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Early life history and settlement of the slender filefish, *Monacanthus tuckeri* (Monacanthidae), at Calabash Caye, Turneffe Atoll, Belize

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Synopsis

We examined early life history traits and patterns of settlement of the slender filefish, *Monacanthus tuckeri*, at Calabash Caye, Turneffe Atoll, Belize. A settlement peak was evident at the new moon, and no settlement occurred at the full moon. However, settlement rates at the quarter moons could not be estimated due to sampling gaps. Many reef fishes show new moon settlement peaks, so *M. tuckeri* shares some characteristics with the primarily perciform species on coral reefs. Pelagic larval duration was long (mean = 42 days) and variable, suggesting that dispersal patterns might be diverse. Size at settlement was large (mean = 32 mm total length) and also variable. Larval duration and size at settlement were outside of the average values exhibited by reef fishes, but are not beyond the extreme end of the range, and might be explained by association with pelagic debris prior to settlement. There were no differences in overall settlement rates on reef and seagrass habitats, and fish settling to either habitat did not differ in larval duration, size at settlement, or larval growth rate. This suggests that settlement to alternative habitats may be random, or driven by availability of suitable microhabitat, rather than habitat quality or individual traits.

Introduction

The early life history stages of marine organisms, including the pelagic larval phase and the pelagic-benthic transition, have long been a focus of marine ecologists, especially those studying coral reef fishes. Historically, these life stages were of interest in explaining spatial and temporal patterns in the structure of benthic populations (reviewed by Doherty 1991). Recently, these life stages have been a focus in understanding larval development, survival and dispersal, and therefore in understanding inter-population connectivity (reviewed by Sale & Kritzer 2003). The diversity of early life history traits and patterns of settlement exhibited by reef fishes reveal that benthic populations can be structured and connected in numerous and complex ways.

Some coral reef fishes are known to utilize not only reef habitat, but also other coastal tropical habitats such as seagrass beds and mangroves. If settlement and demographic rates in non-reef habitats differ from coral reefs, then use of non-reef habitats introduces additional processes determining post-settlement population structure. Use of non-reef habitats by reef fish species also adds another level of complexity to inter-population connectivity by introducing new habitats that can be connected to one another and to coral reefs. Typically, non-reef habitats are thought to be

nursery grounds for coral reef species (see Heck et al. 2003). However, small and site-attached species such as labrids and pomacentrids typically remain in seagrass beds or mangroves when they settle to these habitats (Nagelkerken et al. 2000), and might represent additional, non-reef sources of future replenishment. Whether small-bodied and less mobile species actively choose non-reef habitats as post-settlement habitats, or whether they are delivered to these habitats at random, is unclear.

Fish might choose to settle in different habitats on the basis of post-settlement advantages that the habitat will confer. If so, differences in post-settlement demography would be expected. But it is also possible that individuals settling to different habitats will differ in pre-settlement traits. For example, some habitats might promote additional development of less developed juveniles. If so, these areas might be expected to receive newly settled fish that are on average younger, smaller or that grew more slowly during the pelagic phase. Alternatively, certain habitats might offer post-settlement advantages to all individuals irrespective of pre-settlement traits, but the ability to reach these preferred habitats might differ among individuals. If so, some habitats might be expected to receive individuals that are on average larger or that grew faster during the larval stage. Different habitats could offer comparable post-settlement advantages, or delivery to different habitats could be largely random. In this case, newly settled fish should exhibit no differences in early life history traits among habitats. These alternative possibilities are difficult to assess because, to date, most comparisons of tropical fish populations in reef and non-reef habitats focus on relative abundance of different life stages (i.e., juveniles versus adults), with some limited attention to post-settlement demography. In contrast, little attention has been paid to pre-settlement life history differences among resident individuals in reef and non-reef habitats.

We examined settlement and early life history of the slender filefish, *Monacanthus tuckeri* (Bean, 1906). Coral reef ecologists have paid little attention to cryptic and non-perciform species like *M. tuckeri* (Munday & Jones 1998), so information on settlement and early life history traits for this species will show whether documented patterns in early life history and settlement of commonly studied species apply more broadly. Furthermore, *M. tuckeri* is known to inhabit both coral reef and seagrass habitats as juveniles and adults (Lieske & Myers 1994), so comparing early life history traits between alternative habitats will provide insight into whether settlers in different habitats exhibit different characteristics. This study describes temporal and inter-habitat settlement patterns over one lunar month, and compares pelagic larval duration (PLD), size at settlement, and larval growth rate between fish settling in reef and seagrass habitats.

