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Tidal and diel variations in abundance and schooling behavior of estuarine fish within an intertidal salt marsh pool

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Abstract Tidally driven fluctuations lead to rapid variations in hydrological properties that can have profound effects on the dynamic and functions of salt marshes. During low tides, many nektonic species find refuge from predatory fish in shallow intertidal pools. The utilization of shallow pool refuges also exposes fishes to fitness costs that fluctuate between day and night. Yet, how aggregated fish using an intertidal pool modulate their schooling behavior over the diel cycle remains unknown. Using high-resolution imaging sonar (ARIS), we monitored an intertidal pool over a 3-day period and quantified fish abundance, size, and schooling behavior relative to the diel and tidal cycles. Higher fish abundance was found during low tides than high tides when the section was connected with the subtidal waters. At low tide, no differences in fish abundance and size were detected in the pool between day and night, but larger schools formed at night than day. Our results suggest that biotic and abiotic factors affecting fish schooling behavior in the low tide refuge may vary over the diel cycle. We present possible functional explanations for the shifts in schooling tendency between nocturnal and diurnal utilization of the pool.

Keywords Schooling behavior · Nekton · Salt marsh · Diel cycle · Tidal cycle · Intertidal creek · ARIS

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Introduction

Avoiding predation is considered to be the prevailing explanation for why many fishes form schools (Parrish, 1991; Pitcher & Parrish, 1993). Schooling is mainly presented as an adaptive strategy that enhances fish safety through the action of several anti-predatory mechanisms which include risk dilution (Pitcher & Parrish, 1993), collective predator detection (Webb, 1980; Magurran et al., 1985), confusion effect (Landeau & Terborgh, 1986; Ioannou et al., 2008), or coordinated escape maneuvers (Pitcher & Wyche, 1983; Pitcher & Parrish, 1993). In marine fishes, natural variations in school behavior, internal

organization, and external shape are often reported (Fréon et al., 1992; Misund, 1993; Nøttestad et al., 1996; Makris et al., 2009), with predation and energetic requirements being the most commonly invoked drivers of the observed changes in schooling behavior (Pitcher et al., 1982; Pitcher & Parrish, 1993; Nøttestad et al., 1996).

Under dynamic environmental conditions, schooling fish face the ceaseless challenge of fine-tuning their aggregative tendency to minimize their vulnerability to predation while optimizing their fitness gains. Yet, to date, little is known about the temporal dynamics of schooling behavior of marine and estuarine fish apart from the general trend that most pelagic social fishes disperse at night and form dense and highly cohesive schools during daytime (Blaxter & Batty, 1987; Fréon et al., 1996). In particular, it is unclear how schooling fish modulate their behavior to cope with rapid shifts in predation levels or environmental conditions over the diel cycle. These questions are challenging to address due to the difficulties in observing, tracking, and quantifying the behaviors of aquatic organisms in natural settings.

Diel effects influence the behavior, abundance, and composition of marine and estuarine organisms (Hagan & Able, 2008; Becker et al., 2011; Becker & Suthers, 2014). In estuarine systems, for instance, predatory fish that ambush and chase prey are more active during daytime compared with nighttime, as they rely mostly on vision to detect and capture their prey (Becker et al., 2013; Becker & Suthers, 2014). In schooling fish, vision, hydrodynamic sensing through the lateral line, and auditory cues are presented as the three main sensory mechanisms that enable schooling (Pitcher & Parrish, 1993; Chicoli et al., 2014), but only vision is subject to diel variations (Fréon et al., 1996). Schooling fish can visually gauge the distance to their neighbors or gather predator-related information, making vision critical for the formation, dynamic, and coordinated responses of fish schools.

Many estuarine fishes inhabiting tidally driven salt marshes form mono- or multi-specific aggregations (Bretsch & Allen, 2006a) and, thus, are well-suited models to explore the effects of rapid fluctuations in environmental conditions on schooling behaviors. Salt marshes are highly dynamic complex ecosystems that comprise a mosaic of interconnected habitats that include vegetated marsh surface, marsh ponds and pools, intertidal and subtidal creeks, and open-water

habitats (Minello et al., 2003; Rountree & Able, 2007). These habitats are essential for many transient and resident fish species in providing foraging grounds, migratory routes, nurseries, and predation refuges (Weinstein, 1979; Miller & Dunn, 1980; Kneib, 1987; Hettler, 1989; Catrijsse et al., 1994; Kneib & Wagner, 1994; Kneib, 1997; Allen et al., 2007). Of prime ecological importance are the considerable variations in hydrological properties in salt marshes that occur over relatively small temporal scales (e.g., hours). Tidally driven fluctuations lead to rapid changes in water levels, salinity, temperature, dissolved oxygen, turbidity, and water velocity that can profoundly impact the dynamics and function of the habitat and inhabitants. It has become increasingly clear that changes in water levels over the tidal cycle also mediate predator–prey interactions (Kneib, 1987; Bretsch & Allen, 2006b). Tidal migrations of nektonic species are common in salt marshes and presumably reflect fish responses to local modifications regarding the tradeoff between feeding, reproduction, and survival (Kneib & Wagner, 1994; Gibson, 2003; Bretsch & Allen, 2006a).

