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Early life history of Atlantic reef & pelagic fishes: using otolith microstructure to reveal ecological & oceanographic processes

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Abstract : Otolith microstructure analyses of larval and juvenile fishes from the western Atlantic have revealed the influence of oceanographic features on larval growth, and a combination of these data with the analysis of gut contents has demonstrated that growth is related to the amount and type of prey consumed. For example, larvae of the bluehead wrasse, *Thalassoma bifasciatum* (Labridae), with fuller guts grow faster, resulting in a distinct spatial pattern of growth which tracks environmental prey abundance. Several snapper (Lutjanidae) and barracuda (Sphyraenidae) exhibit similar spatial patterns of larval growth. Similarly, blue marlin (*Makaira nigricans*) larvae feeding on higher proportions of a particular crustacean prey (*Farranula* copepods) grow faster than those feeding on other prey. For billfish larvae, switching early to piscivory enhances survival. As a result of such pelagic processes, fish larvae transitioning to juvenile stages can exhibit considerable variation in early life history traits, setting the stage for trait-based selective mortality of young juveniles. Linking these early stages via otoliths demonstrates that processes occurring in one stage can affect survival in a subsequent stage, with the pattern of selective mortality varying between seasons and among species. Otolith-based studies can further our knowledge of the oceanographic processes affecting a diversity of species.

Introduction

Otolith microstructure studies have the potential to reveal the dynamics of a number of ecological and oceanographic processes that underlie our understanding of the population dynamics of marine fishes. Such ecological and oceanographic processes are increasingly important to effective management and conservation of fish populations in a changing world. A recent review emphasizes the contributions of otolith microstructure studies to ecology, fisheries oceanography, and management by highlighting examples from a diverse range of taxonomic groups and geographic locations (Sponaugle, 2010). For the purposes of this presentation, I am narrowing the scope to briefly outline several recent studies conducted in my laboratory on the early life stages of reef and pelagic species in the western Atlantic Ocean. Although the focus of the present workshop is on pelagic top predators, the reef fish examples I present provide a useful illustration of the overall approach and utility of otolith microstructure studies, particularly as combined with other studies such as diet analyses. Many of the oceanographic processes revealed in these studies are broadly applicable to a diversity of coastal and pelagic species.

The examples, or case studies, presented here are focused on a suite of processes occurring during the pelagic larval stage of a diversity of fish species as well as during the transition between the pelagic larval stage to the reef-associated juvenile stage for several reef fishes. These encompass (1) the physical and biological processes influencing larval growth, and (2) the influence of growth on larval survival, leading to (3) variation in the early life history traits of settlement stage fishes, and (4) differential trait- and behavior-mediated survival of juveniles.

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Case Studies

(1) Larval Growth

The coral reefs of the Florida Keys comprise the most extensive coral reef system in the continental United States, and, interestingly, they exist in a subtropical environment where water temperature fluctuates by ~ 10 ℃ over the year. Recruitment[1] of most reef fish peaks in the warmer summer months, but for some species, settlement of pelagic larvae to the reef occurs year-round. We collected 13 cohorts of juvenile bluehead wrasse, *Thalassoma bifasciatum*, over 4 yrs in the upper Florida Keys (Sponaugle *et al.* 2006). Examination of their otoliths revealed that high variation in larval growth was significantly related to water temperature during the larval period. Variation in mean water temperature explained 78% of the variation in larval growth among cohorts. Further, faster-growing fish in warmer waters had significantly shorter pelagic larval durations (PLDs), with variation in larval growth explaining 85% of the variation in PLD. As a result, the seasonal fluctuation in water temperature of 10 ℃ led to a 15-d difference in the time larvae spent at sea (Sponaugle *et al.*, 2006). With a mean PLD of ~50 d, this represents a 30% difference in the time larvae remain in the dispersive pelagic phase. Such a difference in PLD has the potential to not only affect total mortality during the larval phase, but also the distance over which larvae are transported, resulting in seasonal fluctuations in population connectivity (see Cowen and Sponaugle, 2009).

In another example of the influence of the physical environment on larval growth, we compared the larval growth of *T. bifasciatum* juveniles collected from the upstream Caribbean island of Barbados (Sponaugle and Pinkard, 2004). Water temperatures at this oceanic location are more stable, but transient mesoscale low-salinity current rings frequently impinge upon the island, changing the composition of the nearshore waters. These current rings form as the North Brazil Current (NBC) retroflexes off Brazil to form the North Equatorial Counter Current. NBC rings pinch off low salinity water from the Amazon and Orinoco Rivers and move northwestward up and through the Lesser Antilles island chain, frequently passing directly by Barbados. We recorded the passage of these recirculating rings by the island via the 18-mo. deployment off the island of a deep-water mooring that measured salinity. A NBC ring was considered to be present in the vicinity of Barbados when the salinity at 10-13 m dropped below 34.5. During the 18-mo period, we recorded a total of six low-salinity NBC rings that passed the island. Some passed very quickly, with their signal evident for only a few days, while one ring impacted the surrounding waters over multiple months.