Methods

We collected specimens of newly settled *M. tuckeri* from coral reef and seagrass habitat offshore from Calabash Caye on the southeastern edge of Turneffe Atoll, Belize (17°16.414′ N, 87°48.674′ W) using standard monitoring units for the recruitment of fishes (SMURFs). SMURFs were designed for temperate rocky reef fishes (see Ammann 2004), but we attempted to apply the technique to coral reef fishes. A SMURF is a volume of folded plastic mesh enclosed within an exterior plastic mesh envelope designed to provide an internally complex structure to which larval fish can settle. Each was tethered off the substrate 0.5–2 m. Unfortunately, SMURFs were not used as settlement habitat by most coral reef fishes. However, *M. tuckeri* regularly settled to SMURFs, likely because the apparatus was not rigid and swayed with water movements, mimicking the motion of flexible microhabitats such as vegetation and gorgonian sea fans to which *M. tuckeri* normally settle (Lieske & Myers 1994). This provided a unique opportunity to investigate early life history of a cryptic and poorly understood species.

Because SMURFs replicated and were tethered close to natural benthic substrates, it is possible that post-settlement fish moved into the SMURFs from the benthos and not the plankton. However, both the mean and maximum sizes of fish collected (see Results and Discussion) fell well below the maximum size of 10 cm reported for this species[1].

[1]Froese, R. & D. Pauly (eds.) 2003. FishBase. World Wide Web electronic publication. www.fishbase.org.

Therefore, it is likely that we sampled early post-settlement juveniles and not resident older juveniles and adults.

SMURFs were initially deployed on 12 July 2001. We placed a total of 48 SMURFs within shallow (3–5 m) coral reef habitat and 24 within seagrass beds (2–3 m). We removed fishes every 2 days from half of the SMURFs within each habitat (2D SMURFs) and every 2 weeks from the other half (2W SMURFs) until 10 August 2001. The 2D SMURFs were not cleared on the dates of the 2W SMURFs, 27 July and 10 August, due to time constraints. So we cleared the 2D SMURFs on 29 July, 5 days after their last clearance, and did not clear them again after 6 August due to logistical difficulties. To remove fishes, a SMURF was enclosed within a large, fine mesh bag and detached from the tether rope. At the surface, buckets of seawater were poured through the SMURF repeatedly until no more fishes emptied. Specimens were stored in 95% ethanol, and total length (mm) of each specimen was recorded in the lab.

We removed three pairs of otoliths (sagittae, lapillae, asterisci) from a subsample of 49 fish spread across sampling dates and habitats. We mounted otoliths on a glass microslide in Crystalbond mounting medium for enumeration of presumed daily microincrements. Asterisci were too small to allow clear differentiation of microincrements, so we used only sagittae and lapillae. The senior author performed all readings. Three independent readings were performed of both sagittae and lapillae for 38 of the 49 specimens to compare precision of estimates within each otolith type using the index of average percent error (APE; Beamish & Fournier 1981) and the coefficient of variation (CV; Chang 1982). Furthermore, we compared estimates between otolith types by examining the correlation between mean counts from sagittae and lapillae. Based on these comparisons, we used counts from lapillae except in cases where loss or breakage of lapillae left only sagittae (see Results and Discussion). Final estimates were taken as the mean of the independent readings, provided that the readings did not differ by more than 5% from the mean, in which case the outlying reading was excluded and the remaining readings were used to generate the final estimate.

Validation of otolith increment periodicity was not possible. However, Rogers et al. (2001) have validated daily periodicity of otolith microincrements in the Atlantic monacanthid *Stephanolepis hispidus*, and other studies of tropical reef fishes likewise nearly universally report daily periodicity. Therefore, assuming daily periodicity of microincrements is reasonable. Sample sizes were too small to allow temporal comparisons of life history traits, but pooled samples across the study enabled inter-habitat comparisons. Mean size at settlement, mean age at settlement (i.e., PLD), and mean growth rate during the larval phase (i.e., size at settlement/PLD) were compared between fish settling to coral reef and fish settling to seagrass by *t*-tests.