At low tide stages (e.g., late ebb through early flood), many small nektonic species find refuge against large predatory fish in shallow intertidal pools on the salt marsh surface or in intertidal creeks where pools become isolated from subtidal waters (Boesch & Turner, 1984; McIvor & Odum, 1988; Halpin, 2000; Bretsch & Allen, 2006a). Low water levels prevent large predatory fishes from accessing shallow intertidal pools (Ruiz et al., 1993; Bretsch & Allen, 2006a). However, the utilization of these ephemeral shallow refuges exposes fishes to a series of fitness costs such as hypoxia or suboptimal temperatures during day (Wolf & Kramer, 1987), limited foraging opportunities, reduced ability to visually detect threats or to collect social information due to water turbidity (Godin & Sproul, 1988; Abrahams & Kattenfeld, 1997), or vulnerability to daylight active wading or diving predatory birds (Bildstein et al., 1981; McIvor & Odum, 1988). When increasing water levels with the flooding tide restore the interconnectivity between intertidal pools and subtidal waters, fish usually leave their temporary refuges and move with the flooding tide toward newly inundated intertidal and marsh surface habitats, likely for feeding purposes (Kneib, 1997). In salt marshes, tidal migratory fishes generally feed in flooded intertidal areas and retreat to low tide

refuges with full stomachs which might allow them to cope with limited resources during their isolation in relatively food-poor intertidal pools (Rozas & LaSalle, 1990; Kneib, 1997; Potthoff & Allen, 2003). While it is understood that small fish migrate toward ebbing pools to gain refuge against predators (McIvor & Odum, 1988; Halpin, 2000; Bretsch & Allen, 2006a; Allen et al., 2013), it is unknown how schooling fish respond to small-scale temporal variations in refuge values (i.e., metabolic or predation costs).

Using high-resolution imaging sonar, we monitored a section of a salt marsh intertidal creek over multiple consecutive tidal cycles in a 3-day period. This section was inundated during high tides and became an intertidal pool isolated from the adjacent subtidal creek during low tides. We quantified both fish abundance and size during 4 slack high and 4 slack low tides. In addition, we examined whether schooling fish, remaining in the intertidal pool during low tides, modified their schooling behavior relative to the diel cycle by comparing school size and density during nocturnal and diurnal use of the intertidal pool. We hypothesized that schooling fish would adjust their schooling behavior in response to the changing costs of using the intertidal pool throughout the diel cycle.

Materials and methods

Study site

The study was conducted in North Inlet estuary in Georgetown County, South Carolina, USA between 31 July and 3 August 2012. This warm temperate barrier island bounded system (16.5 km^2) consists mostly of *Spartina alterniflora* marsh (71%); creeks, intertidal flats, and oyster reefs (13%); and open water (16%) (Allen et al., 2013). Semidiurnal tides with a mean tidal range of 1.4 m and a relatively small surrounding watershed result in salinities above 30 PSU most of the time. Because of shallow depth and tidal currents, creeks are well mixed and vertically homogeneous with respect to dissolved substances (Dame et al., 2000). Nutrient and contaminant levels in the estuary are low because of the strong coastal ocean influence and a forest-dominated watershed (Buzzelli et al., 2004). Our study focused on a single intertidal pool (approx. 11 m diameter) located upstream (closest point approx. 22 m) from subtidal
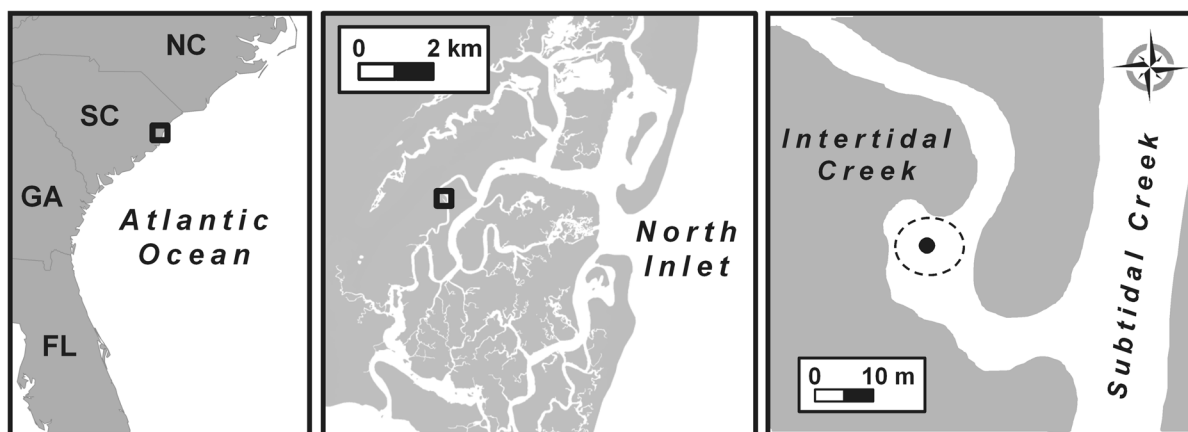
waters at the mouth of the intertidal creek (Fig. 1). This pool was isolated by sections of the intertidal creek bed that were exposed at low tide, whereas the adjacent subtidal creek was always submerged. The center of the pool was approximately 1.8 m deep at high tide (Fig. 2).

