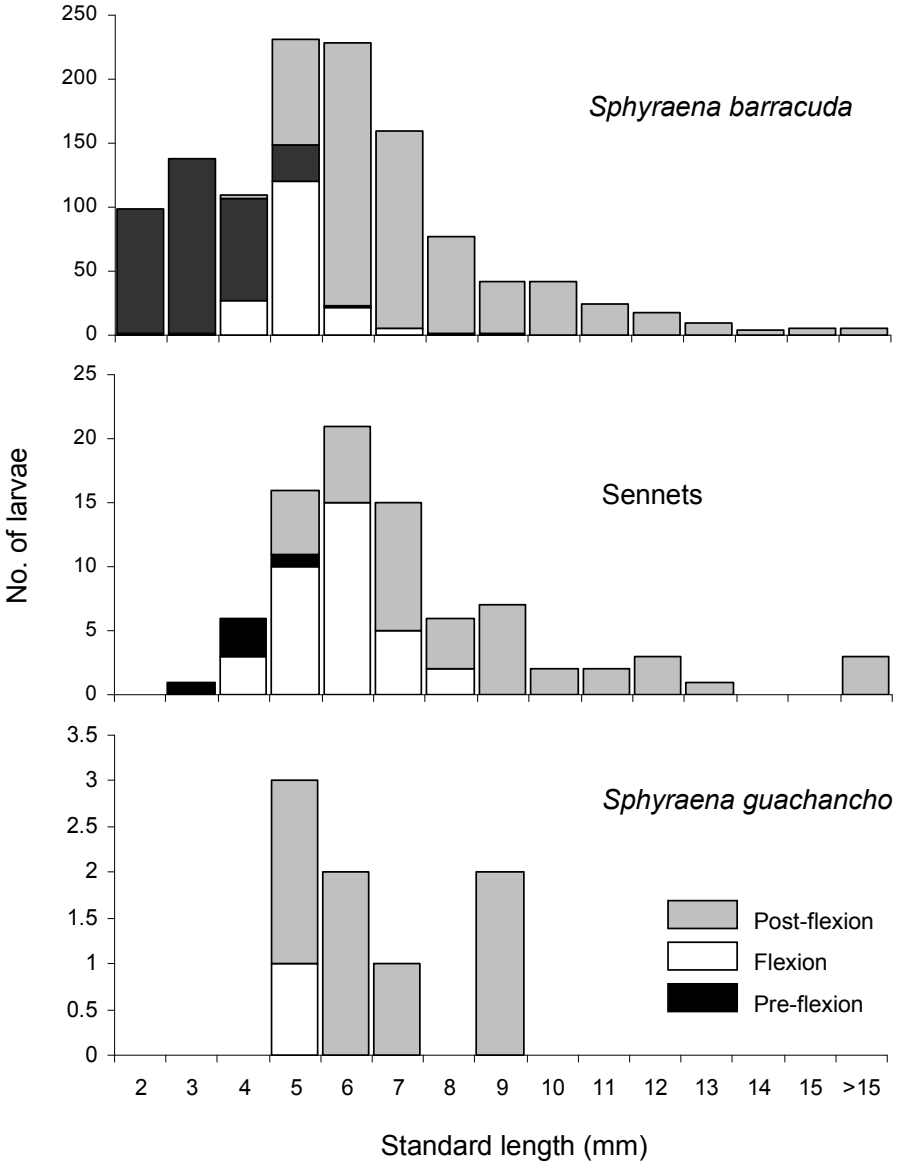


Fig. 3.3. Length-frequency histograms of (a) *Sphyraena barracuda,* (b) sennets, and (c) *Sphyraena guachancho* from all 24 months of sampling across the Straits of Florida.

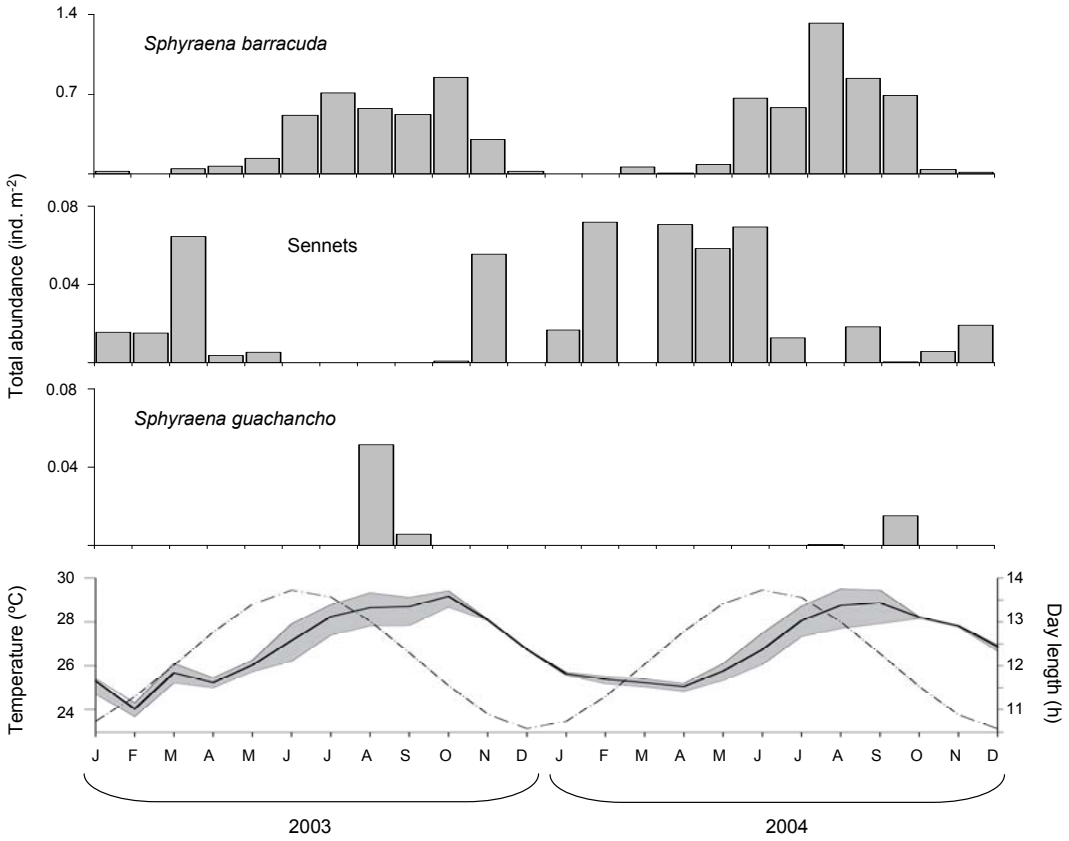


Fig. 3.4 Total larval abundance over time of sphyraenids captured during the 2 yr study (top three panels), and day length (dashed line), mean water temperature (solid line), and temperature range (shaded area) across the Straits of Florida in the upper 50 m of the water column (bottom panel).

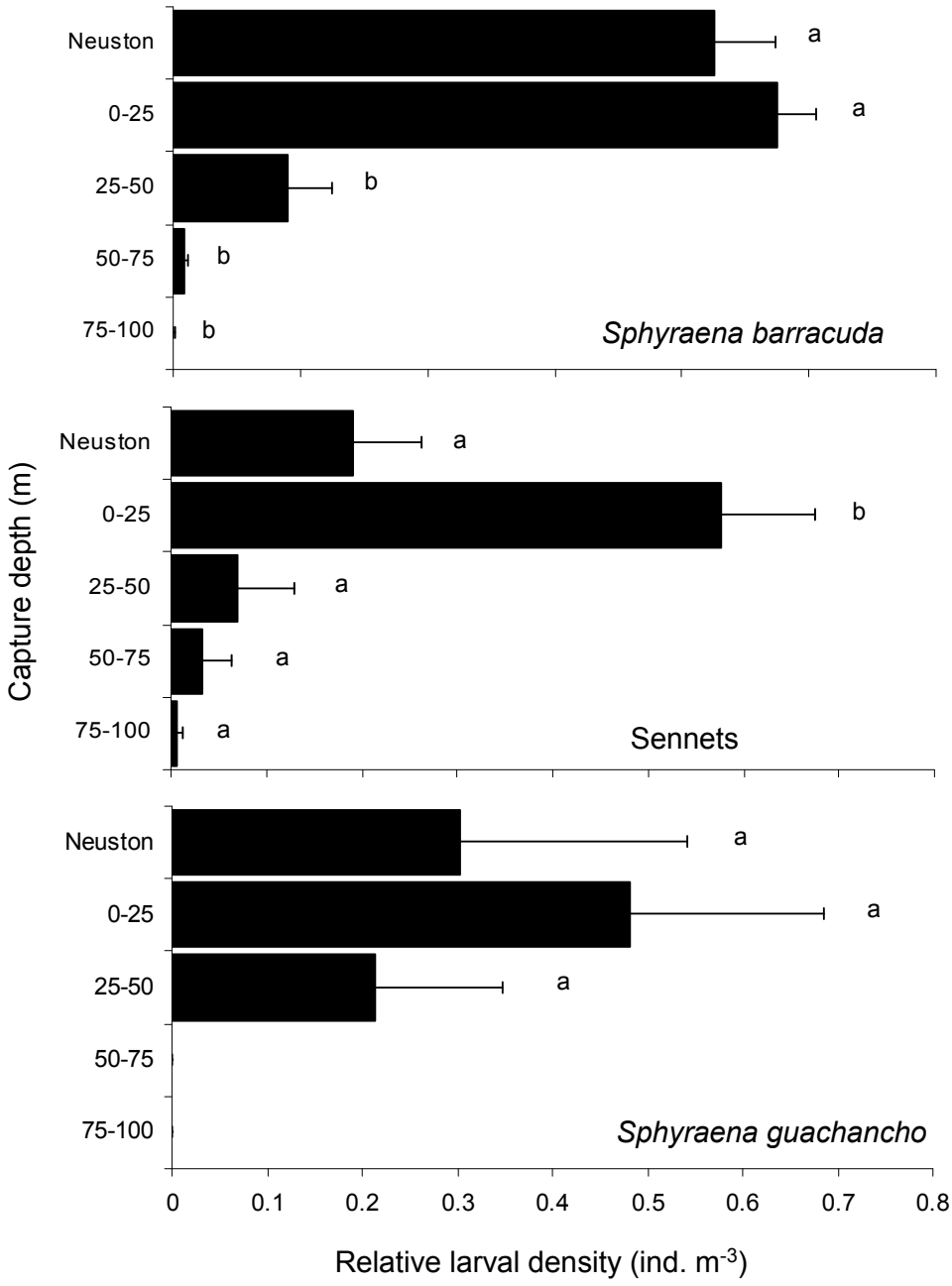


Fig. 3.5. Depth distributions of sphyraenid larvae captured in the Straits of Florida, expressed as proportional densities at depth across all stations and averaged over the main months of occurrence (June-October: *Sphyraena barracuda* and *Sphyraena guachancho*; November-May: *Sphyraena borealis*). Different letters indicate significant differences among depths for each taxon.

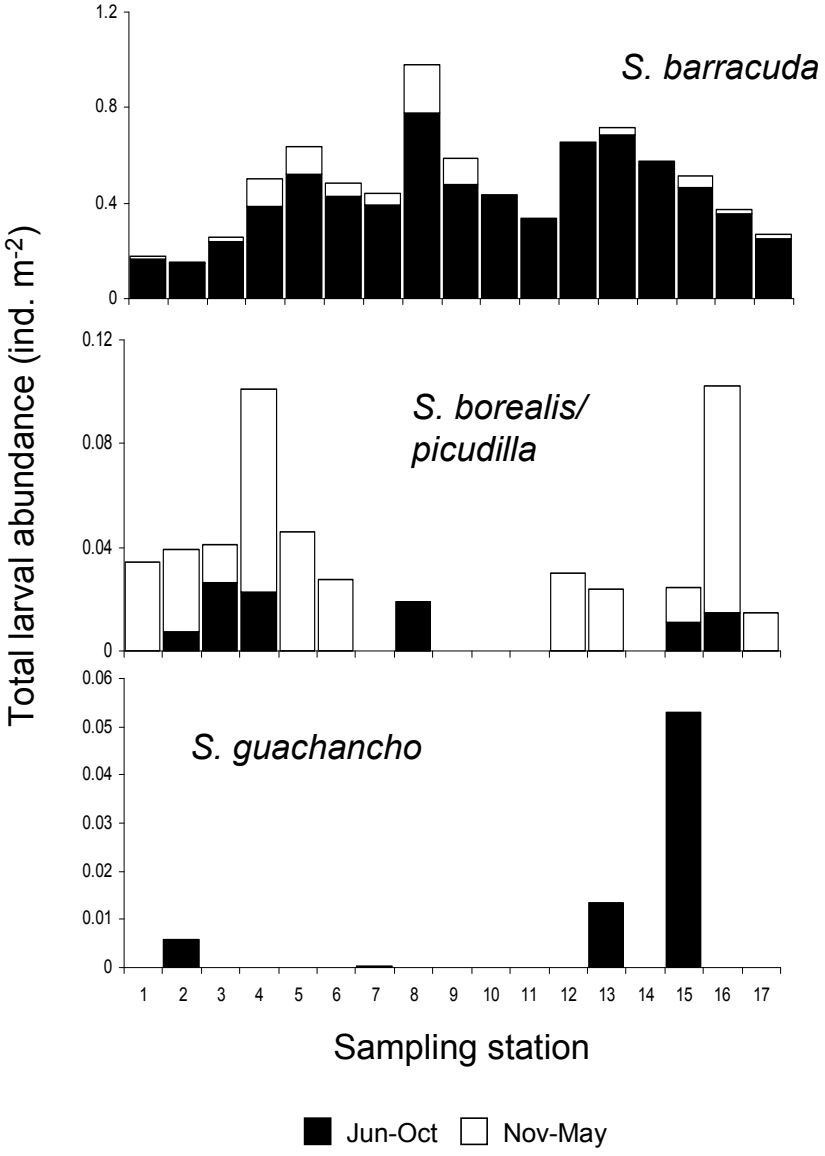


Fig. 3.6. Total larval abundance of sphyraenid larvae collected from 17 stations across the Straits of Florida. Abundances were summed across years and separated into wet (June-October) and dry (November-May) seasons to simplify illustration.

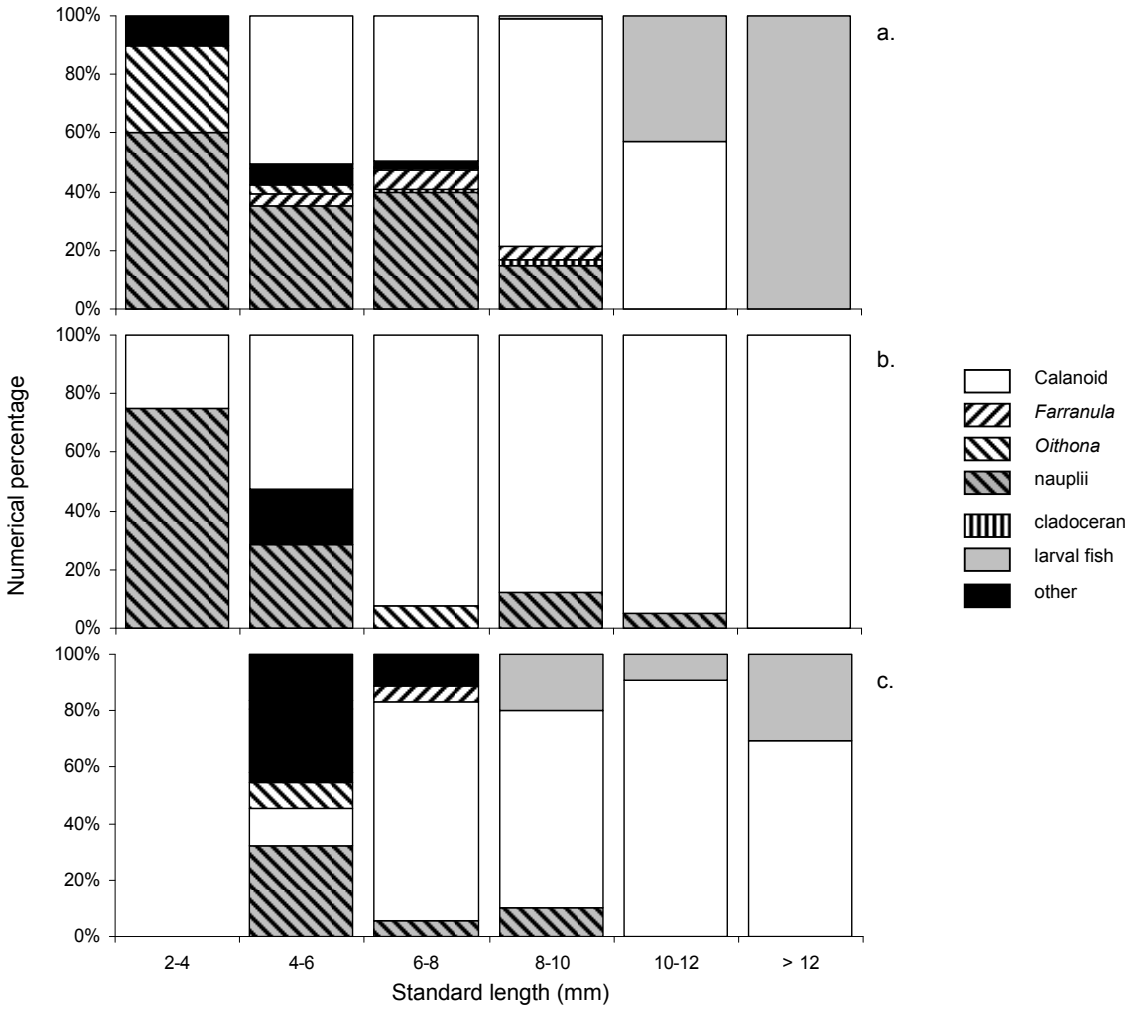


Fig. 3.7. Numerical proportions of prey items in guts of (a) wet and (b) dry season *Sphyraena barracuda* and (c) sennets (*Sphyraena borealis* and *Sphyraena picudilla*) by larval standard length.