Results

Counts of otolith microincrements were very precise when using either sagittae or lapillae (Table 1). The APE index suggested higher precision than the CV, but both metrics were on average less than 5% for either otolith type. Furthermore, very few estimates generated using either otolith type showed precision worse than 10%. Estimates generated using lapillae were generally more precise than those generated using sagittae, with lower values of both the APE and CV and fewer specimens with precision worse than 10%. Therefore, lapillae-based estimates were used preferentially when available. However, age estimates generated for a specimen using lapillae and sagittae were

Table 1. Mean precision of three replicate counts of microincrements within sagittae and lapillae from each of 38 specimens of *Monacanthus tuckeri* as estimated by the index of average percent error (APE; Beamish & Fournier 1981) and the coefficient of variation (CV; Chang 1982). Also presented are the numbers of individuals with precision indices greater than 10% and the correlation coefficient (R) between the mean of each set of three age estimates and their precision.

	Sagittae	Lapillae
APE		
mean (SE)	3.65% (0.61)	2.07% (0.33)
no. >10%	3	1
R with mean age	0.07	0.04
CV		
mean (SE)	4.92% (0.82)	2.74% (0.44)
no. >10%	5	1
R with mean age	0.09	0.04

highly correlated, and exhibited a nearly 1:1 relationship (Figure 1). Therefore, when estimates from lapillae were not available due to loss or breakage, estimates from sagittae were used ($n = 5$). Individual precision values were not correlated with the mean of the age estimates (Table 1), suggesting that the degree of precision is a product of individual otolith characteristics and does not generally become poorer as more increments are formed.

Otoliths of *M. tuckeri* did not exhibit a clear settlement mark. Rogers et al. (2001) provide the only detailed description of otolith microstructure for a monacanthid. They describe a settlement mark matching Wilson & McCormick's (1999) type III, wherein mean increment width gradually decreases following settlement. However, the results of both Rogers et al. and Wilson & McCormick show that the average change in increment width is only discernable after many days post-settlement (20+ days). This is because the potentially high variability in increment width from day to day requires many days worth of data for the general pattern to become evident. For fish collected in the 2D SMURFs, the inability to identify a settlement mark was not a problem because PLD estimates would be overestimated by only a few days at most, if at all. In contrast, PLD estimates for the 2W SMURFs could have been overestimated by as much as 14 days. This limitation of data from the 2W SMURFs proved problematic for description of temporal settlement patterns and early life history.

Sampling difficulties resulted in settlement rate data for only parts of one lunar month from the 2D SMURFs. Catch rates from the 2D SMURFs show a peak at the new moon on 20 July 2001, lower catch rates near the third-quarter moon in mid-July, and no settlement near the full moon in early August (Figure 2). However, 2D SMURF catch data are not available for the first-quarter moon in late July and the next third-quarter moon in mid-August. Catch rates from the 2W SMURFs sampled at these times are higher than any day during the two weeks preceding (Figure 2), suggesting that these SMURFs are storing accumulated catch and not showing settlement peaks near the dates of clearance. Further supporting this hypothesis is the fact that the 2W SMURFs from 27 July, which were preceded by the new moon peak among the 2D SMURFs, experienced higher settlement than the 2W SMURFs from 10 August, for which there was no clear peak among the preceding 2D SMURFs (Figure 2). Also, the 2W SMURFs sampled at the third-quarter moon of 10 August contained nearly twice as many fish as the 2D SMURFs from the previous third-quarter moon of 14 July (Figure 2). The overall mean increment counts of fish collected from 2W SMURFs (50.3 d ± 3.0 SE) was higher than the mean for 2D SMURFs (41.9 d ± 1.8 SE) (one-