Data collection

A high-resolution imaging sonar, ARIS (adaptive resolution imaging sonar, sound metrics corporation, Bellevue, WA, USA), operating at 3 MHz, was mounted to a tripod and positioned 30 cm off of the bottom in the center of the intertidal pool (33.33120, −79.19328) facing toward the mouth of the intertidal creek (beam pointed to 130°) and recording at a rate of approximately 8 frames per second. The ARIS was deployed on 31 July 2012 and left in place undisturbed for monitoring for the duration of the study period (08:00:00/1 August 2012 through 18:00:00/3 August 2012, full Moon phase). Water temperature (Celsius) and light intensity (lumens/ft^2) were measured continuously (every 30 s) during the study period with a single sensor (HOBO Pendant Temperature/Light Data Logger 64K—UA-002-64; Onset) mounted at the same height as the sonar on one side of the tripod. Similarly, water level (m) was measured continuously (every 1 min) throughout the study period with a water level logger (HOBO U20 Water Level Data Logger—U20-001-01; Onset) mounted at the same height on the other side of the tripod. An additional atmospheric reference water level logger was positioned approximately 2 km away at the Baruch Marine Field Laboratory.

Quantification of schooling behavior

The 3-day period of monitoring (1–3 August 2012) was divided into 8 periods of interest: 4 slack high tides (1 August 2012: $n = 1$; 2 August 2012: $n = 2$; 3 August 2012: $n = 1$) and 4 slack low tides (1 August 2012: $n = 1$; 2 August 2012: $n = 2$; 3 August 2012: n = 1). The duration of each period was 13 ± 0.8 min (mean ± SD) and included 6477 ± 401 frames of ARIS imagery. High and low slack tides referred to periods of the tidal phase with little or no horizontal motion of the water, opposed to flood or ebb currents occurring during the rise and fall of the tides. For each period, ten still frames were randomly selected (using

Fig. 1 The location of the ARIS (black dot) in the intertidal pool inside the mouth of an intertidal creek in the North Inlet estuary, Georgetown, SC, on the southeastern US Atlantic coast. The *dashed line* approximates the low tide area (=the pool); the creek bed on either side of and surrounding the *circle* was exposed at low tide. The ARIS was mounted to a tripod and positioned 30 cm off of the *bottom* in the center of the intertidal pool (33.33120, -79.19328) facing towards the mouth of the intertidal creek (beam pointed to 130°)

Fig. 2 Water level, light intensity, and water temperature based on continuous measurements in the pool section of the intertidal creek during the study period (1–3 August 2012)
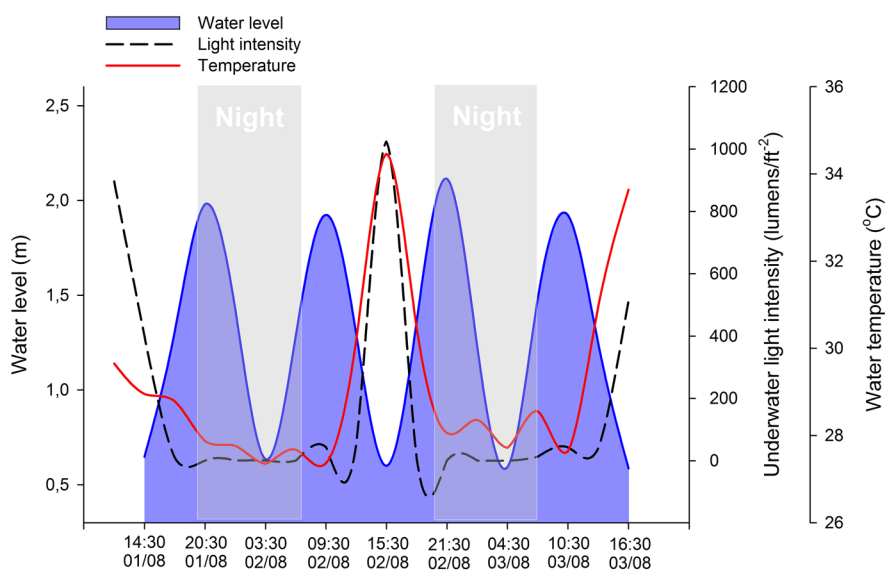
random number tables) from the sonar imaging recordings using ArisFish software (Sound Metrics Corporation, Bellevue, WA, USA). For this study, a total of 80 frames were analyzed. As described in Boswell et al. (2008), a background subtraction algorithm is effective to reduce the effects of static objects (i.e., substrate) and speckle noise. Within ArisFish, a background subtraction algorithm and threshold were applied on each frame to discard static background and all "objects" smaller than 5 cm^2 which were identified as passive particles moving in accordance with the tidal flow (Online Resource 1). This process allowed removal of flooding particles, water movement artifacts, and bottom characteristics of the pool to facilitate the analysis of the frames.

The relative fish abundance (i.e., total number) was estimated using the "MaxN" method described in Cappo et al. (2004) and Cappo et al. (2007). Several previous studies conducted in estuarine systems relied on the "MaxN" method to estimate fish abundance using information collected from high-resolution imaging sonars (Becker et al., 2011, 2013). In order

to include the maximum number of fish present at any time (Becker et al., 2011), we counted the total number of fish observed in the ARIS field of view within each of the 80 frames analyzed (n = 3915 total fish, all frames combined). All fish present in a given frame were counted regardless of their size, swimming activity, or aggregating tendency. Then, for each period of interest, the maximum number of fish in each frame was averaged over the 10 sampled frames giving a mean relative fish abundance estimate, corresponding to the "mean MaxN" described as an accurate estimator of relative abundance (Becker et al., 2011, 2013).