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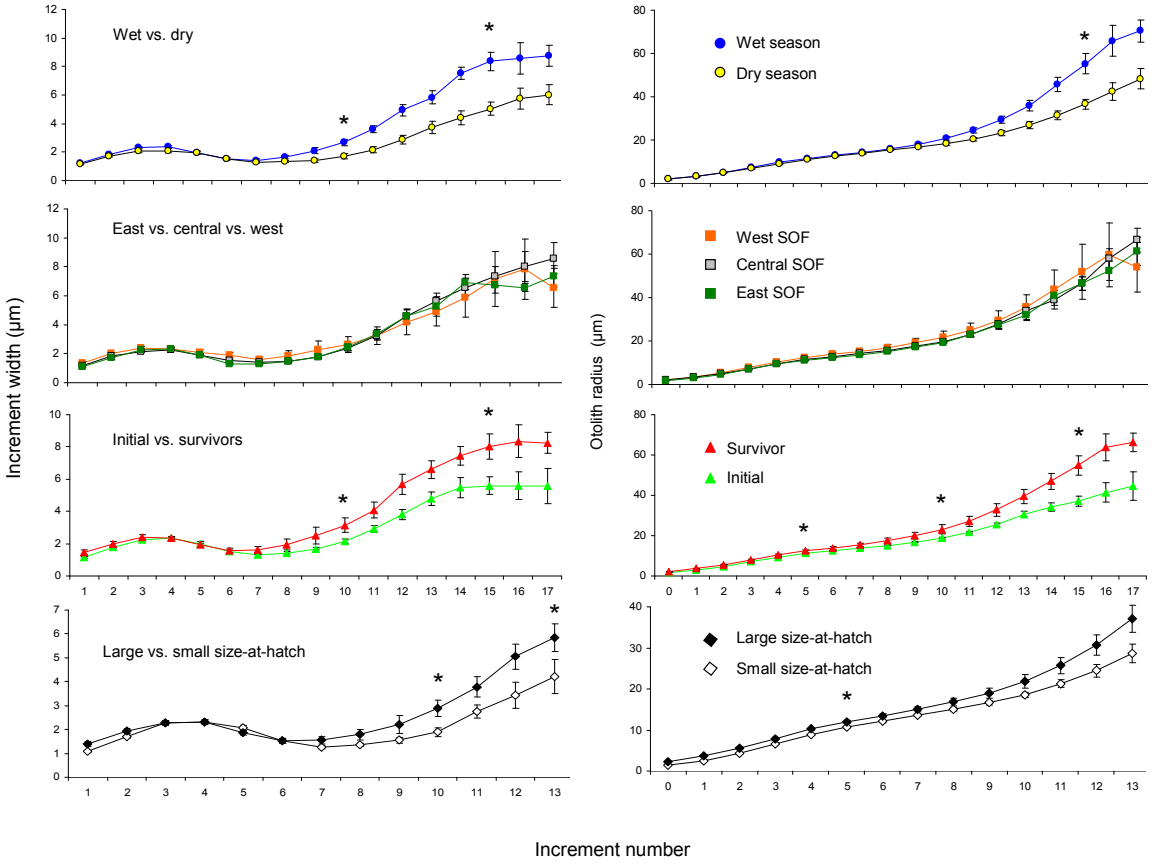

Fig. 3.8. Mean larval growth (otolith increment widths; left panels) and size-at-age (otolith radius at increment; right panels) of *Sphyraena barracuda* in terms of growth in the wet and dry season (wet vs. dry), the western, central, and eastern portions of the Straits of Florida (east vs. central vs. west), larvae with large and small hatch sizes (large vs. small size-at-hatch), and larvae < 8 mm SL and > 8 mm SL (initial vs. survivor). Error bars: SE; * statistically significant differences ($p < 0.05$).

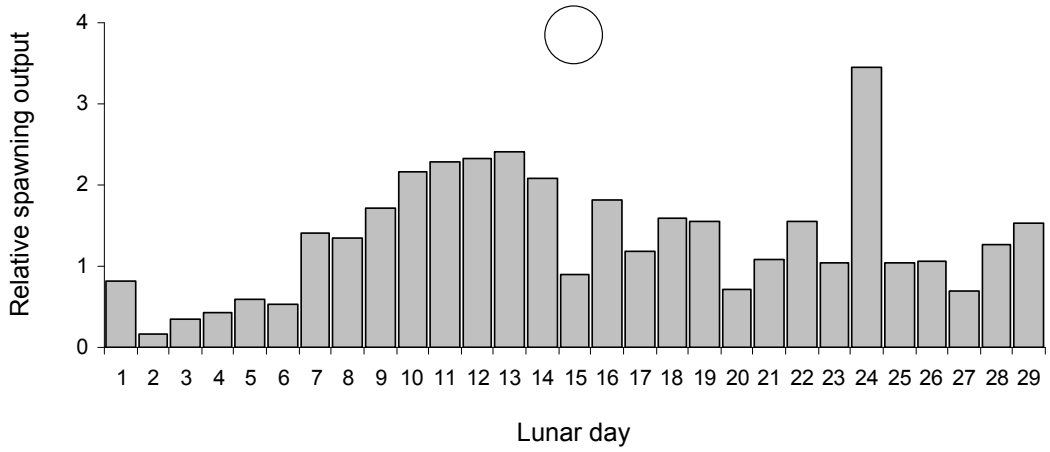

Fig. 3.9. Back-calculated successful spawning output by lunar day for *Sphyraena barracuda*. Lunar day 1 corresponds to the new moon and day 15 to the full moon (circle).

Chapter 4: Comparative Predation Rates on Larval Snappers (Lutjanidae) in Oceanic, Reef, and Nearshore Waters

Background

Most coral reef organisms have complex life histories, whereby relatively sedentary adults produce pelagic eggs or larvae. These larvae often spend days to weeks in the open ocean before returning to reef and/or nearshore environments to settle as juveniles. The pelagic larval phase is a period of extremely high mortality (Houde 1987), and has been recognized over the last century as a major contributor to fluctuations in recruitment. A widely held assumption is that the evolutionary basis for this pelagic phase in reef fishes is to allow eggs and larvae to develop and grow in an environment away from the abundance of predators that typically occupy coral reef habitats (Johannes 1978, Strathmann et al. 2002).

More recently, attention has been directed to the brief (usually occurring during a single night) shift from pelagic larva to bottom-associated juvenile – a transition referred to as "settlement." During this process, settling larvae that are relatively naïve to the juvenile habitat are exposed to a new suite of challenges including different predators, prey, and physical environmental factors. Settlement is often accompanied by very high mortality rates, suggesting that a "predation gauntlet" occurs during and shortly after settlement that may act as a bottleneck for adult populations (Doherty et al. 2004, Osman and Whitlatch 2004, Almany and Webster 2006). Despite the importance of this transition, little is known about the processes involved due in large part to the difficulty involved in unobtrusively tracking and observing larvae at night (Little 1977, Victor 1991, when most larval settlement occurs; Dufour and Galzin 1993, Reyns and

Sponaugle 1999) through sometimes large expanses of open water (but see Acosta and Butler 1999).

Many shallow water snapper (family: Lutjanidae) species and other ecologically and economically important reef fishes and invertebrates (barracuda, groupers, grunts, spiny lobsters) use nearshore back-reef areas as settlement and juvenile habitats before moving to reefs as adults. These larvae must therefore traverse at least the shallow fringing reef tract before reaching nearshore seagrass, algal, and/or hard-bottom habitats. This additional time in nearshore waters may impose particularly high mortality pressure on settling larvae. The overall objective of this study was to examine relative nocturnal mortality rates of late-stage snapper larvae in surface waters of three different cross-shelf habitats. Specifically, we tested the hypothesis that relative predation rates in surface waters differ among oceanic, reef, and nearshore seagrass/hardbottom habitats, with predation intensifying as relatively naïve larvae leave the deep oceanic environment and encounter increasing predator densities in shallow nearshore waters.

Materials and Methods

Study area

The study area encompassed a ~13 km cross-shelf corridor on the Atlantic side (south-southeast) of Sugarloaf Key, lower Florida Keys (FK), USA (Fig. 4.1). This corridor included three distinct habitats: 1) oceanic waters (OC) between the 50 and 100 m isobaths ~13 km from shore; 2) reef waters (RF) located over or directly adjacent to the fringing reef crest (~10.5 km from shore in 3-7 m of water); and 3) nearshore waters (NR) over seagrass/algae/sand/hardbottom ~3.5 km from shore in ~5-7 m of water (Fig. 4.1). The marine environment surrounding the lower FK is a dynamic area affected by

tides, seasonal winds, and the Florida Current (FC) and its associated meanders and eddies. The net westward water movement inshore of the fringing reef is driven by the prevailing westward winds that persist for most of the year (Pitts 1994). The combination of these winds and the east-west orientation of the coastline in the lower FK also causes downwelling along the coast, with onshore flow in the upper layers (Lee et al. 1992). On the outer shelf and often over the fringing reef tract, local wind forcing has little influence on the alongshore flow regime, which is dominated by the FC. In the lower FK, variability in the currents over this area occurs on a 30-60 d time scale due to the passage of mesoscale cyclonic eddies that form along the boundary of the Loop Current as it flows south along the west Florida shelf (Lee et al. 1994, Fratantoni et al. 1998).

Study organisms and field collection

To study predation during settlement, we focused on snappers (Lutjanidae) that are associated with coral reefs as adults. The occurrence of late-stage larvae and newly settled juveniles of western Atlantic and Caribbean snappers in nearshore waters, as indicated by recruitment surveys (Watson et al. 2002), back-calculation of settlement from juveniles (Allman and Grimes 2002, Tzeng et al. 2003, Denit and Sponaugle 2004), channel netting (Halvorsen 1994), and light trap catches (Wilson 2001, D'Alessandro et al. 2007), peaks during warm summer months (July-September) between third quarter to new moon periods. Channel net catches have further shown that ingress of snapper larvae to back-reef habitats through tidal channels occurs mostly at night and in the upper 1 m of the water column (Halvorsen 1994). Therefore, late-stage larval snappers were collected in July-August 2008 and July 2009 between the third quarter and new moons at 1-2 m depth using light traps over the fringing reef crest in the vicinity of American Shoal reef

(Fig. 4.1). Traps were modified from a design by Sponaugle and Cowen (1996b) and consisted of a 1.07 m-long, 0.43 m-diameter cylinder of 500 μm Nitex netting (Sea Gear Corp.), surrounding a 30 cm submersible 5 watt fluorescent light (Bellamare). The net cylinders had six 15 cm funnel shaped openings on the sides, and tapered on the bottom to a 1 L plastic cod-end. Traps were attached to semi-permanent moorings shortly before sunset and retrieved the following morning just after sunrise. Upon retrieval, larval snappers were separated from the rest of the sample, placed into a 220 L cooler of aerated seawater, and transported to shore where they were anesthetized, measured to the nearest 0.5 mm, and tethered (see below). A three-species group consisting of the species *Lutjanus apodus* (Walbaum, 1792), *Lutjanus griseus* (Linnaeus, 1758), and *Lutjanus jocu* (Bloch and Schneider, 1801), was utilized in this study. Morphological differentiation of these larvae to the species level is tenuous, and molecular techniques were not feasible in the present study since live larvae were required for the experiment. The tethering procedure consisted of suturing a 20 cm length of polyester-core thread through the dorsal musculature under the dorsal fin, approximately in line with the first anal spine, avoiding the notochord and major blood vessels (Danilowicz and Sale 1999). Larvae were then allowed to recover in individual 1-L jars of seawater for at least 2 h before experiments began.

Experimental protocol

The experimental design was modified from Acosta and Butler (1999). Eight weighted swivels were attached to a 1.5 m square polyvinyl chloride raft by 10 kg-test monofilament line (Fig. 4.2). Tethered larvae were attached to the swivels upon deployment such that larvae hung 0.5 m below the surface with a 20 cm sphere of free

movement. The raft was equipped with a small mast topped with a light beacon, which flashed every 30 s to facilitate retrieval at night. This beacon sat inside an opaque upward-facing 40 cm diameter funnel to prevent lighting of the area around the experiment (Fig. 4.2). The raft was deployed from an 8 m vessel which waited at least 100 m away with engines and lights shut off during each trial. The raft was allowed to drift for 30 min in each habitat, at which time it was retrieved and the number of larvae remaining on their tethers was recorded. Deployment and retrieval points were recorded to confirm that the device drifted over the intended habitat and to allow assessment of relationships between relative predation rate and the distance/direction of drift. This procedure was repeated in each of the three habitats in random order throughout the course of a single night and constituted one run of the experiment. To coincide with the most relevant time for natural larval snapper ingress and settlement, all experiments were conducted in full darkness after 21:30 h, in the upper 1 m of the water column, and during peak ingress and settlement within the year and lunar cycle. Each fish larva was used only once in one 30 min drift, and experiments were conducted on only relatively calm (< 5 m s^{-1} winds) nights to minimize disturbance to the tethered larvae by waves and shear between water currents and wind.

Preliminary 30 min daytime trials were carried out at the start of experimentation in 2008 and 2009, during which all tethered larvae were carefully and continuously observed in each habitat type for possible experimental bias and among-treatment artifacts. Larvae were not jerked about by movement of the raft, never became entangled or broke free from their tethers, and could move freely in a 20 cm radius around each weighted swivel. Moreover, in the 2-4 h that newly tethered larvae recovered in

individual 1-L jars, they never broke free from their tethers. Therefore, during experimental runs, larvae missing from their tethers upon retrieval of the drifter were considered lost due to predation.

Data analysis

Before testing differences in relative predation rates among habitats, we analyzed the data for relationships with confounding factors. A simple ANOVA and Tukey-Kramer HSD test was used to identify relationships between the distance the drifter traveled and habitat, and Pearson's product moment correlations were used to examine relationships (within habitats) between predation rate and distance the drifter traveled. Because the sensory distance of the predators and thus the true independence of each larva on the raft could not be determined, relative predation data was analyzed both as proportional (proportion of fish preyed upon during each deployment) and binomial (predation occurred or did not occur) datasets. A Pearson's Chi Square test and Tukey-type multiple comparisons for proportions were used in the former case, and a Cochran's Q and similar Tukey-type multiple comparisons in the latter to determine if relative predation was non-uniform between the three habitat types and identify where differences occurred (Zar 1999). To test for size selection by predators, t-tests were used to compare the mean lengths of larvae that were preyed upon with those that survived.

Results

Rafts of tethered larvae were deployed in all three habitats a total of 16 times over 13 nights in July-August 2008 and July 2009 (Table 4.1). These experiments utilized 384 snapper larvae ranging from 11 to 17 mm SL, 51 of which were preyed upon, resulting in an overall predation rate of 13%. The drifter traveled significantly farther in OC than in

RF or NR environments (Fig. 4.3; ANOVA; $p = 0.001$; Tukey-Kramer HS tests: OC vs RF $p = 0.026$; OC vs NS $P < 0.001$; RF vs NS $P = 0.341$), but no significant relationships were identified between relative predation rates and the distance the drifter traveled within each habitat or for all habitats pooled (Fig. 4.4). Likewise, the mean lengths of larvae that were preyed upon and those that survived were not significantly different whether pooled over the entire study (Fig. 4.5; t-test: $p = 0.710$; $df = 243$), or grouped by habitat (t-test: OC: $p = 0.980$ $df = 70$; RF: $p = 0.800$ $df = 48$; NR: $p = 0.270$ $df = 11$).

Both chi-square (proportional data; $\chi^2 = 25.53$; $p < 0.010$) and Cochran's Q tests (binomial data; $Q = 9.8$; $p < 0.010$) revealed that relative levels of predation differed between the three habitat types. Multiple comparisons of data analyzed binomially indicated that probability of predation was significantly higher in OC than in NR (Table 4.2; Fig. 4.6). When data were analyzed as proportions, larvae in OC experienced a significantly higher level of predation than those in either RF or NR (Table 4.2; Fig. 4.6).

Discussion

It is widely held that reef fish possess a pelagic larval stage to reduce mortality rates on their eggs and larvae by spatially separating them from reef-based predators (Johannes 1978, Strathmann et al. 2002). Based on this contention we hypothesized that relative nocturnal predation rates on late-stage snapper larvae in surface waters would differ significantly between open water and shallow nearshore environments, and that these rates would be highest over nearshore reef and seagrass habitats. Our results revealed that relative rates of nocturnal predation on surface larvae differed significantly among habitats, but the pattern was opposite to that predicted. Nocturnal predation on late-stage snapper larvae was highest offshore and decreased closer to shore.

Several factors specific to this study and inherent to tethering studies in general have the potential to bias experimental results. The most obvious is that tethering otherwise mobile organisms introduces experimental artifacts that usually inflate natural predation rates. However, these are cancelled out when applied equally to all treatments as they were here. In contrast, current speeds could not be controlled for and differed between habitats (due in large part to the proximity of OC treatments to the FC), resulting in significantly different distances traveled (and potential exposure to predators) between habitats. However, no significant relationship between distance the drifter traveled and predation rate was identified for the entire study or within any single habitat. Thus, it is unlikely that the distance traveled by the drifter was a causative factor in the observed pattern of relative predation.

