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ORIGINAL PAPER

Swimming abilities of juvenile estuarine fishes: implications for passage at water control structures

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Abstract The capability of early life history stage fishes to access nursery habitat within managed salt marshes is dependent on their ability to negotiate water control structures (WCSs). Knowledge of swimming ability and hydrodynamic preferences is essential to assess the impact of WCSs on fish movement in managed marshes. These data, however, are lacking for many common estuarine fishes, and the utility of the data for the few species examined thus far is limited. We examined critical swimming speeds and derived linear relationships between fish size and swimming speed for juveniles of six common estuarine fish species of the southeast U.S. and northern Gulf of Mexico coasts. White mullet *Mugil curema* displayed the greatest swimming ability among these six species and was able to swim against currents $\geq$ 30 cm s^{-1} higher than the other species examined at the same size. The remaining species displayed lower critical swimming speeds and were classified into groups of moderate (pinfish *Lagodon rhomboides*, striped mullet *Mugil cephalus*) or slow (silver perch *Bairdiella chrysoura*, spotfin mojarra *Eucinostomus argenteus*, spot *Leiostomus xanthurus*) swimmers. Our results suggest that high-flow conditions at WCSs would likely preclude the passage of all but the largest juvenile fishes, and passage for most juveniles would occur under low-flow conditions; these flows at WCSs are dictated largely by site-specific tidal and weather conditions.

Keywords Critical swimming speed · Juvenile fish · Marsh management · Salt marsh · Water control structure

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Introduction

Estuaries are naturally dynamic aquatic environments, where water depth, flow direction, and flow velocity are in constant flux, however, many estuarine habitats are currently under some form of management that regulates water flow and alters natural hydrological conditions (Knudsen et al. 1985; Montague et al. 1987; Cowan et al. 1988; Robinson and Jennings 2012). Approximately 11% of marshes along the southeast U.S. Atlantic coast are under such management (Montague et al. 1987). Estimates of the extent of managed marshes are available for some states such as South Carolina (14%; Robinson and Jennings 2012 and therein) and Louisiana (10–15%; Cowan et al. 1988), but such detailed information on marsh management in other coastal states is lacking.

Fishes in these managed estuarine areas may experience unnatural hydrological conditions at critical access points. In natural, open systems, multiple life history stages of numerous fish species move between interconnected estuarine habitats for refuge, foraging, and reproduction in response to tidal, diel, and seasonal cycles (Able and Fahay 2010). Managed marshes with water control structures (WCSs), however, limit hydrological exchange, and may influence nekton movement patterns, between the managed area and the rest of the estuary (Rogers et al. 1994; Rulifson and Wall 2006; Doehring et al. 2011, Kimball et al. 2010, 2015, 2017). Fishes can avoid entrainment or swim against currents in openings through WCSs only when water velocities do not exceed their swimming capabilities. The swimming ability of fishes, particularly early life history (larval and juvenile) stages, therefore is likely an important factor affecting the distribution of fishes in managed habitats such as salt marshes.

Fish movement through structures such as dams or culverts in freshwater habitats, especially rivers, has received considerable attention (Bunt et al. 2012; Williams et al. 2012). The swimming abilities of larval and juvenile riverine fish species have been extensively evaluated (Wolter and Arlinghaus 2003), and many studies have directly examined the impact of water velocities on fish swimming abilities at fishways (e.g., Mallen-Cooper 1992, 1994; Doehring et al. 2011; Ficke et al. 2011). Hydrologic conditions around fishways in many dams, for instance, are continuously monitored for operations and management purposes, and such monitoring may be used to evaluate the success of fish passage at these structures. As a result, many fish passage structures used in rivers have been designed and tested for effectiveness and passage efficiency for a variety of targeted species (Bunt et al. 2012).