During this same period we surveyed and collected juvenile *T. bifasciatum* from the reefs of Barbados every 2 wks. Because Barbados is upstream of all other reefs, we could assume that larvae that settled to the island were sourced from the island, i.e. were present in the water surrounding the island during their entire larval life. We used otolith microstructure analysis to examine larval growth of these juveniles and compared the growth of fish that encountered a ring as larvae versus those that did not. Fish that encountered a low-salinity NBC ring during their larval life had significantly slower growth than those that did not encounter the water mass (Sponaugle and Pinkard, 2004; see also Sponaugle and Grorud-Colvert, 2006). As there was no significant temperature change between ring and no-ring periods, it may have been due to a shift in prey availability with the changing water masses. Thus, larval encounter with different water masses during larval period can significantly influence larval growth, and consequently, survival.

In addition to the physical larval environment, biological processes can influence larval growth. In this example study, we examined the growth of larval *T. bifasciatum* directly (as opposed to hindcasting larval growth from the otolith record of successfully settled juveniles). Nearshore waters frequently differ from offshore waters in nutrient content so the location of larvae during the pelagic stage has the potential to influence their growth. In the Florida Straits, a major western boundary current (the Florida Current) flows along the coast of

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[1] Recruitment is defined here as the entry of young into the juvenile and adult population after the settlement of pelagic larvae to the juvenile habitat.

Florida, which, together with the passage of recirculating mesoscale eddies results in nearshore upwelling. Enhanced nutrients on the western (Miami side) of the Straits are translated into higher primary production and higher microzooplankton and total plankton in the western Straits than the eastern Straits (Llopiz, 2008). We used ichthyoplankton samples collected monthly along a transect across the Straits of Florida (see Llopiz and Cowen, 2008) to examine larval growth on either side of the Straits of Florida (Sponaugle *et al.*, 2009). We examined the sagittal otoliths and gut contents of larval *T. bifasciatum* collected during two months with similar water temperatures (September 2003 and October 2004). For both months, larvae from the western Straits of Florida grew faster, were larger-at-age, and had fuller guts than those collected from the central or eastern stations. Comparison of prey availability for a sample of stations revealed that gut fullness was directly related to environmental prey availability. These patterns were echoed in a similar study of two commercially important snapper species (D'Alessandro *et al.*, 2010). For both yellowtail (*Ocyurus chrysurus*) and lane (*Lutjanus synagris*) snappers, larval growth was highest in the western Straits of Florida, tracking the abundance of their primary prey, appendicularians (Llopiz, unpubl. data). Thus, for multiple fish species, larvae in proximity to highly productive coastal areas grow faster and attain larger sizes-at-age as a result of increased availability of their preferred prey.

(2) Larval survival

Variable patterns of larval growth can lead to patterns of differential survival for particular individuals. In another analysis of spatial patterns of growth in larval billfishes in the Straits of Florida, and in contrast to our results for reef fishes, we found few significant differences in larval growth between larvae on the western and eastern side of the Straits (Sponaugle et al., 2010). However, it is possible that billfish larvae move frequently among water masses and that their capture location is not where they spent their entire larval period. Therefore, to refine our analysis, we examined "recent growth" during the last two full days prior to capture, being careful to detrend the data to account for different larval ages. This analysis revealed that blue marlin (*Makaira nigricans*) in the western Straits grew more rapidly in the 2 d prior to capture than larvae from the eastern Straits; recent growth of sailfish (*Istiophorus platypterus*) did not differ between the regions. Gut content analysis revealed that the enhanced growth of blue marlin larvae in the western Straits was primarily due to significant differences in smaller larvae consuming zooplankton. Larvae with a higher percent of *Farranula* copepods in their guts grew significantly faster than those with lower proportions of the prey. We also compared growth at particular points in small (< 9 mm SL) and large (≥ 9 mm SL) billfish larvae to examine whether mortality was selective for particular traits. Our sampling design precluded tracking a cohort over time, so instead we combined all larvae collected over the 10 summer cruises and divided them by size, assuming that the larvae experienced similar environments and consistent patterns of selective loss over time, resulting in larger (older larvae) having, on average, a higher likelihood of survival. For both blue marlin and sailfish, growth trajectories diverged at 5-8 mm SL, the size at which the transition to piscivory occurs. By day 7 (sailfish) and 10 (blue marlin) of early life, larvae that survived longer (i.e., attained larger sizes and older ages in our samples and had transitioned to piscivory) grew significantly faster than larvae collected at smaller sizes (younger ages; zooplanktiovorous), indicating that mortality was selective for fast growers. Early onset of piscivory appears to be a critical point in the early life history of billfish. In sum, environmental availability of prey influenced growth of the younger, zooplanktivorous larvae, creating spatial patterns of growth for blue marlin that paralleled environmental productivity. But once larvae switched to piscivory, growth accelerated and spatial differences in larval growth disappeared. However, the timing of this diet transition has the potential to significantly influence larval survival as mortality favors fast growers (Sponaugle *et al.*, 2010).