It is likely that predator guilds in the three environments (treatments) in this study differed in their compositions, opening the possibility for unequal interactions between predators and tethered larvae among treatments, deemed "second order artifacts" (Peterson and Black 1994, Aronson and Heck 1995, Haywood et al. 2003). For example, the late-stage larvae utilized in this study were presumably at or close to competency to settle, and thus undergoing morphological changes (e.g., development of juvenile pigmentation in snappers) to be less conspicuous in the shallow nearshore juvenile environment. If these late-stage larvae were no longer suited to a pelagic existence, moving them back into the oceanic environment and exposing them to oceanic predators would inflate the predation rate in this area. However, because of the large size range (6 mm SL) of the larvae used, lack of size selection amongst preyed upon larvae in any of the examined environments, and largely transparent state of most of the utilized larvae, it

seems unlikely that this potential second order artifact significantly affected the results. To rule out or control for all second order artifacts, the identity and reaction to tethered larvae of all potential predators in each habitat is needed, and this was beyond the scope of this study. Two other studies to date have tethered planktonic organisms to measure relative predation rates in different nearshore environments of the FK, and these utilized preliminary trials, behavioral observations, and experimental assays to evaluate experimental biases and second order artifacts (Acosta and Butler 1999, Bullard and Hay 2002). In both cases, none were identified and tethering was determined to be a valid means of measuring relative predation rates. Ours is the first study to tether larval fish, and while all second order artifacts cannot be ruled out, preliminary trials did not indicate any among-treatment bias or experimental artifacts.

So why then would predation become less intense at the surface as larvae move shoreward? The answer may lie in differences in the distribution of predators between the three habitats such that more predators were concentrated near the surface (and near the experimental drifter) in OC and closer to the bottom in RF and NR. Juveniles and adults of many fish species (potential predators of late-stage larval snappers) commonly aggregate near the surface around flotsam and floating algae in deep oceanic waters (Hunter and Mitchell 1967, Kingsford and Choat 1985, Casazza and Ross 2008). Such drifting communities were abundant and frequently in proximity to the experimental raft in OC during the present study. In contrast, on coral reefs, predators of settling larval fish may be more concentrated near the bottom. Planktivorous fish can cause a near-bottom depletion of zooplankton on some reefs (Holzman et al. 2007, Heidelberg et al. 2010), and much of the mortality associated with settlement of fish larvae is attributed to the

actions of small reef-associated predatory fish (Carr and Hixon 1995, Holbrook and Schmitt 2002). In fact, seven of nine families of reef fishes known to consume larval reef fish in the Caribbean are small bottom dwellers (Randall 1967). In a recent study which involved observation of larval snappers (*Lutjanus carponotatus*) settling during the day, predation and aggressive interactions were only observed when larvae attempted to settle to the benthos and not when swimming over the reef (Quere and Leis 2010), suggesting that predators in this environment stay close to the bottom. Such reef-based predation on small fishes is higher at night (Danilowicz and Sale 1999) when most larval fish settlement occurs. Although transient predators that may hunt above the reef are also an important component of reef-based predation (Hixon and Carr 1997), the extent to which they feed on settling fish larvae is unknown. While depth ranges (and potentially vertical distributions of predators) and relative predation rates and probabilities between RF and NR were similar, back reef habitats are often cited as nursery areas and offer a lower predation risk than shallow reef habitats (Chittaro et al. 2005). Therefore, larvae tethered to within 1 m of the surface likely encountered an increased abundance of predators in OC and fewer in RF and NR where they were separated from the bottom (and presumably the majority of predators). Alternatively, the patterns in relative predation may have simply arisen from differences in the density of relevant predators between the three habitats. Unfortunately, too few data exist as to the identity of major larval fish predators in the study area or relative densities among habitats to confirm or refute this possibility.

Higher predation on surface larvae offshore suggests that to reduce predation mortality, wild settlement-stage larvae should remain at depth offshore, and move into

surface waters as they enter reef and nearshore waters. An upward shift in the vertical distribution of snapper larvae during ingress is supported by several other studies. In tethering post-larval spiny lobsters at varying distances above the bottom along a typical offshore-inshore transport path in the FK (coral reef, coastal lagoon, and bay), Acosta and Butler (1999) also identified a reduction in relative predation with distance inshore and concluded that these organisms likely utilize the surface waters during the darkest lunar phase to reduce risk of predation during inshore migration. Utilizing the upper water column in the shallow nearshore habitats of the lower FK would also allow these post-larvae to take advantage of onshore movement of surface waters typical of this region (Lee et al. 1992, Lee and Williams 1999). While less is known about the ingress of late-stage larval snappers (especially in offshore oceanic waters), younger and smaller (mostly 3-9 mm SL) larvae of reef-associated western Atlantic and Caribbean snappers in deep waters of the FC are concentrated in the upper 25 m of the water column, move to shallower depths with development, and are rarely captured at the surface by neuston nets nocturnally or diurnally (D'Alessandro et al. 2010, Huebert et al. in revision). Direct observation of settling late-stage *Lutjanus carponotatus* larvae revealed that in near-reef areas, they preferred the upper half of the water column, but avoided the upper 2.5 m (Quere and Leis 2010). In contrast, depth-stratified light trapping over reefs (Hendriks et al. 2001) and channel netting in nearshore tidal passages (Halvorsen 1994) revealed that most late-stage snapper larvae are near the surface in these shallow water areas. Combined with these studies, results of our tethering experiments suggest that successful larval snappers avoid the surface in deep oceanic waters until the water column is constrained by the shallow fringing reef crest, and near-bottom predators must be avoided

by moving to shallower depths. By following this cross-shelf migration strategy, larvae could minimize encounters with the highest concentrations of predators and capitalize on onshore transport mechanisms.

Table 4.1. Distance (m) traveled by the drifter (D) and number of larval snapper missing from their tethers (i.e. preyed upon; P) at the end of each of the 16 deployments in each of the three habitats (OC = oceanic; RF = reef; NR = nearshore).

Date	Deployment (running)	OC		RF		NR	
		D	P	D	P	D	P
7/29/2008	1	510	4	200	1	150	0
8/1/2008	2	520	0	590	0	660	0
8/3/2008	3	810	3	410	1	610	1
8/7/2008	4	240	8	280	2	290	0
8/9/2008	5	1120	0	700	0	470	0
8/23/2008	6	690	1	240	1	380	0
8/24/2008	7	1080	0	340	0	300	0
8/25/2008	8	940	0	6	3	450	0
8/26/2008	9	770	4	260	0	4	0
8/27/2008	10	925	3	340	0	580	3
7/16/2009	11	170	3	320	4	400	0
7/16/2009	12	190	4	140	2	430	0
7/17/2009	13	360	0	130	0	160	0
7/17/2009	14	340	0	170	0	210	0
7/18/2009	15	620	1	100	0	590	0
7/18/2009	16	620	2	230	0	660	0
Totals		9905	33	4456	14	6344	4

Table 4.2. Test statistics from multiple comparisons of relative predation between the three habitat types analyzed binomially (probability of predation; Probability) and as proportions (percent of larvae preyed upon; Proportion). Critical values at the $\alpha = 0.01$ level are given in parentheses. Bold type indicates significant differences.

Site	Probability ($S_{\alpha=0.01} = 3.035$)	Proportion ($q_{\alpha=0.01} = 4.12$)
OC v RF	1.16	**4.38**
OC v NR	**3.10**	**7.77**
RF v NR	1.94	3.39

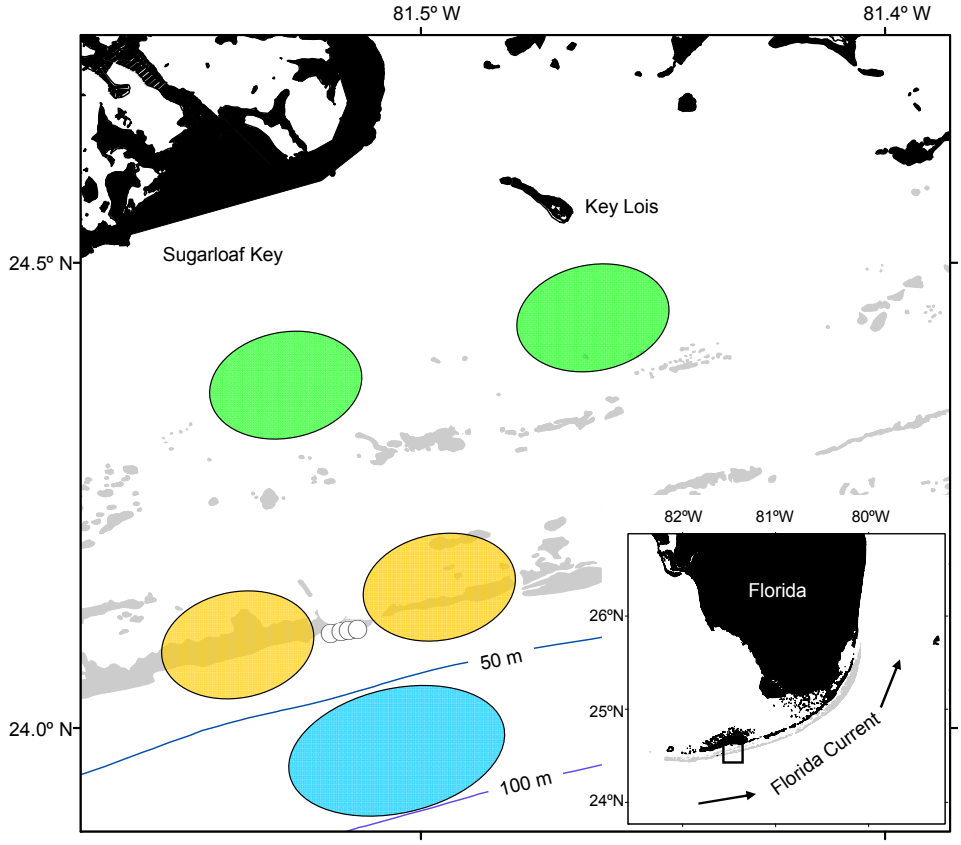

Fig. 4.1. Map of the study area offshore of Sugarloaf Key, Florida, showing light trap moorings (open circles) and the three areas where experiments were conducted: blue water (OC; blue oval), reef (RF; orange ovals), and nearshore (NR; green ovals). Land is shown in black and reef is shown in gray.

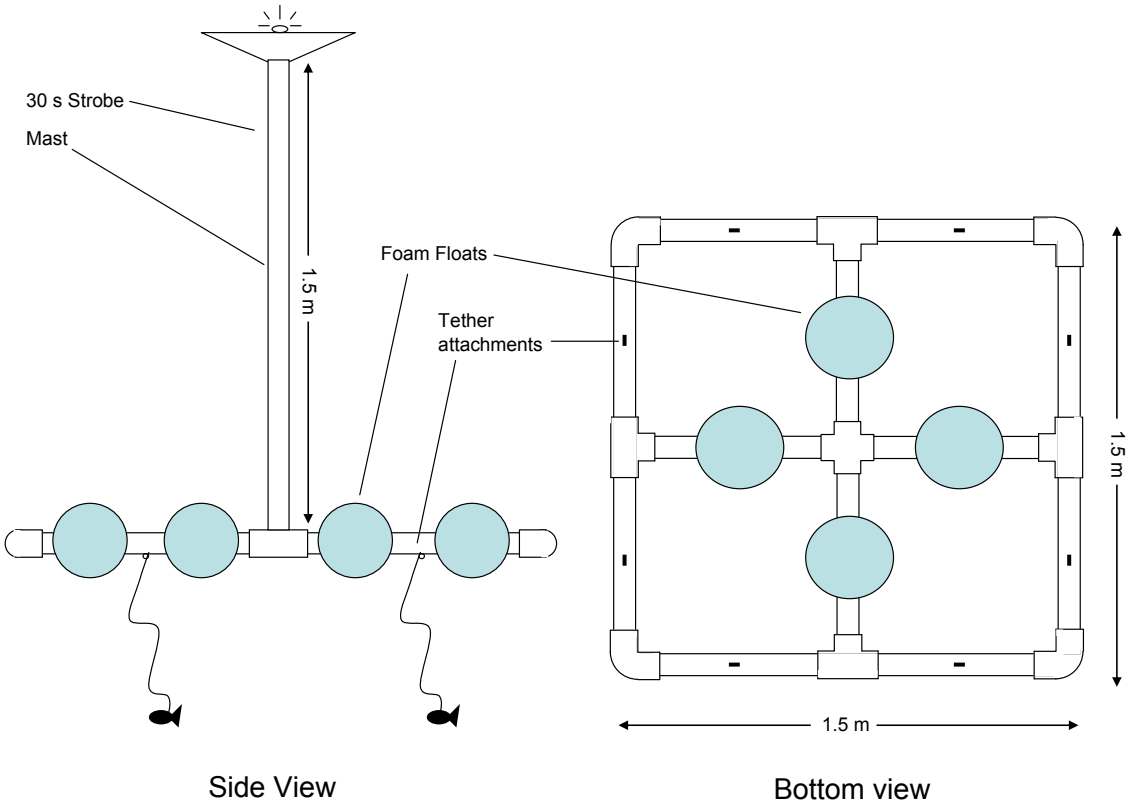

Fig. 4.2. Schematic of the drifting device to which larval snappers were tethered.

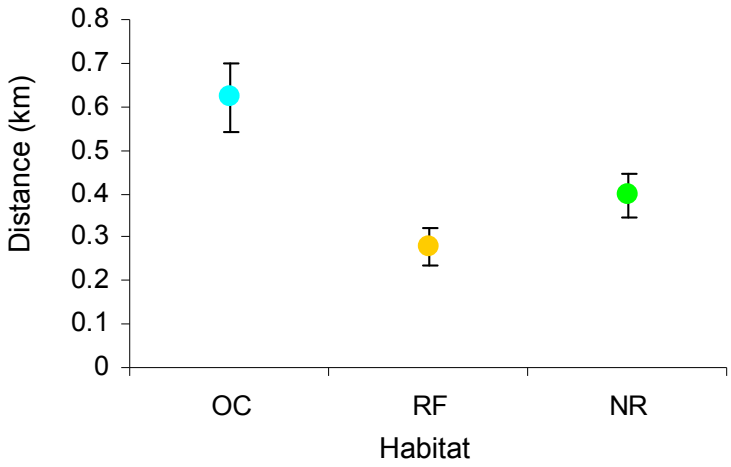

Fig. 4.3. Mean (± SE) distance (km) the drifter traveled in each of the three habitats (OC = oceanic; RF = reef; NR = nearshore).

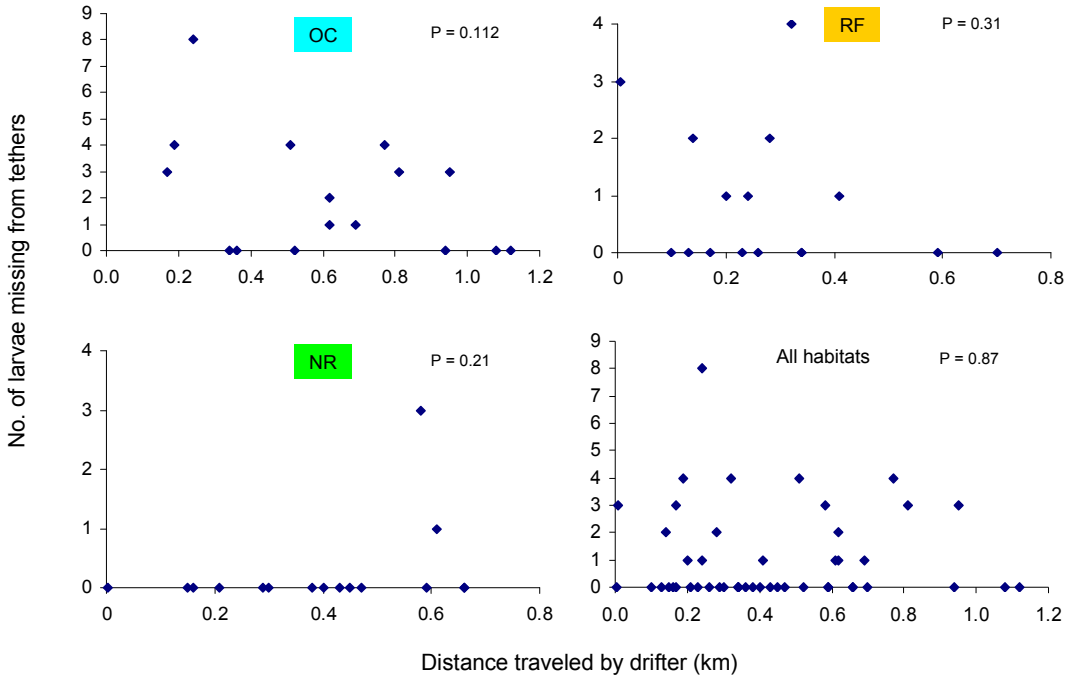

Fig. 4.4. Plots of distance traveled by the drifter versus number of larvae missing from tethers in each of three habitats (OC = oceanic; RF = reef; NR = nearshore) and all three habitats combined (All habitats).