In ArisFish, we manually measured body size (i.e., total body length) of only individuals that were oriented perpendicular to the sonar lens. According to Becker et al. (2011), this procedure minimizes error in obtaining estimates of fish size.

We also counted the number of fish schools observed in each frame. As the number and size of schools observed in the pool section differed from frame to frame, we assigned each school present at the same time in a particular frame a unique identifier code (ID). Our observational approach did not allow us to track any given school over time, therefore school ID only refers to the identity of a fish school present at one particular time. A school was defined as an aggregation of fish presenting polarized, synchronous, and active swimming patterns and in which fish were equally spaced with between-individual distances not greater than one body size (Pitcher et al., 1976; Pitcher, 1983; Pitcher & Parrish, 1993). School sizes were estimated by counting the number of fish present within the boundary of the school. School densities were assessed by measuring the distance to the closest neighbor of each school member. Thereafter, the mean between-individual distance was calculated for each school.

Statistical analysis

Mean values of the hydrological variables (water levels, temperatures, and light intensities) were calculated on data collected (water levels: $n = 13$; water temperatures and light intensities: $n = 26$) over the duration ($\sim$13 min) of the 4 high slack tides and 4 low slack tides monitored. Hydrological data were examined with descriptive statistics.

We used linear mixed effects models (LMEs) to examine the effect of tide level (low tide, high tide), the time of the day (day, night), and the interaction between these two independent variables on fish abundance and body length. Tide level and the time of the day were included as fixed effects in the LMEs. Although each frame could be considered as a unique suite of environmental, hydrodynamic, and biological factors present as suggested by Kimball et al. (2010), it is possible that they may not have been satisfactory independent units of replication. Therefore, we included frame nested within period of interest as a random effect in each LME to control for pseudoreplication and the possible non-independency of the series of frames analyzed for a given period of interest.

We used LMEs to examine the effect of the diel period (day, night), included as a fixed effect, on the school's size and the mean distance between the nearest schooling neighbor for all schools present in the intertidal pool during the periods of interest. School ID nested within frame, nested within period of interest, was included as a random effect in each LME. The structure of the random effect allowed us (1) to control for the eventual non-independency of the randomly chosen frames within each period of interest, (2) to control for the effect of frame as multiple schools within a single frame were quantified and the number of schools was variable among frames, and (3) to assess the between-school variation in size and density within and between frames. All analyses were performed in R 3.0.3 (R Development Core Team, USA), and LMEs were conducted using the package nlme.

Results

The semidiurnal tidal regime induced fluctuations of water levels in the pool section of the creek, with mean water level of 0.62 ± 0.03 m measured at low slack tides and 1.99 ± 0.09 m at high slack tides (mean $\pm$ SD) (Fig. 2). Water temperatures fluctuated over diel and tidal cycles. During low slack tides, water temperature increased inside the pool during the day (31.6 ± 3.2°C; mean $\pm$ SD) and decreased during the night (28.2 ± 0.4°C; mean $\pm$ SD). During slack high tides, water temperature was relatively invariant throughout the diel cycle (day: 27.9 ± 0.2°C; night: 28.2 ± 0.2°C; mean $\pm$ SD). During the day,

underwater light intensities measured during low tides were higher (735.2 ± 547.6 lumens/ft^2; mean ± SD) than during high tides (38.0 ± 6.9 lumens/ft^2; mean ± SD). Peaks in underwater light intensity and temperature were recorded in the pool during the low tide that occurred during the afternoon on August 2, 2012 (Fig. 2). At night, underwater light intensities were null during either low or high slack tides.

Fish abundance in the pool significantly differed between slack low tides and slack high tides ($F_{1,68} = 2.36$, $P = 0.02$), with more fish present in the pool during slack low tide periods (Fig. 3a). No significant difference in fish abundance was detected within the pool between day and night ($F_{1,68} = 0.29$, $P = 0.78$). The lack of a significant interaction between tides and periods of the day ($F_{1,68} = 1.53$, $P = 0.13$) suggests that fish abundance in the pool varied in a similar manner during low and high tides and was not affected by the diel cycle (Fig. 4).

There was no difference in the length of fish that occupied the pool during the low and high tide periods ($F_{1,68} = 0.52$, $P = 0.60$) or between day and night ($F_{1,68} = 0.58$, $P = 0.58$) (Fig. 3b). The interaction between tide and period of the day was not significant ($F_{1,68} = 0.83$, $P = 0.41$), suggesting that, for both high tide and low tide periods, fish of equivalent size used the pool independent of the period of the day (Fig. 4).

No schools were observed during slack high tide periods. A total of 20 schools were observed and quantified over the 40 frames analyzed for the sampled low tides. Each LME was compared to an equivalent model with the same fixed effect structure but that only included school ID nested within frame as a random effect. In each case, the addition of a more complex random effect structure did not significantly increase the fit of the model, and therefore the schooling data were analyzed using the more parsimonious model. School sizes observed in the pool during slack low tides significantly differed between day and night ($F_{18,546} = 3.18$, $P < 0.01$) where larger schools occupied the pool at night compared with day (Fig. 5). Nocturnal schools observed were approximately 1.8 times larger than schools during day, with an average school size of 27 fish at night compared to 15 fish during day. Distance to the nearest school member did not significantly differ relative to the period of the day ($F_{18,548} = 0.64$, $P = 0.52$) (Fig. 5).