The opportunity to assess potential impacts of the hydrodynamics associated with WCSs on fish movement within estuaries, in contrast, is limited. Such efforts require (1) a census of the type and number of WCSs in operation in managed salt marshes, (2) water velocity data collected at openings in WCSs throughout the tidal cycle, and (3) knowledge of the swimming ability and hydrodynamic preferences of estuarine fishes (Doehring et al. 2011; Williams et al. 2012), all of which are lacking. We are aware of no comprehensive catalogue of the various WCSs currently in operation at statewide or regional scales. Detailed information is sometimes available for marsh management projects in specific estuaries, but it often must be gleaned from construction documents and agency reports that are difficult to obtain (e.g., the Cameron-Creole Watershed Project at Calcasieu Lake; see Kimball et al. 2015, 2017). Little is known about water velocities at the various types of WCSs used in estuaries, as water velocity is not often regularly (or continuously) monitored at these structures. Some studies examining fish passage at WCSs include measurements of water velocity, but usually this variable is examined only infrequently during the study period (e.g., Rulifson and Wall 2006; Stevens 2006; Kimball et al. 2010, 2015; Eberhardt et al. 2011). The literature on the swimming ability of estuarine fishes of the southeastern US is sparse. Swimming ability has been examined in the context of transport and settlement of early life history stages of fishes in estuarine nursery habitats (e.g., Wuenschel and Able 2008; Faria et al. 2009). Studies have focused on the swimming ability of juvenile stages of common estuarine species such as striped mullet *Mugil cephalus*, spot *Leiostomus xanthurus*, Atlantic menhaden *Brevoortia tyrannus*, Atlantic silverside *Menidia menidia*, and pinfish *Lagodon rhomboides* (Hettler 1977; Rulifson 1977; Hartwell and Otto 1978, 1991; Mitchell 1989; Nanami 2007). The utility of these studies on juvenile fishes is limited, however, as the methods used to evaluate swimming differed greatly among studies, and these studies often reported only means or ranges in fish size or swimming speed rather than data for individuals. This inconsistency in sampling techniques and limitations in these data preclude using these studies to determine relationships between fish size and swimming ability and makes comparisons among studies and extrapolation among species difficult.

As a first step to better understand fish behavior around WCSs and evaluate potential impacts of the hydrodynamics associated with WCSs on early life stage fish movement within estuaries, we examined the critical swimming speed of juveniles of abundant and widespread estuarine fish species and provide essential information on their swimming ability. Swim speeds were estimated using an adjustable laboratory swim tunnel capable of simulating natural water flow conditions. The swimming capability of fishes is generally related to fish length (size), and critical swimming speed increases with fish length (Wakeman and Wohlshlag 1982; Wolter and Arlinghaus 2003; Fisher et al. 2005). Therefore, by including a range of sizes for each species in our swimming trials, we acquired accurate estimates of relationships between swimming speed and size for juveniles of the target species.

Materials and methods

Fishes were collected for swimming trials using small mesh (< 1 cm) seines and cast nets deployed in shallow (< 1 m deep) tidal creeks of the North Inlet estuary, Georgetown County, South Carolina, USA (33 20 00.08, − 79 11 11.01). Both of these gear types allowed us to effectively, rapidly, and gently capture a variety of juvenile fishes that commonly occur in estuarine habitats. Ubiquitous salt marsh fishes were targeted: silver perch, spotfin mojarra *Eucinostomus argenteus*, pinfish, spot, striped mullet, white mullet *Mugil curema*, Atlantic menhaden, ladyfish *Elops saurus*, and tarpon *Megalops atlanticus*. Target species were examined during their period of residency in the estuary, which varied by species. We selected juvenile fishes 20–100 mm total length (TL) for these trials. We attempted to examine ~ 10 individuals from each 10-cm length increment (e.g., 20–29, 30–39 mm, up to 90–99 mm TL) within this range to include a broad array of sizes for each species.

We determined the swimming ability of these juvenile fishes following critical swimming speed (U_{crit}) methodology, first introduced by Brett (1964) and considered a good estimate of swimming performance capability (Plaut 2001). This method is well suited for comparing swimming abilities among taxa because of its frequently-used, standardized methodology (Underwood et al. 2014). All critical swimming speed trials were conducted using a 5 L Swim Tunnel (Loligo Systems; www.loligosystems.com) at the University of South Carolina's Baruch Marine Field Laboratory from April 2014 through July 2015.