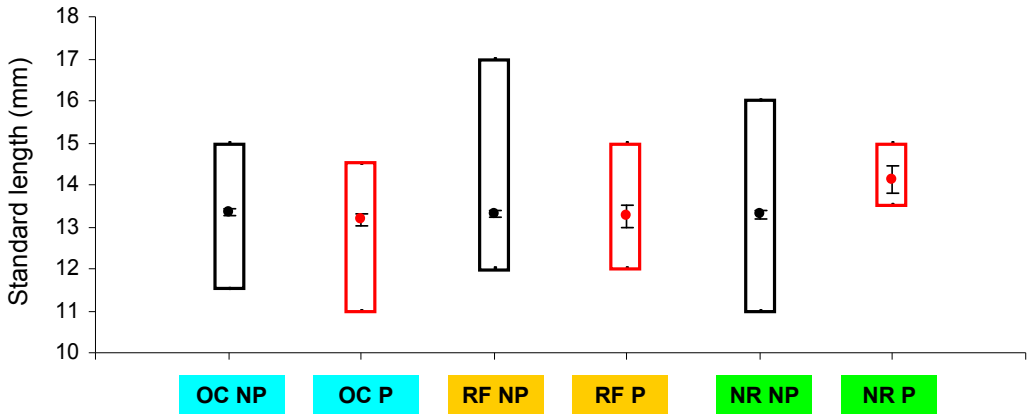

Fig. 4.5. Mean (± SE) lengths of tethered larvae both absent (preyed upon; P; red markers) and present (not preyed upon; NP; black markers) after 30 min of drift over the three habitats: oceanic (OC), reef (RF), and nearshore (NR). Range of data given by thick horizontal bars.

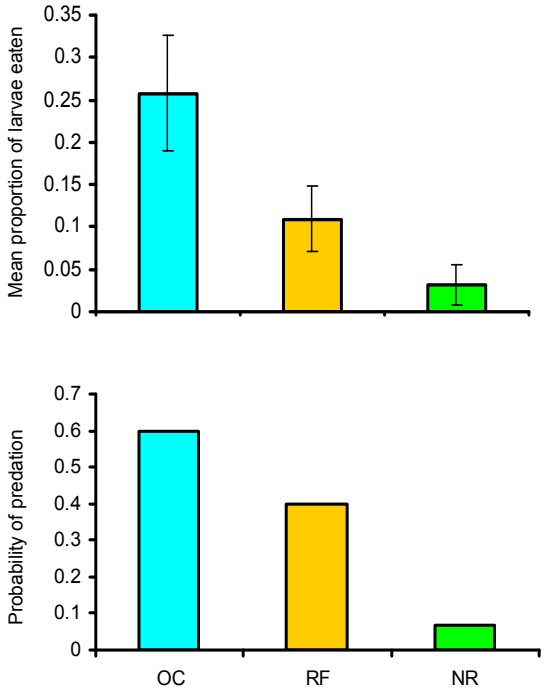

Fig. 4.6. Mean (± SE) proportion of larval snappers preyed upon per drifter deployment (out of eight; top panel), and probability of at least one predation event (binomial representation of data) occurring (bottom panel), over each of the three habitats: oceanic (OC; blue), reef (RF; orange), and nearshore (NR; green).

Chapter 5: Selective Mortality During the Larval and Juvenile Stages of Snappers (Lutjanidae) and Great Barracuda (*Sphyraena barracuda*)

Background

Most marine fishes are characterized by a dispersive pelagic larval stage followed by metamorphosis into the juvenile form, often accompanied by settlement out of the plankton to the benthos. A high degree of inherent variability in fish stocks and poor correlations with recruitment have led fisheries biologists to turn their attention to factors affecting the planktonic larval stage of fishes. Mortality rates in this early stage are extremely high (Bailey and Houde 1989, Leggett and Deblois 1994) owing to predation, starvation, and expatriation. It is now widely accepted that predation is likely the ultimate cause of most mortality, while other factors such as starvation make larvae more or less susceptible to this endpoint (Bailey and Houde 1989). Such high rates of mortality in conjunction with a large amount of variation in larval traits (McCormick 1998), ranging from genetic identity (Vigliola et al. 2007) to experience with predators (McCormick and Holmes 2006), often leads to non-random mortality and preferential survival of certain individuals. The growth-mortality hypothesis (Anderson 1988) provides a conceptual framework to examine selective loss in larval fish and contends that larvae that grow faster (*Growth Rate Hypothesis*; Ware 1975), complete the precarious larval stage faster *(Stage Duration Hypothesis*; Houde 1987), and/or are larger at given ages *(Bigger is Better Hypothesis*; Miller et al. 1988) will preferentially survive. This theory has been supported by numerous temperate (e.g., Hovenkamp 1992, Meekan and Fortier 1996, Hare and Cowen 1997) and some tropical studies (e.g., Meekan et al. 2006), though some experimental studies have found the opposite (Fuiman 1989, Litvak and Leggett 1992,

Pepin et al. 1992), or no selective patterns (Bertram and Leggett 1994, Robert et al. 2010). Thus, extremely high non-random mortality in the planktonic stage of marine fishes suggests that even small changes in size and growth during the larval phase may lead to large fluctuations in juvenile and adult populations (Houde 1989).

Mortality remains extremely high through settlement to the juvenile habitat (reviewed in Almany and Webster 2006), and in combination with a lack of indiscriminate processes like expatriation and a high degree of variability among individuals (Kerrigan 1996), this mortality also has a high potential to be non-random (Sogard 1997). The assumption that faster growth and larger size enhances survival has become pervasive in studies of the juvenile stages of marine fishes as well, and is supported by many recent studies (Searcy and Sponaugle 2001, Vigliola and Meekan 2002, McCormick and Hoey 2004, Hawn et al. 2005, Meekan et al. 2006, Durieux et al. 2009, Johnson and Hixon 2010). However, settlement in reef fishes involves a switch to a more demersal, site attached lifestyle, and confounding effects such as habitat heterogeneity, competition, and density dependence (which are largely avoided by larvae in the diffuse planktonic environment) may mediate or even mask selective processes (Brunton and Booth 2003, Holmes and McCormick 2006, McCormick and Meekan 2007, Samhouri et al. 2009).

While selective mortality has been extensively examined in the early life stages of many temperate commercial and recreation fisheries species (Hovenkamp 1992, Meekan and Fortier 1996, Hare and Cowen 1997), most studies examining selective processes in tropical reef species have focused on small, short lived, and easily sampled reef fishes (Searcy and Sponaugle 2001, Vigliola and Meekan 2002, McCormick and Hoey 2004,

Meekan et al. 2006). These studies have provided many important findings, one of which is the non-static nature of selective patterns, which can change with ontogeny (Gagliano et al. 2007a) and environmental variability (Grorud-Colvert and Sponaugle 2010). Such changes cannot be detected without repeated sampling of life stages and inclusion of multiple cohorts. This is a challenging task as life stages of reef fishes are spatially disparate, with young larvae located offshore in diffuse concentrations, and late-stage larvae and juveniles located near the reef or other shallow nearshore environments. For commercially and recreationally important predatory reef fish, this difficulty is frequently compounded by the relative rarity of both early larvae and post-settled juveniles (Sponaugle unpubl. data). For this reason, most studies of selective mortality in reef fishes have focused on settlement stage larvae and/or post-settled juveniles, and used otoliths (ear stones) to glean information from the early larval stage. While these studies provide insights into the larval traits important for survival to and during the juvenile stage, without larval samples it is not possible to examine selective mortality within the larval stage and how these patterns may change at settlement.

The overall objective of this study was to examine selective mortality across multiple life stages in commercially and recreationally important coral reef associated Lutjanine snappers (family Lutjanidae) and barracudas (family Sphyraenidae). We used multiple sampling techniques to track and repeatedly sample multiple cohorts of these species from early larvae, through settlement, and into the juvenile stage. Specifically, we sought to test the growth-mortality hypothesis within the larval stage in terms of size-at-hatch, larval growth, and larval size-at-age, and in the juvenile stage in terms of the

aforementioned larval traits as well as pelagic larval duration (PLD), size-at-settlement, juvenile growth, and juvenile size-at-age.

Materials and Methods

Study area and focal species

The lower Florida Keys (FK) are a chain of islands running northeast-southwest along the Straits of Florida, opposite the north coast of Cuba. Just seaward of these islands shallow (< 3 m) nearshore seagrass, hardbottom, and mangrove environments give way to Hawk Channel (approximately 1 km offshore and up to 10 m deep), followed by the fringing reef tract (between 5 and 10 km offshore). Seaward of the fringing reef, the continental shelf slopes gradually to a break at 30 m, where it drops off hundreds of meters into the Straits of Florida (Pitts 1994, Lee and Williams 1999). Flow within Hawk channel is influenced mainly by wind and tides, causing a net southwestward flow (Pitts 1997). Currents near and seaward of the fringing reef are dominated by the fast-moving (up to 2 m s^{-1}) northeasterly flowing Florida Current (FC). Flow in these areas may be downstream with the FC or be reversed, depending on the presence of large cyclonic mesoscale eddies that dominate the oceanography offshore of the lower FK on a time scale of several months, and have been implicated in the retention and nearshore delivery of larvae of reef fishes and invertebrates including economically important species (Lee and Williams 1999, Lindeman et al. 2001, Yeung and Lee 2002).

Snappers and barracudas are an important component of commercial and recreational fisheries in the southeast United States and Caribbean. Like many coral reef fishes, their early life history is characterized by a dispersive planktonic larval stage. This stage lasts between 31-42 d in several reef-associated snapper species (summarized in

Lindeman et al. 2001) while the PLD of *Sphyraena barracuda* has been estimated as 17.6 d (range 15-21) from light trap caught late-stage larvae assumed to be competent to settle (Sponaugle et al. 2005b). Although seemingly disparate families, coral-reef associated lutjanids and sphyraenids share an important early life characteristic in that they both settle to shallow nearshore back-reef habitats instead of reefs (hardbottom, seagrass, and mangroves; Lindeman et al. 1998, Nagelkerken et al. 2001a, Bartels and Ferguson 2004). In the FK, these habitats are vast, and densities of newly settled individuals are exceedingly low (Sponaugle unpubl. data). For several years following settlement, these fishes undergo a seaward ontogenetic migration such that large reproductive adults inhabit and spawn at the fringing coral reef and other deeper shelf slope habitats (Cocheret de la Moriniere et al. 2002, Serafy et al. 2003b, Eggleston et al. 2004). In both families, the majority of spawning (Thresher 1984, Kadison et al. 2010) and thus availability of larvae in the FK is restricted to warm summer months (D'Alessandro et al. 2007, 2010; Chapter 2). As larvae, snappers feed mainly on copepod nauplii and appendicularians (Llopiz and Cowen 2009), switching as juveniles and adults to a mixed but exclusively carnivorous diet of invertebrates and fishes (Randall 1967). Young sphyraenid larvae feed mainly on calanoid copepods and copepod nauplii but begin to switch to piscivory at about 8 mm SL (Chapter 3) and are nearly exclusively piscivorous during their juvenile (Schmidt 1989) and adult lives (de Sylva 1963, Randall 1967).

Sample collection and identification

Three sampling methods were employed to target the different ontogenetic stages of lutjanids and sphyraenids. Shipboard plankton tows targeted small pelagic larvae and were carried out during daylight hours on three separate cruises: May 29 - June 15 2007,

July 30 - August 13 2007, and June 17 - July 1 2008. Each cruise sampled 96 fixed stations (and 37 and 21 supplemental stations in the first and second cruises, respectively) encompassing 10 cross-shelf transects along the FK that ranged from the deep oceanic waters of the FC to the nearshore waters inside Hawk Channel (Fig. 5.1). At each station, a multiple-opening-closing-net-and-environmental-sampling-system (MOCNESS) and frame net were used make oblique tows of 20 m depth bins from the surface to 100 m, and horizontal tows of the top ~ 0.5 m of the water column, respectively. Both net systems were towed at a speed of 1 m s^{-1} and were outfitted with continuously recording flow meters, depth and temperature sensors, and contained dual openings with 1-mm and 150-μm mesh nets (MOCNESS – 4 m^2 1 mm mesh and 1 m^2 150 μm mesh (Guigand et al. 2005); Neuston – 2 m^2 1 mm mesh and 0.5 m^2 150 μm mesh). Samples from 150 μm mesh nets were not included in this study. One of the most important assumptions in studying selective mortality is that repeat samples are from the same population (Meekan and Fortier 1996). Recent studies of reef fish population structure revealed no genetic structure within the FK (Purcell et al. 2009, Shulzitski et al. 2009), suggesting that the area comprises one well-mixed population. As a conservative approach, samples of pelagic larvae were selected only from offshore and upstream of the lower FK to correspond spatially with the overwhelming majority of late-stage larval and juvenile snappers collected in the lower FK in both years (see Results).

To target late-stage larvae in the process of settlement, four replicate larval light traps (modified from a design by Sponaugle and Cowen 1996) were deployed nightly at each of two sites over the fringing reef crest in the lower FK for two weeks encompassing the new and third quarter moons in June, July, and August, 2007 and 2008. Traps

consisted of a 1.07 m-long, 0.43 m-diameter cylinder of 500 μm Nitex netting (Sea Gear Corp.), surrounding a 30 cm submersible 5 watt fluorescent light (Bellamare). The net cylinders had six 15-cm funnel shaped openings on the sides, and tapered on the bottom to a 1-L plastic cod-end. Traps were attached to semi-permanent moorings shortly before sunset and retrieved the following morning just after sunrise.

Juvenile snappers and barracuda were captured in shallow (< 2 m) nearshore seagrass and hardbottom habitats during summer months in the vicinity of Big Munson Key using hand nets and the anesthetic Quinaldine or a 21 m (3.2 mm mesh) seine. In addition, a winter (December) collection utilizing only the 21 m seine was carried out in both 2007 and 2008 in this same area to target older juvenile snappers.

Upon collection, all larvae and juveniles were immediately fixed in 95% ETOH and later measured to the nearest 0.1 mm notochord length (NL; pre-flexion larvae) or standard length (SL; post-flexion larvae and juveniles) and identified to species either morphologically using standard larval fish guides (e.g., Richards 2006), or molecularly (all young snapper larvae captured in pelagic tows except *Rhomboplites aurorubens*) following the protocols of D'Alessandro et al. (2010). Most late-stage larvae captured in light traps could be readily identified morphologically, however, one group of snapper species containing *Lutjanus griseus*, *Lutjanus jocu*, *Lutjanus apodus*, and *Lutjanus cyanopterus*, hereafter referred to as "Type G", could not be distinguished confidently without molecular confirmation. Due to the large numbers of type G snapper larvae collected in light traps (see Results) and the prohibitively high cost of molecular identification, only those type G larval snappers selected for otolith analysis were identified to species.

Otolith analysis

Otoliths were removed from all juveniles and a random sub-set of pelagic and light-trap larvae. One sagitta (snappers) or lapillus (barracuda) from each individual was imbedded in crystal-bond thermoplastic glue on a glass microscope slide. Snapper otoliths were polished to a thin transverse section containing the otolith primordium, while barracuda otoliths were laid flat and polished to the primordium on only one side (Fig. 5.2). A 1000X digital image of each otolith was taken using a Leica DMLB microscope equipped with an Infinity 2 digital camera. Otolith increments were enumerated and measured along the longest axis from the primordium to the outer edge using Image Pro 7.0 software (Media Cybernetics). In sectioned snapper larvae, the longest otolith axis shifted progressively with growth. To maintain consistency between individuals of different ages, a non-linear reading axis was created by tracing the longest axis of growth every four increments (Fig. 5.2). Increments were enumerated and measured twice for each otolith by the same person, and if counts differed by ≤ 5%, one count was randomly selected for analysis. If replicate counts differed by > 5%, the otolith was read a third time. If this third read differed by ≤ 5% from one of the other two reads, one of these was randomly chosen for analysis. Otherwise, the otolith was excluded from further analysis.

Daily increments have been previously validated in juvenile *Sphyraena barracuda* (Chapter 3), *L. griseus* (Ahrenholz 2000), *Lutjanus synagris* (Mikulas and Rooker 2008), and *Ocyurus chrysurus* (Lindeman 1997). Therefore, age in days post-hatch (dph) was the total number of increments between the otolith primordium and otolith edge, plus a 2 d correction for time to first increment formation in snapper species

(e.g., D'Alessandro et al. 2010). The spawn date of each individual, estimated as the dph age plus 1 d to account for incubation time (e.g., D'Alessandro et al. 2010), was then used to delineate monthly cohorts (Table 5.1). The daily increments on the otoliths of several snapper species are known to change markedly in width and optical contrast at the time of settlement to juvenile habitat, usually beginning with a conspicuously dark settlement mark (Lindeman 1997, Allman and Grimes 2002, Zapata and Herron 2002, Victor et al. 2009). The otoliths of both snapper and barracuda larvae we examined were consistent with this description. Juvenile age in days post-settlement (dps) was the number of increments between the settlement mark and otolith edge. Regression analysis between SL and otolith radius, SL and age, as well as between residuals of an otolith radius at age regression and residuals of a SL-at-age regression (Hare and Cowen 1995), were carried out for all analyzed species to verify the otolith growth-somatic growth relationship. However, to avoid introducing error in back-calculating somatic growth from otoliths (Chambers and Miller 1995), the distance between each increment was used as a relative measure of larval growth while the otolith radius-at-age was used as a relative proxy for size-at-age.