Discussion

Small estuarine fishes routinely utilized a section of an intertidal salt marsh creek throughout the tidal cycle, regardless of whether it was an isolated pool at low tide or connected with the rest of the creek at higher water levels. Higher fish abundance was observed during low tide than during high tide periods. Generally, comparing fish use of isolated low tide pools and the same areas at high tide is difficult to accomplish with traditional netting techniques (Rozas & Minello, 1997). Using high-resolution imaging sonar, direct quantification of fish habitat use and behavior was made without disturbing or depleting the fish assemblage. The lower fish abundances observed around high tides reflect the tendency for tidal migratory fishes to enter intertidal creeks during the first part of the flooding tide and move further into the creek (Bretsch & Allen, 2006a; Kimball & Able, 2012) and, for some species, onto the flooded marsh (Kneib & Wagner, 1994). Lower fish abundance has been previously reported to occur in the section of creek near the mouth around high tide compared with periods when water levels were lower (Kimball & Able, 2007a, b) As the tide ebbs, fish can either pass through the pool and continue to the subtidal channel (which serves as a low tide refuge for most of the migratory assemblage) or remain there until the next flooding tide (Allen et al., 2007). Higher fish abundances found in our study at low tide indicate that some combination of decreasing water volume in the intertidal creek and habitat selection made by the fishes for the pool resulted in a comparatively high-density aggregation in the pool at low tide.

The lack of a difference in fish abundance in the pool between day and night low tides suggests that there may be an ideal or maximum capacity for occupation, perhaps determined by the size and other physical features of the pool. Earlier, Allen et al. (2007) showed that consistency in the degree of fish use of neighboring intertidal creek basins was determined by certain hydrogeomorphological features. The final numbers of fish that remained in the pool must have been determined as the dropping water level in the creek approached the point when the pool became isolated. During those final minutes of connectivity with the rest of the creek, fish can either decide to remain in the pool with those already occupying the space or move out to the subtidal

Fig. 3 Abundance (**a**) and lengths (**b**) of fishes in the pool section of the intertidal creek during the study period. Abundance values are mean (+SD) numbers of individual per frame for consecutive low and high tides. Length values are means (+SD) for all fishes used to make the abundance determinations for consecutive low and high tides
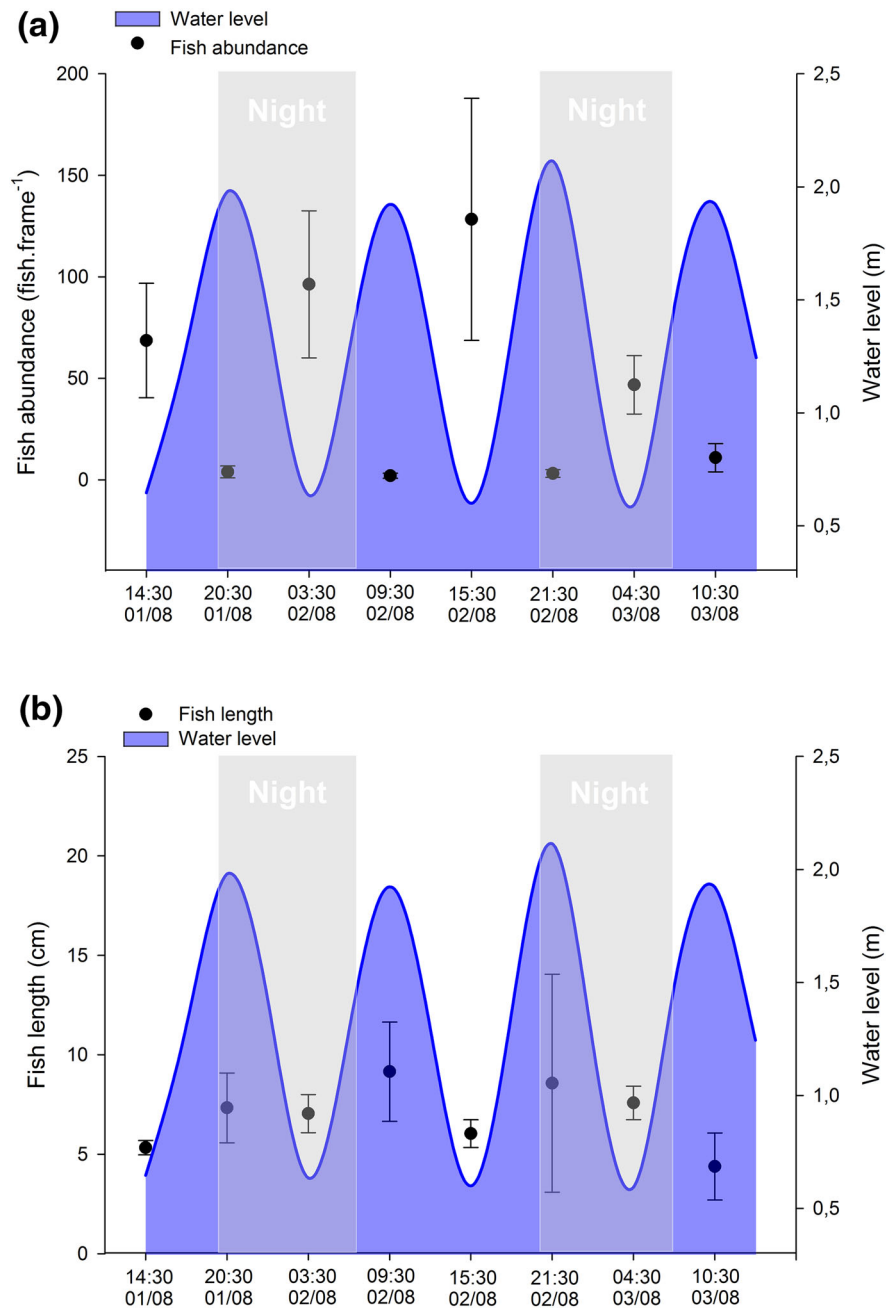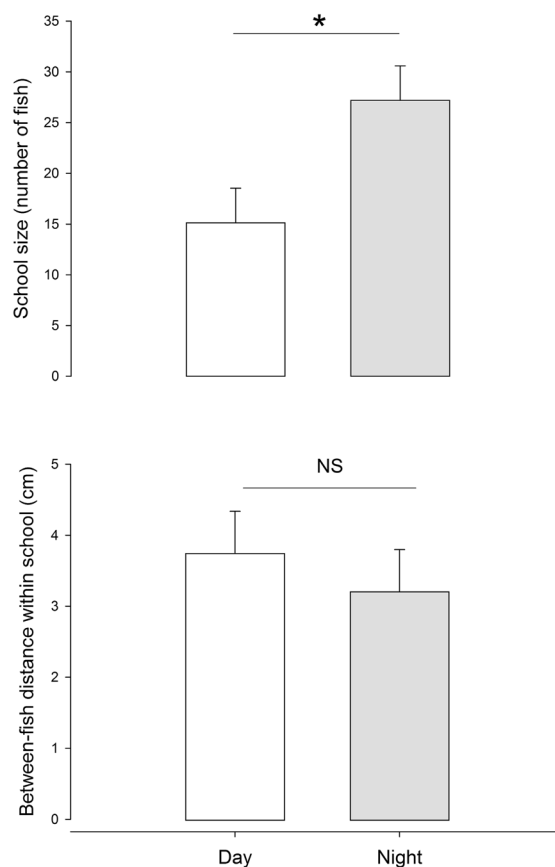