These tight relationships between diet, growth, piscivory, and larval survival are echoed in another top predator, barracuda (*Sphyraena barracuda*). Growth of barracuda larvae collected from the

Straits of Florida varied seasonally with faster growth during the wet season and slower growth during the dry season (D' Alessandro *et al*., 2011). Gut content analysis demonstrated that higher growth during the wet season was associated with the presence of larval fish in the guts of barracuda larvae > 10 mm SL; no larval fish prey were found in barracuda guts in the dry season. Comparison of otolith growth trajectories of younger (initial population) and older (surviving) larvae revealed that, similar to our findings for billfish larvae, mortality is selective and removes slow-growing individuals from the population over time (D' Alessandro *et al.,* 2013).

(3) Variation in early life history traits of settlers

As a consequence of variable pelagic environments, and variable larval growth and survival, late-stage larvae that settle to nearshore juvenile habitats have a range of early life history traits. We divided bluehead wrasse, *T. bifasciatum*, that recently settled to the Florida Keys into those that settled during times of relatively cool water temperatures (22.8-24.8 ℃) versus those that settled during warmer water temperatures (26.4-29.3 ℃) and examined a suite of otolith-derived early life history traits. The traits of the two groups differed substantially, with warmer water fish exhibiting higher larval growth and shorter PLDs than cool water fish (Sponaugle and Grorud-Colvert, 2006). Thus, environments and events encountered by larvae can "carry-over" to influence the composition of young entering the juvenile and adult population.

(4) Trait- and behavior-mediated survival of juveniles

To examine patterns of survival post-settlement, we conducted a number of studies to track cohorts of settlers over time. Comparison of three age groups of juvenile bluehead wrasse, *T. bifasciatum* (young: 0-4 d post-settlement, intermediates: 5-9 d, and survivors: ≥ 10 d; Grorud-Colvert and Sponaugle, 2011), and four age groups of the bicolor damselfish, *Stegastes partitus* (settlement-stage larvae, young settlers: 0-6 d post-settlement, intermediates: 7-13 d, and survivors: 14-20 d; Rankin and Sponaugle, 2011), revealed contrasting patterns of selective mortality. For three traits that can be measured from the otoliths of both species, the traits exhibited by survivors differed significantly from those of the initial (young) settlers or settlement-stage larvae. Surviving wrasse had significantly shorter PLDs, settled at smaller sizes, and exhibited faster early juvenile growth, while surviving damselfish had significantly longer PLDs, settled at larger sizes, and exhibited slower juvenile growth. Experimental behavioral studies provided insight into the proximal mechanism of selection: high condition juvenile wrasse that settled at shorter PLDs and at smaller sizes swam faster and evaded simulated predators more rapidly (Grorud-Colvert and Sponaugle, 2006). While larger territorial juvenile damselfish had higher survival rates (i.e. refuge from gape-limited predators), they spent more time in aggressive interactions with conspecifics, which reduced the energy available for growth (Rankin and Sponaugle, unpubl. data).

Other early life history traits also can influence survival across stages. We recently tracked cohorts of two commercially and recreationally important snapper from the pelagic larval stage through settlement to the older juvenile stage. Otolith microstructure analysis revealed that size-at-hatch not only influenced survival in the pelagic stage but also during settlement and into juvenile life (D' Alessandro *et al.* 2013).

Finally, patterns of trait-based survival can shift seasonally within a species. Seasonal fluctuations in water temperature not only lead to shifts in the distribution of larval and juvenile traits [as illustrated in sections (1) and (3)], but also can influence the strength and direction of selection (Grorud-Colvert and Sponaugle, 2011; Rankin and Sponaugle, 2011). For example, for seven cohorts of *T. bifasciatum*, condition at settlement (as measured by otolith metamorphic band width) varied with water temperature; however, the "optimum" condition level for survival was similar across seasons, resulting in differential patterns of selective mortality during different times of the year. Selective mortality in favor of higher condition was particularly strong in the winter when mean settlement condition was quite low (Grorud-Colvert and Sponaugle, 2011). Likewise, for 16 cohorts of *S. partitus* juveniles, selection on two primary traits (size-at-settlement and juvenile growth) was consistent year-round, while selective loss of two other traits (PLD and larval growth) changed between winter, spring, and summer months (Rankin and Sponaugle, 2011).

Conclusions

Otolith microstructure analysis of multiple life stages enables the close examination of ecological and oceanographic processes that influence survival of young marine fish. Environmental patchiness and fluctuations in water temperature can influence larval growth and survival, and variation in larval traits can carry-over and influence both the composition of settlers and the survival of juveniles. Analysis of otoliths enables the tracking of cohorts and evaluation of their relative success over time. Combining otolith microstructure studies with oceanographic measurements, individual diet and gut analyses, and behavioral experiments provides a powerful means of studying the processes that influence the growth and survival of the young stages of important fish populations. Finally, while much of our work has focused on small reef fishes with limited fisheries applicability, the processes revealed by their study are relevant to a diversity of marine fishes and other organisms.

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