Data analysis

To examine selective loss through ontogeny, larvae were grouped together according to their dph age as initial larvae (Li) or survivng larvae (Ls), and juveniles by their juvenile age in dps as initial juveniles (Ji) or surviving juveniles (Js). Specific ranges of ages varied among species due to sample size constraints (Table 5.1). To identify whether selective loss occurred among ontogenetic groups, we evaluated the samples in terms of size-at-hatch (radius of the primordium), daily larval growth (otolith

increment width), size-at-age (otolith radius-at-age), including size-at-settlement and PLD for older larvae and juveniles. For these analyses, late-stage larvae captured in light traps were assumed to be traversing the reef to settle in nearshore environments. Therefore, their total age in dph was considered to be their PLD, and their total otolith radius was assumed to be their size-at-settlement. Differences in traits among age groups were initially evaluated on a cohort by cohort basis, but this stratification of the data did not change overall trends and shrank sample sizes such that meaningful statistical analysis was not possible in certain cases. Therefore, all larvae and juveniles were pooled across cohorts.

Previous studies have established the strong effect that temperature can have on larval growth of tropical coral reef fish larvae (McCormick and Molony 1995, Sponaugle et al. 2006). To account for this effect, differences in traits among age groups were tested with analysis of covariance (ANCOVA; Systat 11) using temperature as a covariate. Data were first tested for normality and homogeneity of variance (and log transformed where necessary), as well as for significant interaction between temperature and age group (homogeneity of slopes test; Systat 11). When data failed to meet the assumptions of parametric statistics, ANCOVA was used on rank-transformed data (Conover and Iman 1982). To examine whether growth and size at particular days differed among age groups, larval growth and size-at-age trajectories from larval life were plotted and statistically tested at increments 5, 10, and 15. These tests as well as tests of size-at-hatch among age groups used the mean temperature on the date the increment was formed and the date of hatch as covariates, respectively. The presence of linear or non-linear selection on size-at-hatch was also illustrated by generating non-parametric cubic splines

of the fitness function for this trait (Sinclair et al. 2002). These were calculated using a binomial distribution with initial and survivor age groups to obtain relative survival over time (e.g., Gagliano et al. 2007a, Grorud-Colvert and Sponaugle 2010).

To evaluate whether differences in juvenile growth and size among age groups were apparent relative to settlement, growth and size-at-age trajectories of older larvae and juveniles were also aligned by their settlement marks (assumed to be the next daily ring that would have formed in late-stage light trap-caught larvae), plotted, and tested at 5, 10, and 15 dps where possible, and the oldest increment for which there were at least five individuals in each age group. As with tests of larval trajectories, these tests used mean temperatures on the dates of increment formation as covariates. Tests of PLD and size-at-settlement in these late-stage larvae and juveniles used mean temperature experienced during the entire larval duration as covariates. The presence of linear or non-linear selection on these traits was also illustrated with cubic splines. Temperature data were obtained from the National Oceanic and Atmospheric Administration C-MAN station SAN-F1 as daily means, and were assigned to each increment for each individual based on the day of increment formation (date of capture – [total age – increment number]). Although location-specific temperature data at the time of capture was available for MOCNESS collected larvae, these data were not available for juveniles or light trap captured larvae, and fixed station temperature data was chosen to capture relative changes in temperature over time.

Results

Of the 532 MOCNESS- and frame net-captured snapper larvae randomly selected from lower FK station samples, 440 (83%) were positively identified and consisted of

188 *R. aurorubens*, 108 *O. chrysurus*, 92 unidentified, 66 *L. synagris*, 40 *L. griseus*, 27 *Lutjanus analis*, 6 *L. apodus*, 3 *Lutjanus vivanus*, and 2 *Lutjanus campechanus*. MOCNESS-captured sphyraenid larvae were monotypic and consisted of 90 *S. barracuda*.

Light trap catches in 2007-2008 yielded 10,562 lutjanid larvae and 1,884 sphyraenid larvae. Lutjanids consisted of 5,039 *L. synagris*, 4,020 Type G (72 of which were molecularly identified as 68 *L. griseus* and 4 *L. apodus*), 1,089 *O. chrysurus*, 218 *L. analis*, 157 unidentified (due to extensive damage), and 4 *Lutjanus mahogoni* larvae. Sphyraenid larvae consisted of 1,883 *S. barracuda*, and only one *Sphyraena guachancho*. Summer juvenile collections in nearshore environments yielded 208 juvenile snappers and 24 juvenile barracuda. Snappers consisted of *O. chrysurus* (n = 94), *L. synagris* (n = 56), and *L. griseus* (n = 35) and barracudas consisted of only *S. barracuda*. Winter juvenile collections (lower FK only) in both years yielded a total of 59 *O. chrysurus* juveniles.

Sample sizes of four species, *O. chrysurus*, *L. synagris*, *L. griseus,* and *S. barracuda*, contained enough individuals overlapping in at least two of the three ontogenetic stages to be analyzed. A total of 647 snapper (three species combined) and 292 barracuda otoliths were sectioned and read. Of these, 551 of the snapper (85%) and 273 of the barracuda (93%) had reliable otolith reads and were retained for analysis, however, a further 45 snappers and 49 barracuda fell outside of the monthly cohort delineations and were excluded from final analysis. This left a total of 217 *O. chrysurus*, 182 *L. synagris*, 107 *L. griseus*, and 175 *S. barracuda* individuals to be broken into four

age groups (only three age groups for *L. griseus* as only newly settled juveniles < 2 dps were captured; Table 5.1).

All otolith radius-SL regressions ($r^2 = 0.88 – 0.98$; $p < 0.001$), SL-age regressions ($r^2 = 0.77 – 0.94$; $p < 0.001$), and regressions of residuals from the two ($p < 0.01$), were highly significant, indicating that otolith growth is a good proxy for somatic growth in early life stages of these species. Significant patterns in size-at-hatch were identified in all three snapper species such that individuals surviving to the juvenile (Ji) stage had significantly larger sizes-at-hatch than either Li or Ls, and relative fitness increased with increasing size-at-hatch (Fig. 5.3). However, no significant differences in this parameter were identified within the juvenile phase or among any groups in *S. barracuda*.

Larval growth and size-at-age trajectories repeatedly revealed that Li were smaller-at-age and grew more slowly than older groups in two of three examined snapper species (*O. chrysurus, L. synagris*; Fig. 5.4, Table 5.2). For *O. chrysurus*, this pattern was consistent for both larval growth and size-at-age, began early in larval life (increment 5; except Js), and lasted until the maximum age of Li in this species (Fig. 5.4, Table 5.2). Larval growth and size-at-age trajectories of *L. synagris* were similar to *O. chrysurus*, although the slower growth rate of Li than other age groups took longer to appear (increment 10, except Js). As with *O. chrysurus*, differences in growth and size-at-age persisted until the maximum age of Li. Patterns in larval growth and size-at-age in *L. griseus* were somewhat different and more complex than either *O. chrysurus* or *L. synagris*. There were no consistent differences among age groups in growth at particular days and consequently, significant differences in size-at-age fluctuated between larval and juvenile groups (Table 5.2). Similarly inconsistent patterns of larval growth were

apparent for *S. barracuda* larvae and juveniles, resulting in few significant differences in size-at-age (only Ls larger at increment 5 than Li; Fig. 5.4, Table 5.2).

Among Ls and juveniles, there were no significant differences in PLD among age groups for any species examined (Fig. 5.5). Among the snappers, size-at-settlement was significantly greater in Ji than Ls in only *L. griseus. Sphyraena barracuda* survivors exhibited the opposite pattern, whereby Js were smaller at settlement than Ls (Fig. 5.6). Despite the lack of differences in PLD or size-at-settlement among age groups in *O. chrysurus* and *L. synagris*, differences in juvenile growth quickly appeared following settlement. However, these patterns were initially opposite such that surviving *O. chrysurus* juveniles grew significantly slower than Ji for the first 10 dps, while in *L. synagris,* Js grew faster than Ji, and this difference became apparent in size-at-age by 9 dps (Fig. 5.7; Table 5.3). *Ocyurus chrysurus* juveniles also exhibited this pattern of higher growth in juvenile survivors after 10 dps, when the Ji and Js growth trajectories switched. Surviving *O. chrysurus* juveniles also grew significantly faster than Ji at 15 and 20 dps and this trend lasted four wks (29 dps) by which time it had resulted in significantly larger sizes in Js (Fig. 5.7; Table 5.3). Juvenile *L. griseus* only as old as 1 dps were captured in this study, so juvenile groups could not be compared (Fig. 5.7). Similarly, sample sizes of *S. barracuda* juveniles limited the extent to which differences in juvenile growth could be tested, though the one point that was tested (increment 3) revealed no significant differences in growth or size-at-age between Ji and Js (Fig. 5.7; Table 5.3).

In addition to these patterns in growth and size-at-age among age groups, temperature had a significant effect on growth and size-at-age for all four species

consistently during larval life up until the point of settlement (Table 5.2). In contrast, only one test of juvenile growth revealed temperature to be a significant covariate more than four wks after settlement (*O. chrysurus*; Table 5.3).

Discussion

This study represents one of the first attempts to link pelagic larvae of tropical reef fishes with surviving juveniles. By tracking and repeatedly sampling young cohorts of four economically important species through time, we identified species specific patterns of size- and growth-selective mortality in the larval and juvenile stages. Selective mortality began at the initiation of the larval period based on size-at-hatch, as evidenced by a significant trend of larger sizes at hatch in successively older (survivor) groups in all three snapper species. Because size-at-hatch is affected by egg size (Chambers 1997) and energy provisions within eggs (Kerrigan 1997, Gagliano and McCormick 2007), which themselves are primarily determined by maternal quality, age, size, and condition (Marteinsdottir and Steinarsson 1998, McCormick 1999, Raventos and Planes 2008), this result suggests that maternal input had a significant effect on the survival of these fishes past the point of juvenile population replenishment. A recent study of the tropical reef damselfish *Pomacentrus amboinensis* found that smaller size-at-hatch was beneficial to survival when combined with large energy reserves (Gagliano et al. 2007a), thus incorporating larval quality as well as size. Our results suggest a more direct link between size-at-hatch and fitness and are consistent with findings for several other species (Vigliola and Meekan 2002, Macpherson and Raventos 2005, Meekan et al. 2006, Islam et al. 2010). Interestingly, this trend was not significant in *S. barracuda* despite a recent contradicting finding. *Sphyraena barracuda* larvae in the Straits of Florida in 2003 and

2004 that grew faster had larger sizes-at-hatch throughout larval life, and survived to older ages than those with smaller sizes at hatch (Chapter 2). This suggests that fast larval growth, and indirectly, large size-at-hatch conveyed a survival advantage to these larvae. The discrepancy between these results and ours may have stemmed from year to year variability in the intensity of size-selective mortality, which has been identified in several other systems (Meekan and Fortier 1996, Shoji et al. 2005, Robert et al. 2007). Meekan and Fortier (1996) suggested that such inter-annual differences were the result of fluctuating environmental conditions (i.e., temperature, food availability) which in some cases can depress larval growth, at which time predators selectively remove slower growers. If conditions remain favorable, no such selection occurs (Shoji et al. 2005). Alternatively, but not mutually exclusively, differences in the sampling and analysis between the two studies may have caused the contradictory results. Our study focused only on three cohorts and sampled these repeatedly through time in a quasi-longitudinal manner, while in Chapter 2 larvae were sampled monthly for two years and grouped together in a more cross-sectional approach. The latter method likely encompassed more off-peak spawning during presumably less favorable times of the year when selective mortality may have been stronger.

Re-constructed larval growth and size-at-age trajectories showed that both growth- and size-selective mortality was present in all species examined. The most common pattern that emerged was selective loss of larvae with the slowest growth and smallest sizes-at-age, as evidenced by the significant difference in these parameters between Li and all other groups in *O. chrysurus* and *L. synagris*. This selectivity, which acted in the first few weeks of larval life, both inflated and homogenized larval growth

among age groups by removing smaller, slower growing larvae. Selective mortality favoring fast growth early in the larval period was also found in Atlantic mackerel *Scomber scombrus*, where it homogenized growth of survivors, and obscured the relationship between fast larval growth and recruitment (Robert et al. 2007).

In contrast to *O. chrysurus* and *L. synagris*, patterns of larval selective mortality were not as consistent in *L. griseus,* and were nearly absent in *S. barracuda*. Instead, clear directional selective mortality did not act on these species until the transition from larval to juvenile phase. Both mortality and trait variability, the raw materials of selection, are typically high at settlement in reef fish (Kerrigan 1996, Almany and Webster 2006), often resulting in strong selective mortality during this transition (Searcy and Sponaugle 2001, Grorud-Colvert and Sponaugle 2010). Coefficients of variation in size-at-settlement of snappers (9.2-13.7 %) and *S. barracuda* (13.3%) in our study were similar to each other, and to those found for *T. bifasciatum* in the region (9.9-10.5%; Sponaugle and Grorud-Colvert 2006), despite the highly plastic nature of the PLD and early life history of this species (Victor 1986a). No differences among age groups in size-at-settlement were found in *O. chrysurus* or *L. synagris*. However, had the slower growing and smaller larvae lost to selective mortality during the first 2 wk of larval life in survived to settlement, this variation would have presumably been much greater, leaving a greater scope for selective mortality to act. In contrast, strong growth- or size-selective mortality was not identified in the larval stage of either *L. griseus* or *S. barracuda*, but age groups differed significantly in size-at-settlement.

While *L. griseus* displayed a size-selective advantage for larger individuals at settlement (consistent with the growth-mortality hypothesis), the pattern of size-at-

settlement in *S. barracuda* was opposite to what is predicted by the growth-mortality hypothesis, and larger individuals were selectively lost from the population at this point. Several studies of temperate species identified survival advantages for small larvae (Fuiman 1989, Litvak and Leggett 1992, Pepin et al. 1992, Takasuka et al. 2004), and suggested that the mechanism behind this pattern of selectivity is a size-mediated decrease in encounter rate, a primary component of predation events (reviewed in Bailey and Houde 1989). Predator selection for larger prey is also consistent with optimal foraging theory, because larger prey provide more energy when the costs are equivalent (reviewed in Takasuka et al. 2004). Grorud-Colvert and Sponaugle (2006) found that smaller, high condition *T. bifasciatum* escaped predators more readily and exhibited less risk-taking behavior. Assuming predation is the major constraint at settlement, we do not know whether smaller sized *S. barracuda* larvae were simply inferior in terms of energy content, or whether their behavior created a refuge from predators as they settled to nearshore seagrass and mangrove environments. However, processes beyond settlement in *S. barracuda* and *L. griseus* must be interpreted with caution due to the small sample sizes of juveniles in several of the cohorts.

Despite the small amount of variability in growth and size at the time of settlement of *O. chrysurus* and *L. synagris*, patterns of juvenile growth-selective mortality emerged as early as the day after settlement. This pattern of mortality was independent of size as significant differences between age groups emerged only after 1-3 wks. Such a rapid appearance of growth-selective loss following settlement, as well as rapid reversals in the direction of selection, must have been the result of a strong environmental factor affecting growth itself. Temperature variability, although important

to selective processes across life stages, is negligible during summer months in shallow waters of the FK. Predation seems a more likely explanation for the observed patterns, as the days following settlement to juvenile habitat are extremely dangerous for young reef fish as they encounter a suite of new predators (reviewed in Almany and Webster 2006). However, it is unlikely that a predator has any means of evaluating differences in growth among individuals independent of size. The most parsimonious explanation is that growth was affected by feeding success, as a function of individual behavior. Feeding (or lack thereof) can have immediate and lasting effects on growth (Shoji et al. 2005) as well as swimming speed, responsiveness to predatory attacks, and overall survival (Booth and Hixon 1999, Chick and Van Den Avyle 2000). This suggests that in *L. synagris*, individuals that fed most successfully and/or frequently preferentially survived. This is consistent with the existing paradigm that faster growing individuals gain a survival advantage over slower growing ones, and within one week, this growth advantage translated into a size advantage. This finding is consistent with many recent studies (Searcy and Sponaugle 2001, Durieux et al. 2009, Grorud-Colvert and Sponaugle 2010) and with conventional ecological theory that faster growing and thus larger individuals should be susceptible to fewer predators due to gape limitation, be better able to escape predation, resist starvation, and tolerate physiological extremes (reviewed in Sogard 1997).

Although *O. chrysurus* shares this pattern of advantageous fast growth later in juvenile life, initially during the first 10 d immediately following settlement, slower growth was favored. After 10 d, the pattern switched abruptly back to favoring fast growth, and translated into a size advantage that favored survival within about 3 wks. A

similar result was obtained in an 8-yr study of damselfish (*Stegastes partitus*) populations in the Bahamas, where faster growing juveniles had higher mortality, but larger adults had higher survival rates. Based on complimentary laboratory experiments, it was concluded that this pattern of selectivity resulted from more risk-prone feeding behavior in faster growing juveniles, whereas larger adults were better competitors and were less susceptible to gape-limited predators (Johnson and Hixon 2010). Thus, a trade-off may exist in recently settled *O. chrysurus* juveniles, whereby avoiding predation during this vulnerable stage (by sheltering more than feeding, or associating with habitats with lower predation risks, but sub-optimal feeding), although detrimental to growth, is beneficial to overall survival (e.g., Werner and Hall 1988). Alternatively, slower growth may have resulted from allocation of more energy to development, or activity (reviewed in Arendt 1997), such as territorial defense as was found in another recent study of *S. partitus* in the FK (Rankin 2010).