channel. As evading predation by large piscivorous fish is the common explanation for why many fish retreat to natural intertidal pools (Paterson & Whitfield, 2000; Potthoff & Allen, 2003; Bretsch & Allen, 2006a), fish that occupy these ephemeral refuges face the tradeoff between the costs associated with overcapacity (i.e., degrading water quality) in the pool or threat of predation in subtidal waters. While the sonar

imagery does not provide sufficient resolution to precisely identify fish species, the processing approach employed allows for accurate fish length measurements and then inferences about the species identity can be made with knowledge of the fish community. Young of the year (YOY) mullets are by far the most abundant fish in the tidal migratory assemblage at this site in August (Allen et al., 1992),
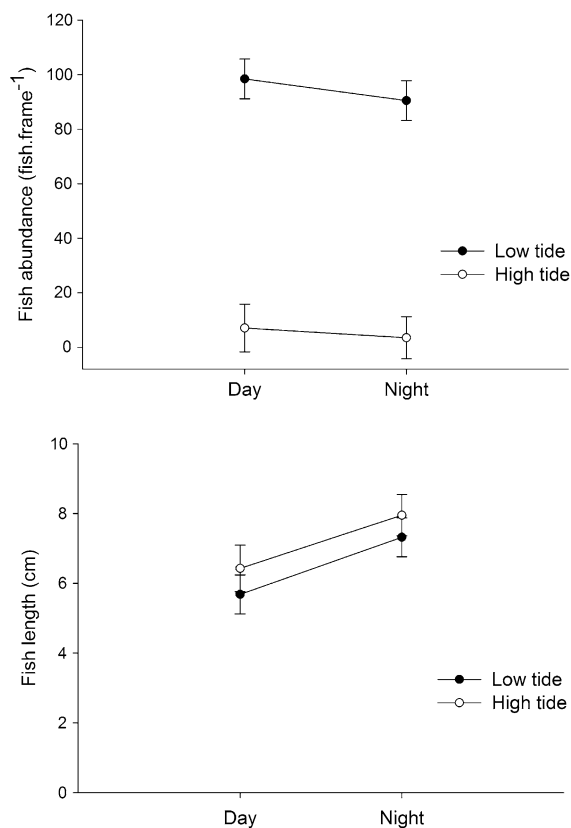
Fig. 4 Mean (+SD) abundances and lengths of fishes in the pool section of the intertidal creek at low and high tide during day and night

Fig. 5 Mean (+SD) school size and distance between individuals fishes in the pool section of the intertidal creek between day and night during low tide periods. *Asterisk* indicates a significant difference between day and night

and they form fast-moving schools in the water column of intertidal creeks. Seine and cast-net collections from the pool after the sonar equipment was removed indicated the dominance of YOY mullets within the familiar assemblage of water column fishes. This observation was consistent with quantitative long-term studies in a nearby creek. From 1983 to 2002 biweekly, low tide seine collections at a similar intertidal creek pool yielded consistently high abundances of YOY striped mullet (*Mugil cephalus*) and white mullet (*Mugil curema*) in July (combined 91%, 2.8 SE) and August (combined 91%, 3.7 SE) among the other water column fishes collected (i.e., *Menidia* spp., *Brevoortia* spp., and *Anchoa* spp.) (BMFL Data Archive: http://www.baruch.sc.edu/biological-databases). In addition, YOY mullets were similarly abundant in net collections targeting juvenile fishes for a concomitant 2012 tagging study in this and nearby intertidal creeks.