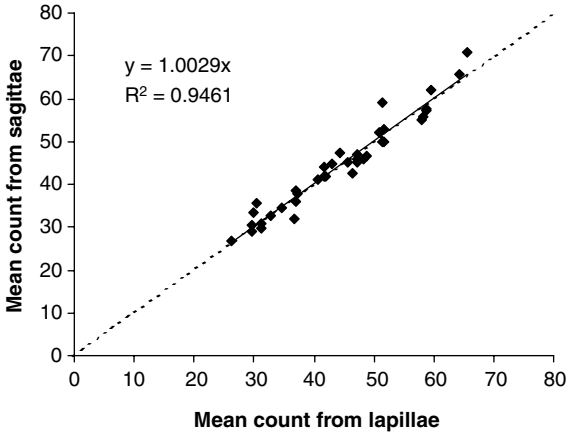

Figure 1. Relationship between the mean of three replicate counts of microincrements within sagittae and three replicate counts from lapillae for each of 38 specimens of *Monacanthus tuckeri*. solid line = linear regression of mean count from sagittae on mean count from lapillae (i.e., less precise method regressed on more precise method; see Table 1), broken line = 1:1 relationship.

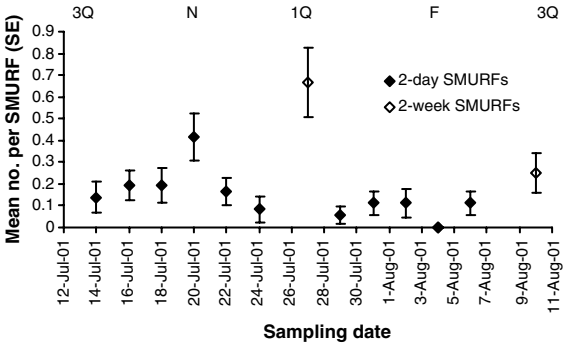

Figure 2. Mean catch rates of *Monacanthus tuckeri* by standard monitoring units for recruitment of fishes (SMURFs) sampled every 2 days and every 2 weeks over one lunar month in July–August 2001. Lunar phases are indicated: 1Q = first quarter moon, 3Q = third quarter moon, N = new moon, F = full moon.

tailed t-test: $df = 47$, $t = 2.84$, $p = 0.006$), suggesting that the counts for the fish from the 2W SMURFs include the PLD plus some time post-settlement.

Ammann's (2004) experiment examining SMURF clearance intervals showed that, while some species remained resident in a SMURF for up to one month, others left the SMURF after only a few days. If the latter were true for *M. tuckeri*, then the high catch rates on 27 July represent a first-quarter moon peak and not accumulation from the new moon peak. We can be certain that there was a peak of settlement near the new moon and little settlement near the full moon (Figure 2). However, we cannot unequivocally determine how the magnitude of the new moon peak compares with the quarter moons due to the absence of 2D SMURF data coinciding with the 2W SMURF data.

Given the uncertainty of the actual settlement date of fish from the 2W SMURFs, we exclude those fish from analysis of early life history traits. This resulted in a pooled sample size of 30 fish from the 2D SMURFs, with 17 fish from the reef and 13 from the seagrass beds. Although these habitat-specific samples sizes are small, mean age and, especially, mean length characteristics can be measured with relatively high precision using small sample sizes and provide useful initial demographic information for a population in the absence of large numbers of fish (Kritzer et al. 2001). The overall mean PLD was fairly high at approximately 42 days (Table 2). Individual PLDs differed by more than twofold, and short PLDs were about as common as long PLDs, as indicated by the lack of strong skew in the distribution. Also, both short and long PLDs were nearly as common as average PLDs, given that the distribution was fairly flat (i.e., negative kurtosis).

It does not seem likely that the range of PLDs reflects differences in larval growth to an optimal settlement size. Sizes at settlement were large and nearly as variable as PLDs (Table 2), so there is no evidence that all fish settle once reaching a critical size. Furthermore, although there was a statistically significant relationship between PLD and larval growth rate, the slope of the relationship is nearly flat and it explains very little variability (regression analysis: $b = -0.003$, $R^2 = 0.14$, $df = 1,28$, $F = 4.50$, $p = 0.043$). Therefore, there is no strong evidence that fish with longer PLDs were growing more slowly and therefore in need of more time in the plankton. Despite a 50% difference in the maximum and minimum larval growth rates estimated, larval growth rates showed high precision and a very peaked distribution (Table 2). This suggests that most fish that survive to settle grow at similar rates during the pelagic phase.