Opposite patterns in growth-selective mortality shortly after settlement in two closely related species that settle to similar habitat at similar sizes (based on sizes of late-stage larvae in light traps; Sponaugle & D'Alessandro unpubl. data), suggests that they are under different selective pressures in similar habitats. Differences in selective processes for closely related species occupying similar habitats have also been found for two tropical wrasses, *T. bifasciatum* and *Halichoeres bivittatus*, where the latter exhibited a survival advantage for fast larval growth and the former did not (Searcy and Sponaugle 2001). This difference was attributed to differences in juvenile ecology and behavior between the two species, which caused them to be exposed to different predator guilds, rates of predation, and selective pressures. Differences in predators were also found to

influence patterns of selective mortality of a newly settled damselfish (McCormick and Hoey 2004). It is likely then, that despite settling to the same habitats, some aspect of the morphology of these two species (early juvenile pigmentation differs between species: a single yellow mid-lateral stripe in *O. chrysurus*, and a dark dorso-lateral spot in *L. synagris*) or behavior caused them to be vulnerable to different predators, or experience different rates of predation, and thus experience different patterns in selective mortality.

It is often difficult to disentangle the relative effects of the three major components of the growth-mortality hypothesis, as they are all highly correlated and likely act synergistically (Hare and Cowen 1997, Takasuka et al. 2004). Still, many recent studies have taken great pains to do so and the importance of growth rate, even in the absence of size and PLD differences, is becoming prominent in the literature (Takasuka et al. 2003, 2004, Islam et al. 2010). Such selection was evident in our study of *O. chrysurus* and *L. synagris*, where significant differences between age groups were identified in juvenile growth but not size-at-age. However, the opposite trend was occasionally apparent in the larval stage where larval size-at-age (including size-at-hatch) differed among age groups but growth did not (increment 5 in *S. barracuda* and *L. synagris*, increment 15 in *L. griseus*, and size-at-settlement in *S. barracuda*). There was no evidence in our study of the advantages of a short PLD (i.e. stage duration hypothesis), as no significant differences in PLD were found between age groups for any species. Thus size-selective mortality may have played a dominant role in the larval life of *S. barracuda*, *L. griseus*, and *L. synagris*, but growth-selective mortality seemed to be the major selective force in juvenile *O. chrysurus* and *L. synagris*. Our results illustrate

how selective processes may switch between stages and survivors may ultimately face conflicting pressures over time.

Despite the relatively small seasonal temperature variation in the sub-tropical FK, and small temperature range within the seasonal scope of our study (1-3 ºC), temperature was often a significant covariate in tests of larval growth rate and larval size-at-age, and this result is consistent with findings of another study which examined the effects of temperature on larval growth in *Thalassoma bifasciatum* in the FK (Sponaugle et al. 2006). In contrast, during the early juvenile phase for the three species examined, temperature was rarely a significant covariate. The effect of temperature may have been tempered by a decrease in trait variability resulting from selective mortality in the larval stage (at least for *O. chrysurus* and *L. synagris*), or dampened by increased importance of other factors such as resource availability and competition in the juvenile environment. Temperature can serve as a mediating factor of selective mortality in reef fishes, changing the intensity (Gagliano et al. 2007b) and pattern of selective loss of individuals (Grorud-Colvert and Sponaugle 2010). While the intensity of selective mortality during the larval stage may have been affected by ambient water temperature in our study, it is unlikely that patterns or direction of selective loss were affected, as growth and size-at-age trajectories were similar among cohorts, and significant patterns emerged despite pooling of the data.

This study is the first examination of selective processes in commercially and recreationally important tropical reef fish species. By examining otolith-based growth and size-at-age throughout the pelagic larval and early juvenile stages, we have demonstrated that, in three species of snapper and one species of barracuda, selective

mortality plays an important role in determining which individuals survive both the pelagic larval and early juvenile stages. These results have important implications for the overall ecological understanding of these species as well as their management. There was a high degree of variability in selective patterns between species, highlighting the potential pitfall of applying patterns gleaned from single species studies in a general manner to other, even closely related, species. Despite this species-specific variability, faster growth and larger sizes-at-age were selected for in the larval and juvenile stages of *O. chrysurus* (after the first 10 dps) and *L. synagris.* Many recent studies have re-enforced the link between early growth rate and recruitment magnitude in fishes (Bergenius et al. 2002, Vigliola and Meekan 2002, Wilson and Meekan 2002, McCormick and Hoey 2004, Sponaugle and Pinkard 2004, Raventos and Macpherson 2005, Jenkins and King 2006, Sponaugle et al. 2006, Tanaka et al. 2006, Robert et al. 2007), and consistent patterns in selective mortality such as these may have important predictive value for future recruitment if used in conjunction with larval surveys. Effects of temperature on larval growth (and selective mortality) like those identified here, are important in understanding how fisheries will react to predicted future global climate change. Perhaps most importantly, the significance of size-at-hatch, and possibly maternal contribution, to survival through the larval and into the juvenile stage in *O. chrysurus*, *L. synagris*, and *L. griseus* has important implications for the management of these heavily fished species. Current single species management relies on the minimum size at sexual maturity to apply size limits to the exploitable stage in most fishes, and assumes that every spawning female is equivalent. It has been shown in other species that larger, older, or higher condition females produce larger eggs and larvae (Marteinsdottir

and Steinarsson 1998, Berkeley et al. 2004, Raventos and Planes 2008). If this correlation exists in the snapper species examined here, then current size limits should be adjusted to protect not only immature fish that have not had a chance to spawn, but also larger, older fishes that would effectively contribute more offspring to the juvenile population. More research is warranted to determine if a correlation between larger, older females and larger sizes-at-hatch of larvae exists, and if the pattern of size- and growth-selective mortality remains consistent to the point of sexual maturity, thus determining which individuals effectively contribute to ecologically meaningful persistence of the population.

Table 5.1. Temporal spawning range, mean water temperature from the NOAA C-MAN station SANF1, mean pelagic larval duration (PLD), and sample sizes of initial pelagic larvae (Li), surviving pelagic larvae (Ls), initial post-settled juveniles (Ji), and surviving post-settled juveniles (Js) of each species studied by cohort. Cut-off ages for each age group designation for each species are given in parentheses: Li and Ls in days post hatch (dph); Ji and Js in days post settlement (dps).

	Spawn date range	Mean temp.	Li	Ls	Ji	Js	PLD
Ocyurus chrysurus			(< 22)	(> 22)	(< 50)	(> 50)	
Cohort 1	5/13/07-6/12/07	27.9	15	45	14	0	28.5
Cohort 2	7/3/07-8/3/07	30.4	25	26	8	5	26.0
Cohort 3	5/18/08-6/17/08	28.6	29	31	5	14	26.9
Sample totals			**69**	**102**	**27**	**19**	**24.1**
Lutjanus synagris			(< 22)	(> 22)	(< 10)	(> 10)	
Cohort 1	5/29/07-6/15/07	28.4	0	25	17	6	29.0
Cohort 2	7/1/07-7/29/07	30.4	30	31	12	0	25.3
Cohort 3	5/31/09-6/23/09	29.1	0	24	24	13	28.1
Sample totals			**30**	**80**	**53**	**19**	**25.2**
Lutjanus griseus			(< 22)	(> 22)			
Cohort 1	7/2/07-7/27/07	30.3	27	31	0	0	
Cohort 2	7/21/08-7/30/08	29.6	0	27	22	0	27.4
Sample totals			**27**	**58**	**22**	**0**	**27.4**
Sphyraena barracuda			(< 20)	(> 20)	(< 4)	(> 4)	
Cohort 1	5/12/07-5/29/07	26.9	24	27	7	7	22.1
Cohort 2	7/14/07-7/28/07	30.4	29	31	0	1	21
Cohort 3	6/2/08-6/24/08	28.6	31	17	1	0	21
Sample totals			**84**	**75**	**8**	**8**	**22.0**

Table 5.2. p values of ANCOVAs (p) for differences between age groups (A), temperature as a covariate (T), and the location of significant differences (pattern) between initial larvae (Li), surviving larvae (Ls), initial juveniles (Ji), and surviving juveniles (Js) in larval growth rates (increment widths) and larval size-at-age (otolith radii) at selected increments. Significant values are bold. FST indicates that the relationship between the covariate and dependent variable differed between the two groups, and ANCOVA was not possible.

Species/cohort	Daily growth (increment widths)			Size-at-age (otolith radii)		
	p (A)	p (T)	pattern	p (A)	p (T)	pattern
Ocyurus chrysurus						
Increment 5	**< 0.001**	**0.001**	(Li<Ls<Ji) = Js	**< 0.001**	**0.002**	(Li<Ls<Ji) = Js
Increment 10	**< 0.001**	**< 0.001**	Li < (Ls=Ji=Js)	**< 0.001**	**< 0.001**	Li < (Ls=Ji=Js)
Increment 15	**< 0.001**	**< 0.001**	Li < (Ls=Ji=Js)	**0.001**	**0.001**	Li < (Ls=Ji=Js)
Lutjanus synagris						
Increment 5	0.232	0.003		**< 0.001**	0.167	(Li,Ls) < (Ji,Js)
Increment 10	**0.017**	**< 0.001**	(Li<Ls=Ji) = Js	**0.002**	**< 0.001**	Li < (Ls,Ji,Js)
Increment 14	**0.018**	**< 0.001**	Li < (Ls=Ji=Js)	**0.003**	**< 0.001**	Li < (Ls=Ji=Js)
Lutjanus griseus						
Increment 5	FST			FST		
Increment 10	**0.002**	**0.037**	Ls < (Li,Ji)	**0.004**	**0.002**	(Li,Ls) < Ji
Increment 15	0.149	0.866	Li = Ls = Jy	**0.040**	0.181	(Ls<Ji) = Li
Sphyraena barracuda						
Increment 5	0.346	0.067	Li=Ls=Ji=Js	**0.007**	0.337	(Li<Ls) = Ji,Js
Increment 10	FST			FST		
Increment 15	0.256	**< 0.001**	Li=Ls=Ji=Js	0.167	**< 0.001**	Li=Ls=Ji=Js

Table 5.3. p values of ANCOVAs (p) for differences between age groups (A), temperature as a covariate (T), and the location of significant differences (pattern) between initial juveniles (Ji) and surviving juveniles (Js) in juvenile growth rates (increment widths) and juvenile size-at-age (otolith radii) at selected increments. Significant values are bold.

Species/increment	Daily growth (increment widths)			Size-at-age (otolith radii)		
	p (A)	p (T)	Pattern	p (A)	p (T)	Pattern
Ocyurus chrysurus						
Increment 5	**0.016**	0.090	Ji > Js	0.697	0.467	Ji= Js
Increment 10	0.876	0.109	Ji = Js	0.765	0.569	Ji = Js
Increment 15	**0.022**	0.106	Ji < Js	0.286	0.054	Ji = Js
Last (30)	**0.023**	**0.022**	Ji < Js	**0.018**	0.284	Ji < Js
Lutjanus synagris						
Increment 5	**0.030**	0.593	Ji < Js	0.442	0.062	Ji = Js
Last (10)	0.736	0.936	Ji = Js	**0.031**	0.786	Ji < Js
Sphyraena barracuda						
Last (4)	0.983	0.248	Ji = Js	0.223	0.503	Ji = Js

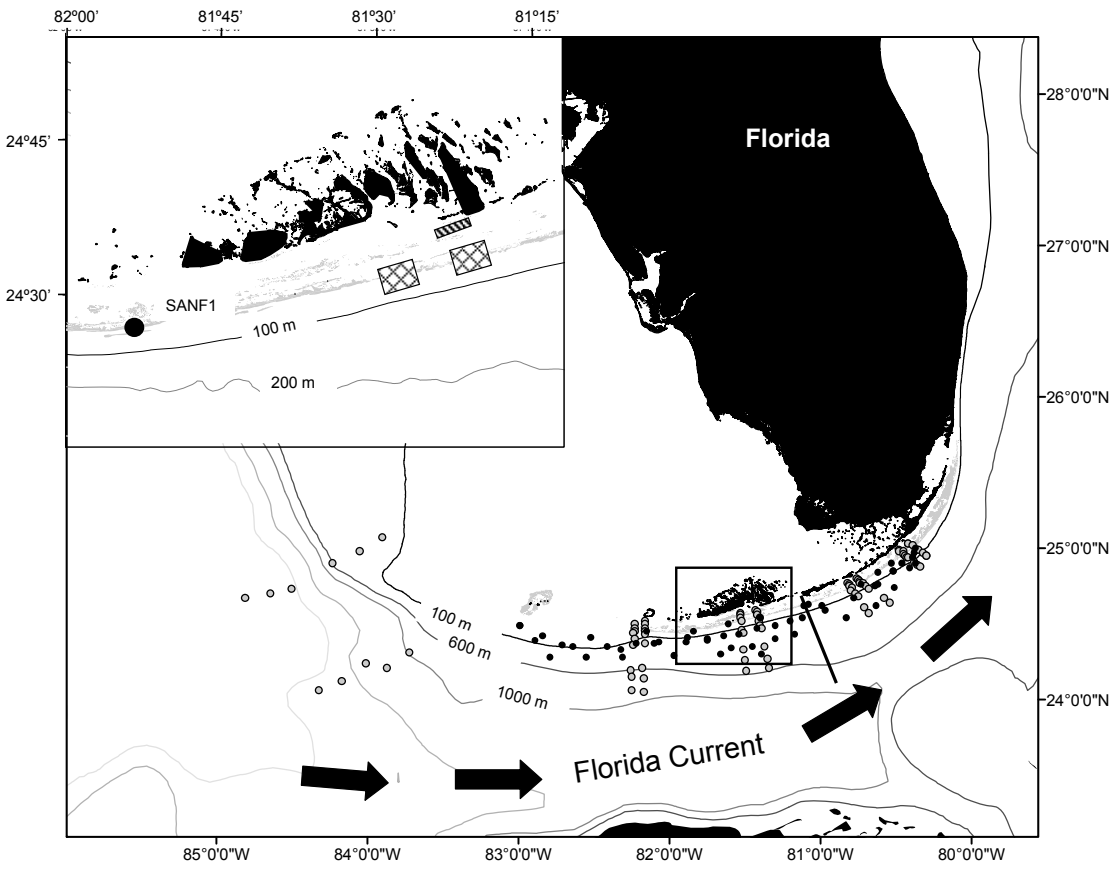

Fig. 5.1. Map of the study area. Black represents land and grey represents coral reef. Grey circles and black dots represent 96 fixed and 58 supplementary stations sampled by MOCNESS during 2007 and 2008, respectively. Samples from stations only to the west of the bold line were utilized in the present study. On the inset, the large black circle represents the location of the NOAA C-MAN station SANF1 where temperature data were obtained, cross-hatched boxes are where light traps were deployed, and the striped box is where juvenile surveys and seines were performed.

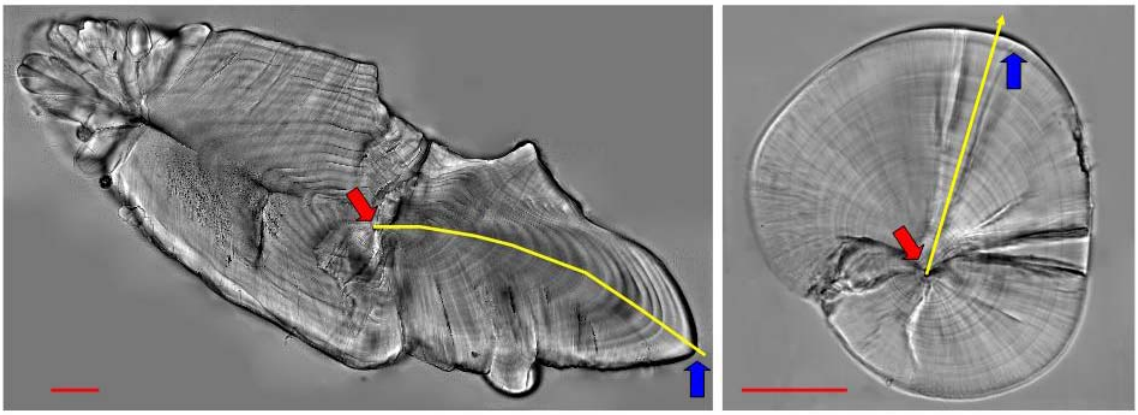

Fig. 5.2. Transverse section of a sagittal otolith from a juvenile *Ocyurus chrysurus* (left image) and lapillus from a juvenile *Sphyraena barracuda* illustrating reading axes from the primordium (red arrows) to the otolith edge (blue arrows) along which daily increments were enumerated and measured. Red lines are 50 μm scale bars.