While many other pelagic species occur in much lower densities and many demersal fishes co-occur along the bottom of pools, these do not form fast-moving schools as mullets commonly do. Mullets regularly school (Thomson, 1955; Whitfield et al., 2012), and *M. cephalus* has been reported to use tidal flats and estuarine shallow banks during low tides (Thomson, 1955). In addition, rapid variations in school shape and general schooling tendency are common in this species (Thomson, 1955; Whitfield et al., 2012). Other schooling species that inhabit salt marsh creeks such as bay anchovies (*Anchoa mitchilli*), Atlantic silversides (*Menidia menidia*), and mummichogs (*Fundulus heteroclitus*) might have been present in the pool, but these were likely eliminated from the image frames analyzed by pre-

filtering all targets <5 cm^2. Sonar records of schools consisting of small fish (body size < 9 cm; Fig. 4) were also consistent with the occurrence of YOY striped and white mullets in the creeks at the time of the study. The acoustic imaging also revealed that no large predatory fish (body size > 30 cm) co-occupied the pools. Typically, low water levels deter most large predatory fish from using shallow-isolated intertidal pools (Ruiz et al., 1993; Paterson & Whitfield, 2000; Bretsch & Allen, 2006a). Our results agree with previous studies conducted in the North Inlet estuary which demonstrated a synchrony between fish habitat use and tidally driven fluctuating water levels (Bretsch & Allen, 2006a). Typically, schools of fish are not common in the lower sections of intertidal creeks around high tide. Indeed in the present study, few fish were present, and no fish schools were observed in the studied section during high tide periods when the pool was completely inundated and connected with the subtidal waters. We observed schools of juvenile mullets moving up the intertidal creek during most of the flooding tide, with no evidence that they paused at the location of the pool in the flooded creek.

This study also provides the first evidence of diel changes in the schooling behavior of fishes in salt marsh creeks. Differences in the schooling behavior of fish occupying the intertidal pool were observed between day and night. During low tides, schooling fish formed larger schools at night compared with day, suggesting that biotic and abiotic factors affecting schooling behavior in the low tide refuge may vary over the diel cycle. These factors may include activity of avian predators, presence of other nekton within the pool, or fluctuation in abiotic variables such as dissolved oxygen. Interestingly, despite variations in school size, we found that school density remained constant over the diel cycle. This result contrasts with previous studies reporting changes in school internal structure (e.g., between-fish distances, degrees of polarization and alignment between neighboring fish) in pelagic fish in response to variations in predation risk or environmental factors (Fréon et al., 1992, 1996; Soria et al., 2003; Paramo et al., 2010).

The functional significance of changes in group sizes in response to environmental conditions and predation risk has been extensively investigated in shoaling fishes (Pitcher & Parrish, 1993; Pitcher et al., 1996; Hoare et al., 2000; Krause et al., 2000; Svensson et al., 2000), depicting shoaling behavior plasticity as

an adaptive feature. Hence, variations in school sizes observed in the intertidal pool over the diel cycle may reflect adaptive responses to balancing the security benefits of grouping against the possible costs associated with refuge use. Ascertaining the real cause for shifts in schooling behavior during the diel cycle requires further investigation, but several possibilities can be considered.

Even though piscivorous fish (e.g., ladyfish *Elops saurus*, red drum *Sciaenops ocellatus*, spotted seatrout *Cynoscion nebulosus,* or bluefish *Pomatomus saltatrix*) large enough to consume small mullets do not remain in low tide pools, other small predatory fishes and crabs that occupy pools with mullets can be intimidating. It is possible that fish schooling behavior could change in response to a switch in diel activity levels of juvenile pinfish (*Lagodon rhomboides*), spot (*Leiostomus xanthurus*), silver perch (*Bairdiella chrysoura*), blue crabs (*Callinectes sapidus*), or adult striped mullet which typically co-occupy deep intertidal creek pools at low tide (Bretsch & Allen, 2006b; Allen et al., 2007). For instance, gut-content analyses of blue crabs in the Chesapeake Bay highlight a day/night pattern in crab foraging behavior, with individuals being more active at night when exposed to higher risk of predation (Ryer, 1987). In combination with the reported daily cycle in foraging activity of blue crabs, Clark et al. (1999) found a peak in agonistic behavior soon after feeding periods. Given the high sensitivity of mullets to disturbance, even non-predaceous actions of co-occupants such as blue crabs during certain periods could elicit changes in swimming and schooling behavior. Disturbance through intimidation by other animals in the pool could explain why mullet schools were larger at night.

Another explanation for the diel shift in school sizes is that aggregated fish responded to the perceived change in predation pressure exerted by avian predators between day and night. Fish in shallow waters are vulnerable to wading and diving birds. For instance, egrets and herons are often observed hunting in the salt marsh intertidal pools in the North Inlet estuary during the day (Bildstein et al., 1981; McIvor & Odum, 1988). Predation pressure from visually mediated predators is marked by a strong diel component, with the highest activity during day (Benfield & Minello, 1996). Due to higher light intensities in the pool during the day, large schools become more conspicuous against the visual background (Pitcher & Parrish, 1993), making it easier