Fishes were collected from the estuary and housed in aerated tubs overnight (minimum 12 h) before beginning swim speed trials. Ambient seawater was used for housing fishes and conducting experiments to ensure fishes experienced similar water quality during the period (~ 24 h) from capture to release. Temperature (°C), salinity, and dissolved oxygen (mg L^{-1}) in the swim tunnel were measured once for each individual fish (e.g., trial) with a YSI Model 85 handheld meter (Yellow Springs Instruments). Turbidity was not measured, but we used clear ambient seawater in all trials. All fishes were swum individually and only for a single experimental trial. Prior to the start of each trial, an individual fish was placed in the 30 cm × 7 cm × 5 cm test section of the swim tunnel and allowed to acclimate 3 min at low flow rates (≤ 5 cm s^{-1}). After this acclimation period, the trial was initiated and water velocity was incrementally increased by 5 cm s^{-1} every 3 min until the fish no longer maintained position in the swim tunnel and became impinged on the rear screen. The velocity and time (min:s) spent in the final velocity increment were recorded. After exhaustion, individuals were removed from the swim tunnel, measured (mm TL), returned to an aerated holding tank, and later released back into the wild.

Critical swimming speed (U_{crit}) for each individual fish was calculated using these data and the equation from Brett (1964), which is:

$$U_{crit} = U + (T/T_i \times U_i)$$

where U is the penultimate speed, U_i is the velocity increment (5 cm s^{-1}), T is the time swum in the final velocity increment, and T_i is the set time interval for each velocity increment (3 min).

We used linear regressions to examine the relationship between swimming ability, U_{crit} (in absolute terms; cm s^{-1}), and fish length (mm TL) for six primary species (*B. chrysoura*, *E. argenteus*, *L. rhomboides*, *L. xanthurus*, *M. cephalus*, and *M. curema*). In addition, an Analysis of Covariance (ANCOVA) was used for these six species to examine differences in the slopes and intercepts of the swimming ability—size relationships among species. When significant effects in slope or intercept were detected in this analysis, we used Tukey–Kramer tests to compare differences among species. Too few individuals ($n \leq 10$) of three species (*B. tyrannus*, *E. saurus*, *M. atlanticus*) were collected and available for swimming trials to obtain accurate relationships; thus we report only mean U_{crit} values (with standard error) and size range for these species. All statistical analyses were conducted using SigmaPlot v12.5 (Systat Software Inc., San Jose, CA, USA) and SAS v9.4 (SAS Institute Inc., Cary, NC, USA).

Results

Swimming trials were conducted under similar water quality conditions for all the species included in our study (Table 1). The high salinity values (> 30) we recorded reflect the ocean-dominated conditions typical of the North Inlet estuary during the period (April–October) these swimming trials took place.

Regardless of species, all fishes used in the swimming trials displayed similar behavior during the critical swimming speed experiments. They often appeared startled and swiftly swam around the inside of the entire test section for a brief period (< 30 s) when initially placed into the swim tunnel. By the end of the 3-min acclimation period, most individuals were oriented into the current, moving only slightly, and positioned at the rear of the test section near the bottom. When exposed to low water velocities, fishes were observed swimming slowly (low tailbeat frequencies) in the middle of the test section, often near the bottom or in the water column. As water velocities were increased, individuals swam more rapidly (high tailbeat frequencies) and positioned themselves at the front of the test section and higher in the water column. At water velocities near the limit of their swimming ability, they were no longer able to maintain their position at the front of the test section and slowly began to lose ground and move closer to the rear screen at the end of the test section, at which point they would burst forward and return to the earlier position in the front of the test section. This cycle would continue until water velocities increased to levels where individuals could only maintain a position immediately in front of the rear screen at the back of the test section. After a relatively brief period, these individuals would become impinged on the screen, and the trial would end.