Table 2. Mean pelagic larval duration (PLD), size at settlement and larval growth rate of 30 newly settled *Monacanthus tuckeri*, and the range, coefficient of variation (CV), skew and kurtosis of the sets of estimates.

	PLD (days)	Size at settlement (mm)	Larval growth rate (mm d^{-1})
mean (SE)	41.9 (1.7)	31.7 (1.3)	0.76 (0.014)
range	26–60	20.5–47.2	0.62–0.93
CV	23%	22%	10%
skew	0.15	0.28	−0.017
kurtosis	−0.99	−0.98	0.78

Fish settling to reef and seagrass habitats showed no differences in PLD (one-tailed t-test: $df = 28$, $t = 0.83$, $p = 0.41$), size at settlement ($df = 28$, $t = 1.31$, $p = 0.20$), or mean growth rate during the larval period ($df = 28$, $t = 1.31$, $p = 0.20$). Therefore, there is no apparent early life history difference between fish settling to reef and seagrass habitats. Also, mean catch rates of 2D SMURFs did not differ between reef and seagrass (one-tailed t-test: $df = 12$, $t = 1.78$, $p = 0.28$), so the magnitude of settlement did not differ between habitats.

Discussion

Settlement of *M. tuckeri* to SMURFs showed a peak at the new moon and no settlement at the full moon, but quarter moon patterns are ambiguous given the sampling limitations of our study. Doherty (1991) reviewed lunar settlement patterns for a variety of coral reef fishes, and found that peaks at the new moon are the most common pattern, but peaks at the quarter moons are also evident for some species. Therefore, the broader reef fish literature supports the likelihood of a new moon settlement peak, but also precludes discounting the possibility of quarter moon peaks.

Additional sampling would have allowed us to resolve the ambiguities concerning quarter moon settlement rates, as well as establish the generality of the full and new moon settlement patterns. Unfortunately, the failure of SMURFs to sample other coral reef fishes led to abandonment of the technique by the larger sampling program within which this study took place.

At approximately 42 days, the mean PLD of *M. tuckeri* was quite long, given that most reef fish PLDs are between 20 and 30 days (Victor 1991), and there was considerable variability about the mean value. Other Caribbean reef fishes, including the labrid *Thalassoma bifasciatum* (reviewed by Philibotte 2002) and the gobiid *Gnatholepis thompsoni* (Sponaugle & Cowen 1999), also have very long and variable PLDs. Sponaugle & Cowen (1999) speculate that such patterns reflect the need to maintain flexibility in larval duration in the face of extended developmental periods in order to achieve successful transport to settlement habitat. Long and variable PLDs within a species create the potential for diverse patterns of dispersal and inter-population connectivity. Specifically, variable PLDs allow the possibility of local retention among individuals with short PLDs while increasing the likelihood of very long distance transport among individuals with long PLDs (e.g., Doherty et al. 1995).

The mean size at settlement was over 30 mm, which is considerably larger than the range of settlement sizes for most reef fishes (7–12 mm; Victor 1991). Even the smallest settlement size was well above the typical range, and the largest size (47 mm) approaches the largest settlement sizes reported for reef fishes (≈ 60 mm for some triggerfishes and butterflyfishes; Victor 1991). Given that sizes at settlement were so variable, and that larval growth rate did not correlate strongly with PLD, it is unlikely that the variability in PLD is due to individual variability in other life history traits. Instead, it is more likely that the variability in PLD is due to variability in transport processes or active choices about when and where to settle (Sponaugle & Cowen 1999).

Little is known of the early ontogeny of monacanthids, so it is difficult to evaluate the role of development in driving the extended PLDs and large sizes at settlement. However, pre-settlement monacanthids, including *M. tuckeri*, have been known to associate with drifting algae and other debris during their pelagic stage (reviewed by Castro et al. 2002). This presents a mechanism for both the extended PLDs and larger sizes at settlement observed. The protection and food sources offered by mobile shelter provide for greater survivorship and growth (Castro et al. 2002), which places fewer constraints on finding benthic habitat and ending the pelagic phase. This ultimately allows for greater flexibility in making the transition to reef or seagrass environments.