for visually targeting predators to localize large prey aggregations than smaller ones or solitary prey (Turner & Pitcher, 1986; Pitcher & Parrish, 1993). In addition, during diurnal low tides, water turbidity increases in shallow pools and contributes to reduced ability of avian predators to spot small prey aggregations (Minello et al., 1987; Benfield & Minello, 1996; Abrahams & Kattenfeld, 1997). Water turbidity is known to reduce schooling fish survival due to an altered information transfer of predator cues among school members (Abrahams & Kattenfeld, 1997). The formation of smaller and less conspicuous schools during the day could be an adaptive strategy which relaxes schooling fish from the risk of being captured by avian predators. Predation pressure from birds has the potential to act additively to the tidal component in explaining variations in the relative value of refuge in salt marsh systems and can be important in structuring patterns of habitat selection and anti-predatory strategies of small fishes over the diel cycle (McIvor & Odum, 1988; Clark et al., 2003). To better understand how prey species retreating to intertidal pool refuge balance protection benefits toward predatory fish against metabolic costs and avian predation risk (Werner et al., 1983), studies quantifying predation rates of wading and diving birds in shallow intertidal pools are needed.

Recently, a mechanistic approach has been proposed to understand the variations in shoal size and density induced by the interplay of simple individual behavioral rules based on attraction and repulsion toward nearby fish (Katz et al., 2011) and attraction to external stimuli such as food resources (Rieucau et al., 2014c). When schooling fish are strongly motivated to feed, the relative attraction to conspecifics is expected to decrease resulting in more individualistic and exploratory behavior, leading to less dense aggregations (Robinson & Pitcher, 1989; Sogard & Olla, 1997; Hensor et al., 2003). Although little is known about their foraging periodicity, mullets forage in the bottom, scrape consumables from surfaces of submerged objects, and draw in fine materials floating at the water's surface (Whitfield et al., 2012). These opportunities exist in intertidal creek pools regardless of stage of tide or time of day. Foraging motivation probably does not account for the observed differences in schooling tendency between day and night in the intertidal creek pool.

Independent of the activities and perceived threats of other organisms to small schooling fish species, changes in environmental conditions could trigger changes in aggregative behavior. Abiotic factors can mediate nektonic migrations and habitat use (Craig & Crowder, 2000), and it can be assumed that they may also affect fish schooling behavior in intertidal pool refuges. During darkness, water temperatures and dissolved oxygen levels typically decrease in isolated intertidal creek pools, and other changes in water chemistry occur with the shift in algal metabolism from photosynthesis to respiration at night (Allen et al., 2013). Hypoxia not only has a profound effect on fish metabolism and the general level of activity (Lefrançois & Claireaux, 2003; Smith & Able, 2003) but also known to affect fish anti-predatory behavior, prey responsiveness, and vulnerability, see Shingles et al. (2005). For example, hypoxia plays a critical role on the outcome of predator–prey encounters for the striped mullet (*M. cephalus*) (see Domenici et al. (2007) for a review). Interestingly, hypoxia can also trigger acute cascading effects on fish schooling dynamics and school structure. Common responses of schools to hypoxia include an increase of school volume or greater spacing between neighboring fish (Domenici et al., 2000, 2002, 2007). Increases in individual distance can reduce the detrimental effect of oxygen depletion especially at the center of dense pelagic shoals (Dommasnes et al., 1994; Brierley & Cox, 2010). Despite the growing body of evidence presenting the role hypoxia in schooling behavior, it remains unclear how the security benefits of school formation, for example, through increased packing density (Rieucau et al., 2014b), could be mitigated by the detrimental effect of hypoxia in natural conditions (Domenici et al., 2007). In our study, no change in school internal structure (i.e., school density) was detected between day and night suggesting that nocturnal decrease in dissolved oxygen concentration in isolated intertidal creek pools may not be the primary abiotic factor mediating schooling tendency. More work is needed to adequately portray the role of recurring nocturnal physical and chemical signals on the behavior of schooling fish in salt marsh systems.

Acoustic technology represents an alternative to the traditional intrusive sampling approaches (e.g., active net gears) to collect high-quality data describing nekton size, abundance, and behavior across a wide range of temporal scales in shallow coastal waters (Boswell et al., 2007, 2008; Kimball et al., 2010; Becker et al., 2011; Becker & Suthers, 2014). Over the

years, the use of acoustics has offered a unique opportunity to monitor patterns and dynamic behavior of organisms and fine-scaled prey–predator interactions in aquatic ecosystems with no direct disturbance (Simmonds & MacLennan, 2005; Handegard et al., 2012; Becker et al., 2013; Becker & Suthers, 2014; Rieucau et al., 2014a). Yet, to further the quantitative power of the acoustic approach for time-series analysis of fish active behavioral patterns, the development of automatized individual-based tracking systems is required.

Our study only presents a snapshot of the potential behavioral and ecological processes occurring in salt marsh creeks over tidal and diel cycles. Consequently, replicating our research effort in other intertidal pools over different temporal scales is required to generalize our findings. However, this study appears to be the first attempt to describe fine scale patterns of schooling in intertidal salt marsh habitats, and it provides a foundation for future research. Our study contributes to strengthening the current knowledge about refuge use in estuarine nektonic species by providing new insight on how schooling fish adjust their behavior over the diel cycle when in a pool refuge. The functional significance of shifts in schooling tendency between nocturnal and diurnal utilization of the pool, however, still needs to be ascertained. Particular attention should be devoted at unraveling the specific role of both abiotic and biotic factors on the value of refuge creeks in salt marshes. This will help to better understand nekton migratory patterns, predator–prey interactions, and other ecosystem processes in estuaries.

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