A total of 386 individuals of the six primary species was tested in the swimming trials (Fig. 1, Table 2). All six species displayed significant positive linear relationships between fish size and critical swimming speed (all slopes not equal to zero; $p \leq 0.0002$). Analysis of Covariance did not detect a significant difference among the slopes for these six species ($p = 0.0686$); therefore a common slope model was fitted to the data (Table 3). The common slope (0.7981) was significantly different from zero ($p < 0.0001$), and the differences among the regression lines (i.e., the intercepts) were significantly different ($p < 0.0001$). At any given size, *M. curema* had greater swimming abilities than the other species examined (all Tukey–Kramer tests $p < 0.0001$). The remaining five species had significantly different ($p < 0.05$) swimming abilities with a few exceptions. The swimming ability of *B. chrysoura* was similar to that of *E. argenteus* ($p = 0.9900$) and *L. xanthurus* ($p = 0.1708$). *Mugil cephalus* and *L. rhomboides* had similar swimming abilities to one another ($p = 0.7443$). The swimming ability of *E. argenteus*

Table 1 Mean and one standard error (in parentheses) for temperature, salinity, and dissolved oxygen recorded in the swim tunnel for each individual (N) used in swimming trials for each species

Species	N	Temperature (°C)	Salinity	D.O. (mg L^{-1})	Months
Bairdiella chrysoura	50	23.2 (0.2)	32.7 (0.2)	7.0 (0.1)	Jun–Sep
Brevoortia tyrannus	10	23.3 (0.0)	35.3 (0.1)	7.7 (0.0)	Jun
Elops saurus	6	23.8 (0.0)	35.7 (0.0)	7.1 (0.0)	Jul
Eucinostomus argenteus	51	23.1 (0.1)	33.4 (0.1)	7.1 (0.1)	Jul–Oct
Lagodon rhomboides	87	23.5 (0.1)	32.1 (0.2)	7.2 (0.1)	May–Sep
Leiostomus xanthurus	89	22.9 (0.2)	31.4 (0.3)	7.4 (0.1)	Apr–Oct
Megalops atlanticus	10	23.4 (0.0)	32.6 (0.0)	6.8 (0.1)	Aug–Sep
Mugil cephalus	49	23.8 (0.1)	33.2 (0.3)	7.8 (0.1)	May–Oct
Mugil curema	60	23.7 (0.1)	33.8 (0.3)	7.6 (0.1)	May–Oct

The months during the study period when individuals were collected and trials took place are also indicated for each species