The lack of a difference in magnitude of settlement or life history traits between fish settling to different habitats might reflect limited ability of larvae to precisely select their settlement habitat. In other words, larvae with weak swimming abilities might effectively be randomly distributed among habitats within a given area. However, J.D. Hogan has recently examined swimming abilities of late stage larvae of Caribbean reef fishes[2]. His study includes one monacanthid species, *Stephanolepis setifer*, the critical swimming speed of which is approximately 35 cm s^{-1}. Ocean current speeds in the vicinity of Calabash Caye during summer months can be as high as 46 cm s^{-1}, but are generally well below the 35 cm s^{-1} critical swimming speed Hogan measured for *S. setifer*[3]. Therefore, if swimming abilities of larval *M. tuckeri* are comparable to *S. setifer*, then fish should have adequate capacity to select a preferred habitat under most oceanographic conditions. The potential for these fishes to drift with floating objects could also affect the interaction between swimming ability, current speeds and selection of a settlement site, depending upon when and where they disassociate with objects to make the transition to benthos.

It is possible that there are no consistent differences between reef and seagrass beds that will select for active habitat selection by *M. tuckeri*. Chittaro et al. (2004) found that predation rates on juvenile smallmouth grunts, *Haemulon chrysargyreum*, showed complex spatio-temporal patterns among several reef and non-reef habitats (mangroves and seagrass beds) in the vicinity of

[2]J.D Hogan, Department of Biological Sciences, University of Windsor, unpublished data.

[3]P.F. Sale et al., Department of Biological Sciences, University of Windsor, unpublished data.

Calabash Caye. High variance in predation rates precluded identification of clear and consistent advantages of non-reef habitats. Species like *M. tuckeri* might be even less susceptible to any habitat-specific predation pressures that do exist because their cryptic nature reduces predation risk (Munday & Jones 1998). Food availability could also create differences in habitat quality for *M. tuckeri*. However, Barrett (1999) found that food was not a limiting factor in growth of a temperate monacanthid in Australia, and Bullard et al. (1999) found that an Atlantic monacanthid could readily consume a wide array of available microinvertebrate prey. *M. tuckeri* has a broad diet including algae, detritus and invertebrates[1], so food is likewise unlikely to be a limiting resource for this species.

What might be more important, then, is simply locating suitable microhabitat for shelter. Heck et al. (2003) discovered that the biggest difference between seagrass beds and other habitats is the abundance of species held in common, and not growth or survival rates within each habitat. They argue that differences in abundance are often driven by availability of microhabitat with suitable general structure, but not by availability of any specific microhabitat. Gorgonian sea fans on coral reefs and seagrass blades might provide comparable shelter for *M. tuckeri*, but with different densities within each habitat. Those larvae that do not locate a gorgonian as they pass over the reef might readily settle amidst the higher density microhabitat within the seagrass beds, with no distinct demographic advantage provided by either habitat. Clearly, additional research on post-settlement ecology is needed to test these ideas.

Despite the fundamental taxonomic difference between the tetraodontiform *M. tuckeri* and the predominantly perciform reef fish community, settlement of *M. tuckeri* exhibited a peak at the new moon as is typical of many reef fishes. Unfortunately, whether settlement also peaks at the quarter moons in unclear. The early life history traits of *M. tuckeri* were different from those exhibited by many perciform species, including a long and variable PLD and large size at settlement. However, these patterns have been found among some perciform species, and therefore do not represent unique tetraodontiform characteristics. Instead, these characteristics might be due to use of floating algae and debris by pre-settlement fish as an aid in dispersal, which would allow greater flexibility in the length of pre-settlement life history. If so, these traits should be similar among other species with similar behavior. Despite the documented importance of larval life history traits in determining early post-settlement ecology, there were no obvious differences between fish settling to coral reef and seagrass habitats. It is therefore possible that either habitat is comparably suitable for juvenile *M. tuckeri*. Of course, it is also possible that these habitats will confer different post-settlement advantages that were not documented in the present paper, but any potential habitat-specific differences cannot be linked with aspects of larval life studied. This study presents a first look at the early life history of a cryptic coral reef fishes, and raises questions concerning whether utilization of different habitats is driven by important habitat differences or primarily random processes.

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