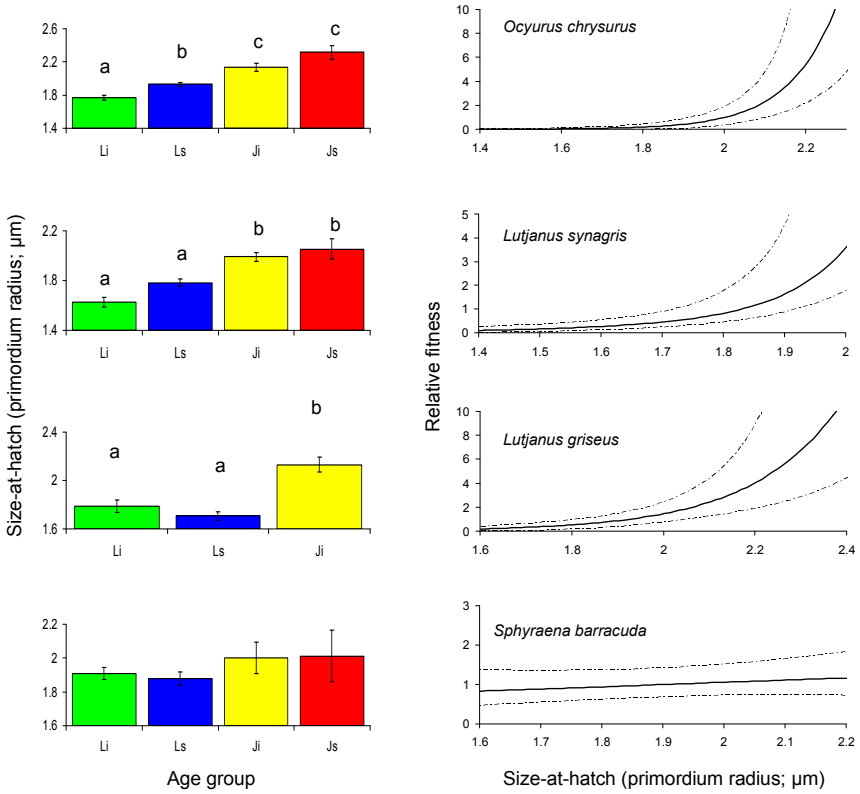

Fig. 5.3. Left panels: mean size-at-hatch of examined species illustrating differences among initial larvae (Li; green), surviving larvae (Ls; blue), initial juveniles (Ji; yellow), and surviving juveniles (Js; red). Where ANCOVAs were significant (all p's < 0.01), letters indicate patterns. Right panels: Fitness functions created using cubic splines. Dashed lines indicate 95% confidence bands.

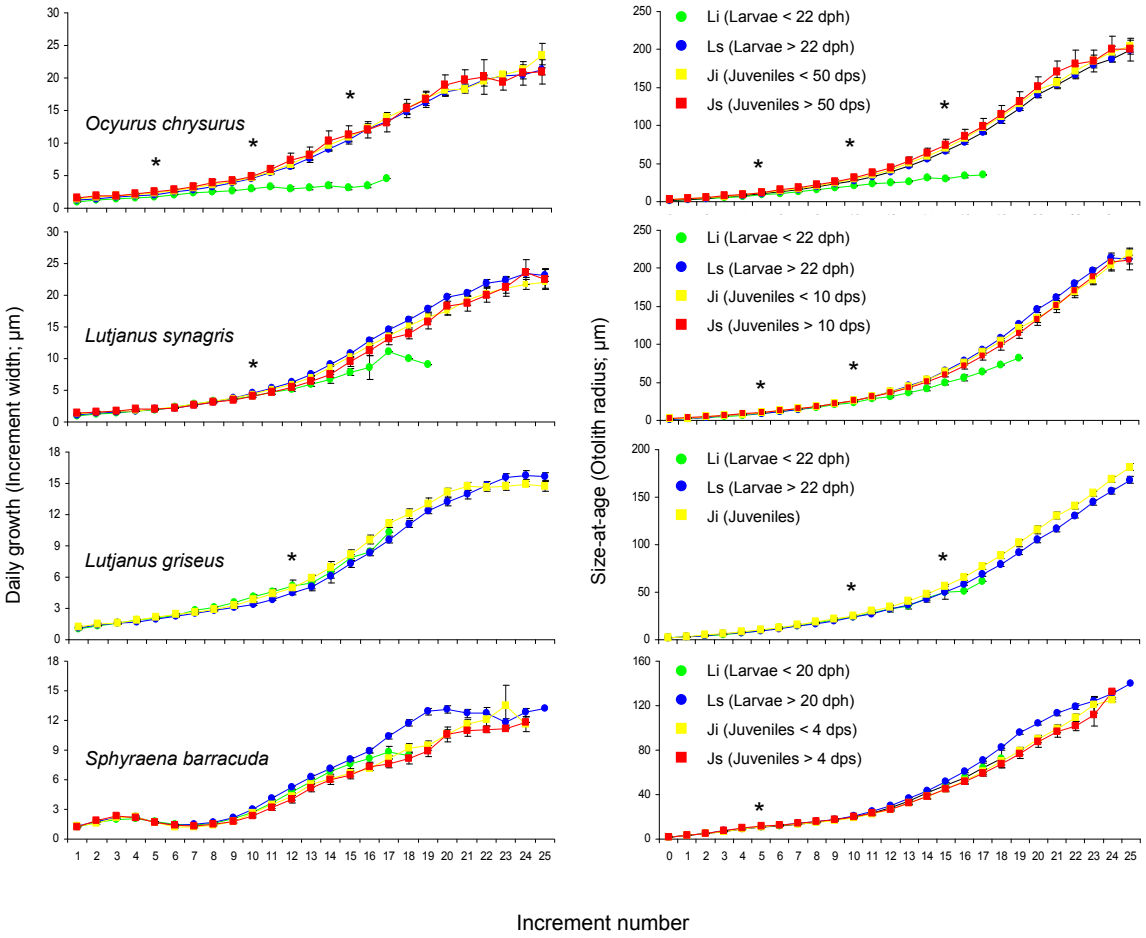

Fig. 5.4. Larval growth (left panels) and size-at-age (right panels) trajectories of initial larvae (Li), surviving larvae (Ls), initial juveniles (Ji), and surviving juveniles (Js) of the four studied species. Increments 5, 10, and 15 in both larval growth and size-at-age were tested using ANCOVA, and significant differences ($p < 0.05$) among groups are indicated with *. Exact p values and patterns among groups are given in Table 2.

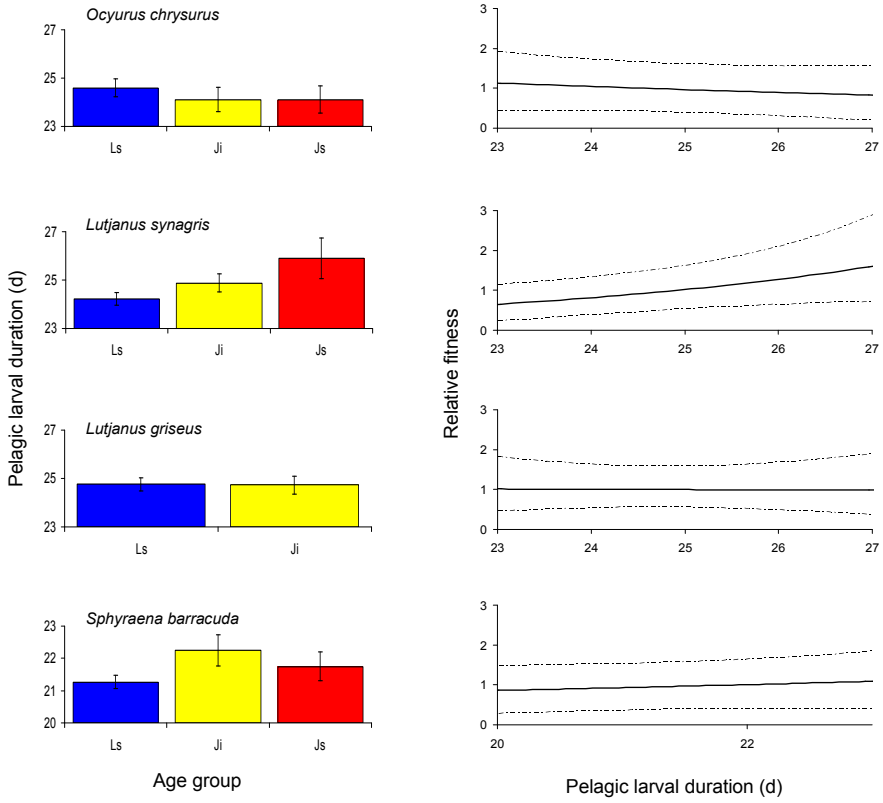

Fig. 5.5. Left panels: mean pelagic larval duration of examined species illustrating differences among initial larvae (Li; green), surviving larvae (Ls; blue), initial juveniles (Ji; yellow), and surviving juveniles (Js; red). Where ANCOVAs were significant (all p's < 0.01), letters indicate where significant differences among groups exist. Right panels: Fitness functions created using cubic splines. Dashed lines indicate 95% confidence bands.

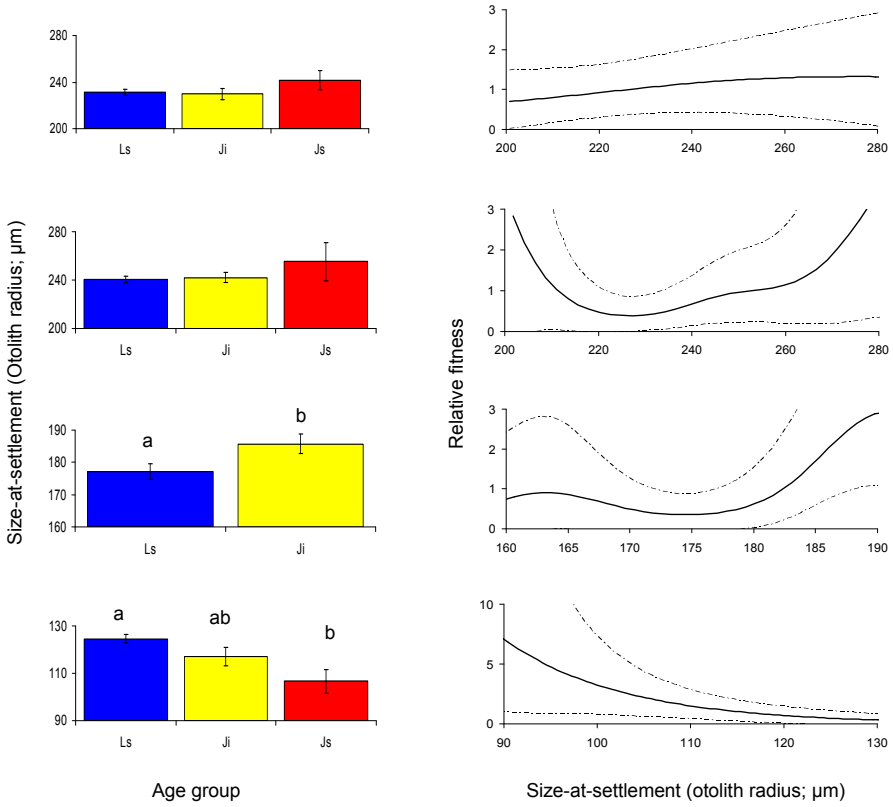

Fig. 5.6. Left panels: mean size-at-settlement of examined species illustrating differences among initial larvae (Li; green), surviving larvae (Ls; blue), initial juveniles (Ji; yellow), and surviving juveniles (Js; red). Where ANCOVAs were significant (all p's < 0.01), letters indicate where significant differences among groups exist. Right panels: Fitness functions created using cubic splines. Dashed lines indicate 95% confidence bands.

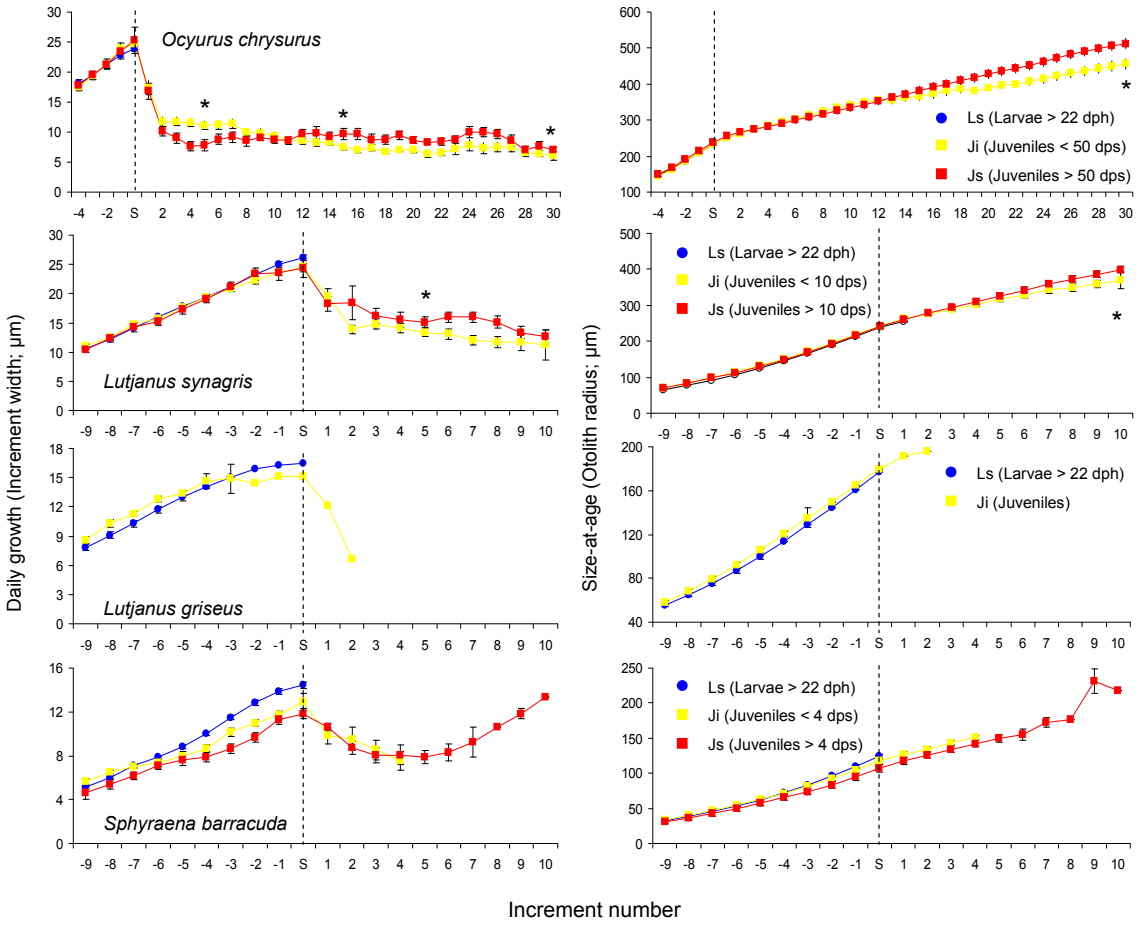

Fig. 5.7. Late larval and early juvenile growth (left panels) and size-at-age (right panels) trajectories aligned by settlement (S) of surviving larvae (Ls), initial juveniles (Ji), and surviving juveniles (Js). ANCOVAs were used to test for significant differences between juvenile groups at 5 days post settlement (when possible) and the last increment for which at least 5 individuals remained in each group. Significant differences ($p < 0.05$) are indicated by * and exact p values and patterns are given in Table 3. Dashed lines represent settlement.

Chapter 6: Summary and Conclusions

Ecology of the pelagic larval stage of snappers and barracudas

The pelagic larval stage of coral reef fishes has important effects on juvenile and adult populations through its influence on larval dispersal, recruitment, and population connectivity, yet is poorly described for most species. Pelagic larvae of snappers and barracudas from 2 yrs (2003-2004) of monthly ichthyoplankton samples at 17 fixed stations across the Straits of Florida (SOF) revealed consistent spatial and temporal patterns of abundance and growth. Both snappers and *Sphyraena barracuda* exhibited peak larval abundances during the warm wet season months (June-September), and were scarce in dry season samples (November-May), indicating a similar seasonal pattern in spawning. This agrees well with studies of adult gonads and recruitment of young in *S. barracuda* (de Sylva 1963, Kadison et al. 2010), published literature on snapper reproduction (reviewed in Lindeman et al. 2006), and appearance of late stage larvae near reefs (D'Alessandro et al. 2007). The abundance of all larval fishes, including reef fishes, also decreased in the dry season in ichthyoplankton samples from the Florida Current (FC; Llopiz and Cowen, unpubl. data), and for late-stage larvae of several reef fish families (Pomacentridae, Lutjanidae, Sphyraenidae, Monacanthidae, Labrisomidae, Scorpaenidae, and Gerreidae) in near-reef light trap catches (D'Alessandro et al. 2007), suggesting that this pattern of reproduction and larval abundance is common in the study area. Waters offshore of the Florida Keys (FK) lack the seasonal predictability in primary production thought to dictate reproductive patterns in higher latitude marine systems (Cushing 1990), and temperature (6 ºC seasonal temperature change that exists in the upper 50 m of the open waters of the FC) may be the major driving force behind the

seasonal pattern in larval fish abundance. While higher temperatures would increase growth rates, enhanced growth would also make larvae more susceptible to starvation, and the broad peak in reproduction in these species (over 4 months) may represent a bet-hedging strategy to cope with unpredictable larval food conditions. In contrast, by spawning mostly in winter months, sennets may be trading higher summertime growth for some other benefit such as a reduction in high mortality by predators.

Five of six examined snapper species exhibited significant lunar cyclic patterns in back-calculated reproductive output which agree well with observed lunar patterns of spawning at aggregations (Domeier and Colin 1997, Heyman and Kjerfve 2008) and back-calculated spawning in other studies (Denit and Sponaugle 2004). However, no significant patterns were found for the deepest dwelling western Atlantic snapper species, *E. oculatus*, or for *S. barracuda*. In addition to synchronizing reproduction, lunar or tidal periodicity in spawning is thought to be related to transport processes (maximize flushing away from the reef and associated predators, increase larval retention, etc.) or to minimize predation on spawning adults (Johannes 1978, Robertson 1990). For snappers, bottom associated adults make a rush up through the water column and release their eggs during only parts of the lunar cycle, highlighting the importance flushing eggs away from the reef in these species (Domeier and Colin 1997). While spawning has never been observed in *S. barracuda*, it is semi-pelagic and often found close to the surface in deep waters. Therefore, its vertical or horizontal distribution likely does not need to be altered to enhance transport of eggs off the coral reef, and its position near the top of the food chain may alleviate pressure to spawn at times of minimal ambient light or stay in the

vicinity of benthic cover. In the deep habitats (> 150 m) occupied by *E. oculatus*, lunar illumination and tidal cycles may be of little consequence to spawning activities.