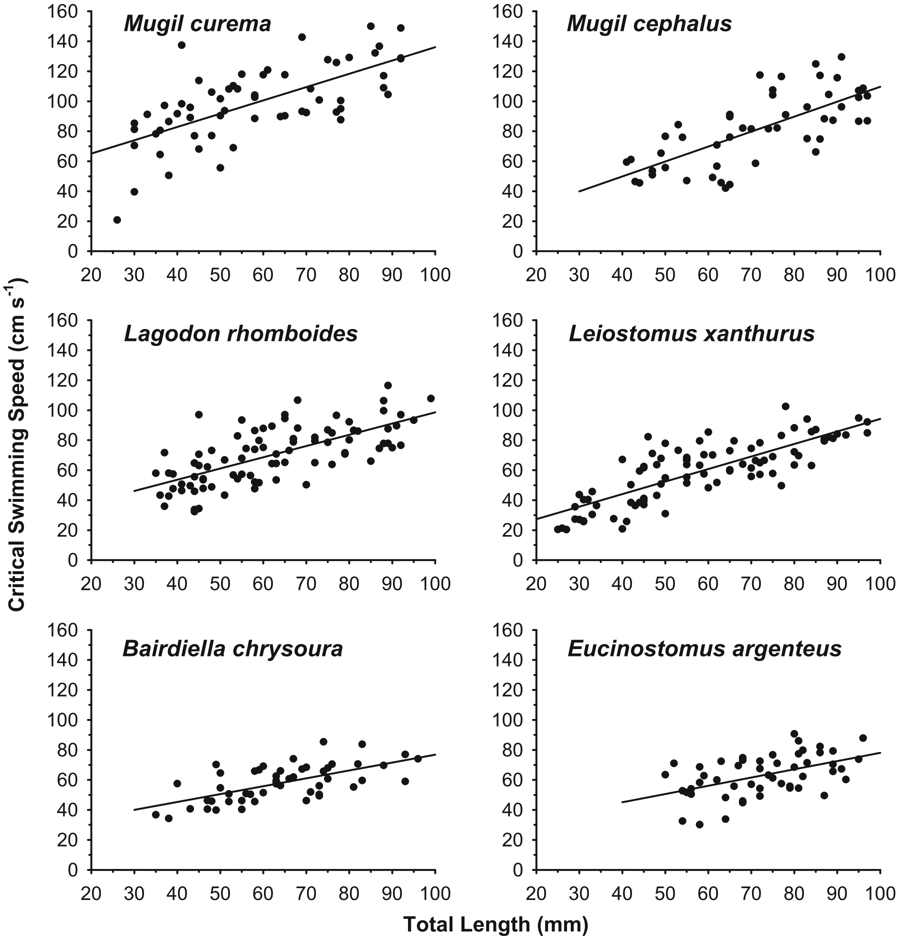

Fig. 1 Relationship between critical swimming speed (cm s^{-1}) and total length (mm) for juveniles (20–100 mm total length) of six species of estuarine fish

Table 2 Linear relationship between critical swimming speed (cm s^{-1}; U_{crit}) and total length (mm) for juveniles of six species of estuarine fish

Species	N	Size range (mm TL)	Relationship	R^2
Bairdiella chrysoura	50	35–96	$U_{crit} = 24.2747 + 0.5253$ (mm TL)	0.4027
Eucinostomus argenteus	51	50–96	$U_{crit} = 23.1551 + 0.5487$ (mm TL)	0.2473
Lagodon rhomboides	87	35–99	$U_{crit} = 23.6901 + 0.7490$ (mm TL)	0.4687
Leiostomus xanthurus	89	25–97	$U_{crit} = 10.6299 + 0.8355$ (mm TL)	0.6521
Mugil cephalus	49	41–97	$U_{crit} = 9.9380 + 0.9976$ (mm TL)	0.5006
Mugil curema	60	26–92	$U_{crit} = 47.4233 + 0.8863$ (mm TL)	0.4481

The number of fish tested (N), size range (mm TL), and R^2 of the relationship also are provided

was significantly different from that of *L. xanthurus* ($p = 0.0331$), although absolute swimming speeds of these two species were comparable.

A total of 26 *B. tyrannus*, *E. saurus*, and *M. atlanticus* individuals also were tested in swimming trials (Table 4). Some individuals of these three species were identified as nonperformers; they refused, or were reluctant, to swim, or did not respond well to being confined in the swim chamber (e.g., swam frenetically trying to escape), which is not

Table 3 Analysis of covariance (ANCOVA) results to fit a common slope model for the six species of estuarine fish: U_{crit} = Intercept + 0.7981 (mm TL)

Species	Intercept estimates	Standard error
Bairdiella chrysoura	6.7798	3.40
Eucinostomus argenteus	5.0081	3.68
Lagodon rhomboides	20.6354	3.06
Leiostomus xanthurus	12.8197	2.91
Mugil cephalus	24.1982	3.66
Mugil curema	52.5520	3.09

uncommon behavior in swimming speed studies (Ficke et al. 2011). These nonperformers were excluded from our analysis. Therefore, we were able to examine the swimming ability of only a small number and limited size range of these species.

Discussion

The swimming abilities of the primary targeted estuarine fishes, determined through examination of critical swimming speeds (U_{crit}), varied greatly among species. *Mugil curema* displayed the greatest swimming ability and was able to swim against currents ≥ 30 cm s^{-1} higher than the other species examined at the same size. The remaining five species displayed lower critical swimming speeds at a given size, and could be further divided into groups of moderate (*L. rhomboides*, *M. cephalus*) and slow (*B. chrysoura*, *E. argenteus*, *L. xanthurus*) swimmers. For example, using the common slope model (Table 3) at a size of 50 mm TL, *M. curema* had a U_{crit} of 93 cm s^{-1}, the mean U_{crit} of the moderate group was 62 cm s^{-1}, and the slow group had a mean U_{crit} of 48 cm s^{-1}. At larger sizes (e.g., 80 mm TL), the U_{crit} values for these three groups were 116, 86, and 72 cm s^{-1}, respectively.