The spatial distribution (vertical and cross-SOF) of larvae of both snappers and barracudas tracked adult distributions. For coral reef and continental shelf-associated snappers and sennets, larvae were most abundant in the 0-25 m depth range and away from the extremely deep middle SOF, which likely represents a biogeographical barrier for these species. Larvae of deeper dwelling snapper species were distributed at deeper depths in the water column (becoming progressively deeper with ontogeny), and larvae of *E. oculatus* (the deepest living western Atlantic snapper species), were evenly distributed across the SOF. Adult *E. oculatus*, though bottom associated, are not as constrained by depth as other snapper species, as they are found to 450 m and possibly deeper (Gobert et al. 2005). Adult *Sphyraena barracuda* are also found in deep offshore waters (though still near the surface; de Sylva 1963), and larvae were abundant at stations towards the middle of the SOF.

Larvae of both snapper and barracuda, like those of many reef fishes, were most abundant in the upper 25 m of the water column. This is not surprising as most reef-associated fishes, including snappers, live and spawn in habitats < 50 m depth and produce pelagic eggs (Leis 1987, Clarke et al. 1997, Cowen 2002). Even in species that form spawning aggregations near deep drop-offs, adults rush up from the bottom and release gametes into the upper 25 m of the water column (Heyman and Kjerfve 2008). Observed vertical patterns, therefore, may be due not to larval preference or distributions of predators or prey, but rather to a lack of significant vertical movement after hatching. Spawning has not been observed in barracudas or deeper dwelling snapper species, and

the distribution of most of their larvae in the upper 25 m (upper 50 m in some snapper species) may be indicative of deeper spawning and positively buoyant eggs, or spawning in the upper 25 m of the water column as well (involving a vertical migration upward in the case of deeper dwelling snapper species).

Of the larval snappers and barracuda, only four snapper species (two reef-associated and two deep species) exhibited ontogenetic changes in vertical distributions. For coral-reef associated snappers and barracudas, larval distributions largely in the upper 25 m of the water column means that as larvae approach the shelf, whether by horizontal swimming or passive transport, the shoaling of the water column would eventually bring them to or over the fringing reef crest. For species that settle to back-reef habitats, it may be advantageous to move into shallower waters with ontogeny, as was seen in *O. chrysurus* and *L. apodus*, to facilitate movement across the reef. However, results of Chapter 4 indicated a pattern of higher mortality seaward of the reef for late-stage larval *L. griseus* at the surface, suggesting that surface waters should be avoided until the reef is encountered. For the two deeper dwelling snapper species, *Pristipomoides* spp. and *E. oculatus*, being distributed mainly in the upper 50 m of the water column, and presumably settling to the benthos at much deeper depths (based on their absence in shallower environments) means that horizontal shoreward movement and passive shoaling of the water column would not be effective in delivering larvae to suitable settlement habitat. Active vertical movement by larvae would be required for successful settlement, and this was evident in observed changes in ontogenetic vertical distribution.

Spatial patterns in larval growth in several snapper species, and a seasonal pattern in *S. barracuda*, were attributed to larval diet and food availability. In snappers, larval

growth was higher towards the western SOF where their primary prey, appendicularians (Llopiz and Cowen 2009), were most abundant (Llopiz et al. 2010). While water temperature plays an important role in the larval growth of tropical reef fishes (Meekan et al. 2003, Sponaugle et al. 2006), the importance of food to larval fish growth (especially in temporally limited studies, or species with limited seasonal reproductive windows) is becoming more apparent (Sponaugle et al. 2009, 2010).

Of all the Sphyraenidae and Lutjanidae, larvae of *S. barracuda* were by far the most abundant. Nearly twice as many (n = 1,239) were collected in 2003-2004 than all coral reef-associated snapper larvae combined (n = 762). This pattern also remained consistent in ichthyoplankton samples collected along the FK in 2007 and 2008 (data not shown). While larval mortality of *S. barracuda* is low relative to most of the snapper species (except *E. oculatus*), comparing such rates between different species or families is tenuous. Apparent mortality rates, for example, incorporate increasing swimming and sensory capabilities and net avoidance with ontogeny (Houde et al. 1979), and these abilities may differ substantially between species (Fisher et al. 2000, Fisher et al. 2005). More likely, this striking difference in abundance may be reflective of adult spawning stocks. Nearly all species of snappers are heavily targeted by fisherman, and several species have been reported as overfished in the FK (Ault et al. 1998). In contrast, the risk of ciguatera poisoning associated with eating *S. barracuda* has largely released it from fishing pressure in the United States and Cuba and, in concert with a presumed competitive release caused by overfishing of other large predatory fishes at the same trophic level (e.g., sharks, large groupers, and snappers), has allowed the population of *S. barracuda* to increase rapidly in the study area in recent years (Ault et al. 1998).

Consequently, the spawning stock of *S. barracuda* may be far healthier than that of most snappers, which if all other factors (i.e., spawning frequency, fecundity) are comparable between these species, may contribute to the observed difference in larval abundances.

Habitat-specific relative mortality of settling snapper larvae

The process of settlement is considered to be highly risky for reef fishes as larvae encounter high rates of predation mortality associated with shallow nearshore habitats (Almany and Webster 2006). This potential bottleneck may be particularly significant for many tropical reef species that bypass the reef to settle to very nearshore seagrass and mangrove areas. Results of tethering experiments of late-stage *Lutjanus griseus* larvae at the surface indicated that both relative predation rate and probability of predation in oceanic areas seaward of the reef were significantly greater than over reef or nearshore seagrass/hardbottom habitats. These unexpected results led to the hypothesis that successful late-stage larvae avoid surface waters in deep areas, and move up in the water column when the fringing coral reef is encountered. This idea is consistent with observations that late-stage Caribbean snapper larvae on an outer reef edge, inside a lagoon (Hendriks et al. 2001), and passing through a tidal channel (Halvorsen 1994) were captured mostly near the surface, and young larvae in the SOF avoided surface waters (Chapter 2).

The tethering experiments had several limitations caused by availability of live late-stage larvae and manpower, and were forced to rely on certain assumptions. Firstly, we assumed that second order artifacts did not significantly bias the experiments based on similar tethering studies in the area utilizing planktonic invertebrates (Acosta and Butler 1999, Bullard and Hay 2002). However, to definitively rule out such effects and

gain a better understanding of the predation causing settlement mortality for larval fish, potential predators in each habitat should be surveyed and predation events recorded using infra-red cameras. Secondly, the presumption that predation risk was lower at depth offshore (Hunter and Mitchell 1967, Kingsford and Choat 1985, Casazza and Ross 2008) and higher close to the bottom in nearshore environments (Carr and Hixon 1995, Holbrook and Schmitt 2002, Quere and Leis 2010) does have support in the literature, but has not been shown for the study area and species used. Ideally, several depth stratifications would have been investigated simultaneously to gain a more three dimensional picture of predation risk for settling larvae. In conjunction with depth and cross-shelf stratified light trapping, such depth-stratified tethering experiments could effectively test the hypothesis of upward movement in the water column as larvae move shoreward for settlement. Thirdly, the spatial extent of the experiment was somewhat limited, and predation rates may differ in deeper areas of the SOF and different regions of the fringing reef and back-reef. Lastly, only *L. griseus* larvae were consistently available in sufficient numbers to achieve the replication needed for statistically meaningful analysis. Two additional runs of the experiment were carried out, one with *L. synagris* and one with *O. chrysurus*, and both of these exhibited the same pattern as *L. griseus* (diminishing predation with distance inshore). *Sphyraena barracuda* could not be examined in these experiments due to unreliable catches in light traps and difficulty in tethering dorso-ventrally compressed larvae. However, considering that smaller *S. barracuda* preferentially survived during settlement in direct contrast to snapper (Chapter 5), it is likely that the dynamics of ingress over shallow water habitats also differs substantially from snappers in this species.

Selective mortality throughout the early life history

Intense mortality during the early life history stages in marine fishes (Houde 1987), coupled with a high degree of phenotypic variability (e.g., McCormick 1998), often results in selective mortality (reviewed in Anderson 1988, Sogard 1997). Frequently, a larger size-at-hatching (Meekan and Fortier 1996, Vigliola and Meekan 2002, Raventos and Macpherson 2005), shorter pelagic larval duration (PLD; Meekan and Fortier 1996, Shima and Findlay 2002), faster larval growth (Meekan and Fortier 1996, Searcy and Sponaugle 2001, Shima and Findlay 2002, Raventos and Macpherson 2005), larger size or higher condition at settlement (Searcy and Sponaugle 2001, McCormick and Hoey 2004, Sponaugle and Grorud-Colvert 2006, Hamilton et al. 2008), or faster juvenile growth (Searcy and Sponaugle 2001, Grorud-Colvert and Sponaugle 2006, Sponaugle and Grorud-Colvert 2006) enhances survival of young fishes, in agreement with the growth-mortality hypothesis (Anderson 1988).

Trait mediated selective mortality was evident in four species examined here (*O. chrysurus*, *L. synagris*, *L. griseus*, and *S. barracuda*), although the timing and pattern of selective mortality varied among species, and was not always consistent with the growth-mortality hypothesis. Larger size-at-hatch was the only trait that conveyed a significant survival advantage to all examined species. For the three snapper species, older larvae and older juveniles exhibited larger sizes-at-hatch indicating that selective mortality removed smaller individuals at hatch over time, consistent with the growth-mortality hypothesis. In *S. barracuda*, this advantage was only evident indirectly in larval samples from 2003-2004 in that larvae that were larger-at-hatch grew faster throughout larval life, and larvae that were older (survivors) were those that grew faster (Chapter 3). A trend for

survivors to have larger sizes-at-hatch was also visible in the 2007-2008 data set (Chapter 5), but was not statistically significant. Differences between these two datasets may have arisen from differences in the temporal scale (June-July in 2007-2008 and year-round in 2003-2004), or that only young pelagic larvae were being examined in a cross-sectional (as opposed to semi-longitudinal) manner in the 2003-2004 data.

Growth-selective mortality removed smaller, slower growing individuals during the larval life of *O. chrysurus* and *L. synagris*. In contrast, in *L. griseus* patterns of selective mortality after hatching were not evident until settlement, when larger sizes-at-settlement produced a survival advantage. The absence of selective mortality in tethering experiments (Chapter 4) suggests that this selective mortality acted after settlement to the benthos. However, tethering of these organisms may have confounded advantages conveyed by faster growth or larger size and precluded natural selective processes.

Several contradictions of the growth-mortality hypothesis were identified in that smaller *S. barracuda* preferentially survived at settlement and slower growth was favored shortly after settlement in *O. chrysurus*. Such contradictions have been identified for other reef fishes as well (e.g., Grorud-Colvert and Sponaugle 2006, Grorud-Colvert and Sponaugle 2010, Johnson and Hixon 2010, Rankin 2010). Faster growth rates can sometimes have detrimental developmental effects (Arendt 1997), and larger individuals may be more conspicuous during high mortality transitions (e.g., Fuiman 1989). Further, these contradictions of the growth-mortality hypothesis in *O. chrysurus* and *S. barracuda* represent switches in selective pressures with ontogeny, a result that has been found in several other reef fishes (e.g., Gagliano et al. 2007a, Johnson and Hixon 2010). In addition to ontogenetic changes in selective mortality, mortality was not consistently

selective over time in *S. barracuda* in that growth- and size-selective mortality was identified in pelagic larvae collected in 2003-2004 (Chapter 3), but not in pelagic larvae collected in 2007-2008. Inter-annual inconsistencies in selective mortality have been identified in other fish species (Meekan and Fortier 1996, Shoji et al. 2005, Robert et al. 2007) and attributed to fluctuations in environmental conditions. Such fluctuations can increase variability in larval growth, increasing susceptibility to trait-based selective mortality. Such switches in selective mortality with ontogeny and over time may be a mechanism by which phenotypic variability is maintained.

Synthesis and future directions

This dissertation represents the first attempt to link early pelagic larvae with settlement stage larvae and juveniles of long-lived, economically valuable tropical reef fishes. In the patchy and seasonally unpredictable subtropical pelagic environment of the FK, two years of monthly sampling across the SOF revealed consistent spatiotemporal patterns in growth and abundance of snapper and barracuda larvae. A tethering experiment utilizing *L. griseus* larvae in surface waters revealed that relative rate of predation as well as probability of predation decreased as larvae left deep oceanic waters and entered shallow nearshore environments. Finally, repeated sampling of larvae and juveniles from several snapper and barracuda cohorts in 2007-2008 revealed patterns of selective mortality that began at hatching and most often followed the growth mortality hypothesis. However, these patterns were not always consistent, allowing for the persistence of phenotypic variability over time.

Because most reef fishes are relatively site-attached as adults, the pelagic larval stage is the major mechanism of dispersal, and consistent spatiotemporal patterns in

larval distribution, abundance, and growth may have direct and important implications for population connectivity. Connectivity in turn, plays a central role in population dynamics and structure, genetic diversity, and resilience of populations to exploitation (Botsford et al. 2001, Cowen et al. 2007, Cowen and Sponaugle 2009). Spatial management, including marine protected areas, has become popular in recent years due to its potential to simultaneously preserve biodiversity and help to manage fisheries (Fogarty and Botsford 2007). However, resolving dispersal and subsequent population connectivity for populations of interest remains a central obstacle in evaluating the design and potential benefits of such spatial management strategies, and understanding population dynamics of marine organisms in general (Sale et al. 2005, Cowen et al. 2007). Due to the complexity involved in the pelagic larval environment, understanding dispersal and population connectivity necessitates an integrated interdisciplinary approach that incorporates high-resolution biophysical modeling and empirical data (Cowen and Sponaugle 2009). Early models treated larvae as passive particles (Roberts 1997), but it is now understood that larval behavior can play an important role in connectivity, and even small underdeveloped larvae with little horizontal swimming ability can affect their dispersal by modifying their vertical distributions (Paris and Cowen 2004). Newer models that incorporate larval behavior and sensory capabilities are providing valuable data for broad-scale patterns of connectivity (Cowen et al. 2006), including for Cuban snapper populations just south of the study area (Paris et al. 2005). However, the effectiveness of these models depends on accurate species-specific data on reproductive patterns, larval mortality, larval growth rates, larval distributions, larval behavior, and PLDs such as those provided in this dissertation.

A critical area in which knowledge of both biological and physical processes is lacking is the shallow nearshore environment. This area includes the starting and ending points for larval dispersal, and is characterized by complex physical oceanography (due to the interaction of frictional forces of coastal topography, stratified water columns, tidal forces, wind, buoyancy, surface waves, and turbulence; Gawarkiewicz et al. 2007). The arrival in this nearshore environment of late-stage larvae competent to settle adds an element of complexity to understanding dispersal. Such larvae are strong swimmers (e.g., Fisher and Wilson 2004) capable of substantially influencing their horizontal and vertical distributions based on a suite of well developed senses that operate on a variety of different spatial scales (Atema et al. 2002, Kingsford et al. 2002, Lecchini et al. 2005). Thus, the process of settlement is a critical link in coupling large-scale oceanic processes and small-scale nearshore processes in biophysical models (Gawarkiewicz et al. 2007). Chapter 4 of this dissertation took an important first step towards understanding the process of settlement, but much work remains to be done on identifying larval capabilities (but see Fisher et al. 2005), natural vertical distributions of late-stage larvae, and three dimensional patterns of predation risk of settling larvae.

Perhaps most importantly, the significance of size-at-hatch, and possibly maternal contribution, to survival through the larval and into the juvenile stage in *O. chrysurus*, *L. synagris*, and *L. griseus* has important implications for the management of these heavily fished species. Size-at-hatch is determined by egg size (Chambers 1997) and energy provisions within eggs (Kerrigan 1997, Gagliano and McCormick 2007), which themselves are influenced by spawning females. Studies have shown that maternal quality, age, size, and condition have important effects on egg size and provisions within

eggs, as well as hatch size and survival of larvae. In a number of species, larger, older, higher condition females produce larger eggs and larvae (Marteinsdottir and Steinarsson 1998, McCormick 1999, Berkeley et al. 2004, Raventos and Planes 2008). Assuming this relationship holds for snapper, these results suggest that maternal input has a significant effect on the survival of snapper and barracuda larvae through to the juvenile stage. Current single species management relies on the minimum size at sexual maturity to apply size limits to the exploitable stage in most fishes, and assumes that every spawning female is equivalent. Preferential survival of large hatch size larvae suggests that current size limits should be adjusted to protect not only immature fish that have not had a chance to spawn, but also larger, older fishes that would effectively contribute more high quality offspring to the juvenile population. More research is warranted to determine if a correlation between larger, older females and larger sizes-at-hatch of larvae exists in snappers and barracudas. Further, cohorts in this study were only sampled into the juvenile stage, thus their ultimate contribution to the population and subsequent reproduction is unknown. It would be useful to track cohorts past the point of reproductive maturity to determine which traits, if any, continued to convey a survival advantage. Results of this study are the first step to building a fuller understanding of these economically important species. Identifying predictable patterns in abundance, growth, and survival in the early life stages of snapper and barracudas advances the understanding of not only these families, but early life stages of fishes in general, and can help direct future studies and management of these economically important species.

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