Despite being ecologically and morphometrically similar, the swimming abilities of *M. cephalus* differed greatly from *M. curema*. The two species commonly co-occur in a variety of estuarine habitats as juveniles and have similar diets (see review by Whitfield et al. 2012), but to date no life history trait or ecological context has been identified to explain this difference in swimming ability. Four previous studies reported on swimming performance of *M. cephalus*, and despite differences in methodologies, two of these reported swimming speeds for this species (51 cm s^{-1}, Rulifson 1977; 46 cm s^{-1}, Hettler 1977) similar to our study (50 cm s^{-1}, using the linear regression); one estimated a somewhat greater speed (64 cm s^{-1}, Nanami 2007) for individuals 40 mm TL in size, but all three studies classified *M. cephalus* as a moderate swimmer. Mitchell (1989) reported a much slower swimming speed (20 cm s^{-1}) for *M. cephalus* of this size (40 mm TL), but this result appears to be an outlier.

In comparisons of similar sized individuals of *L. xanthurus*, earlier estimates of swimming speeds were lower (38 cm s^{-1}, Rulifson 1977), even by almost half (23 cm s^{-1}, Hettler 1977) of our estimate (44 cm s^{-1}, using the linear regression); all these results, however, are consistent in grouping this species as a slow swimmer. Although we considered *L. rhomboides* a moderate swimmer, individuals (40 mm TL) included in earlier studies were reported to have lower swimming speeds (38 cm s^{-1}, Rulifson 1977; 43 cm s^{-1} Hettler 1977) than our estimate (54 cm s^{-1}, using the linear regression). Taken together, these results suggest that this species may be on the slower end of the moderate group. The general agreement of these earlier studies with our results supports the utility of the linear relationships between fish size and swimming speed derived herein (both the linear regressions for individual species and the common slopes model) for future work.

Table 4 Mean, one standard error (in parentheses), and range of size and critical swimming speed (cm s^{-1}; U_{crit}) for juveniles of three species of estuarine fishes

Species	N	Size (mm TL)		U_{crit} (cm s^{-1})	
		Mean (SE)	Range	Mean (SE)	Range
Brevoortia tyrannus	10	49 (2.1)	40–65	61.5 (4.9)	32.3–80.3
Elops saurus	6	112 (6.5)	95–135	48.8 (4.0)	37.6–61.6
Megalops atlanticus	10	85 (5.1)	63–106	31.5 (2.1)	20.7–40.6

The swimming performance of the primary species included in our study could be used to represent (or estimate) the swimming abilities of juveniles of similar benthic-oriented or water column-oriented species of similar size occurring in estuaries, but this should be done with caution. This approach would be especially useful when trying to estimate the swimming abilities of species that do not respond well to handling stress and transport from field sites (e.g., *B. tyrannus*) or those species that do not perform in the artificial conditions presented in swim chambers (e.g., *E. saurus*, and *M. atlanticus*). For example, there was no consensus regarding *B. tyrannus* swimming performance, as our coarse estimate (mean = 62 cm s^{-1}) was between earlier estimates of 88 cm s^{-1} (Hartwell and Otto 1978) and 46 cm s^{-1} (Hettler 1977) for individuals ~ 50 mm TL. The differences we documented between *M. curema* and *M. cephalus* show that even closely related species of similar shape can vary significantly in swimming performance. Therefore, fish morphology may not always correlate well with swimming ability.

The fishes targeted in our study are commonly found in managed marshes and around WCSs in US Atlantic (McGovern and Wenner 1990; Robinson and Jennings 2014) and northern Gulf of Mexico (Herke et al. 1992; Kimball et al. 2010, 2015, 2017) estuaries. Based on the limited water velocity information collected at WCSs in managed marshes, it appears that early life history stages of these species may be negatively impacted by flow conditions in and around WCSs, at least some of the time. Water velocities at these structures, which are driven by tidal conditions, vary from almost no flow to velocities $\geq$ 100 cm s^{-1} (e.g., Rulifson and Wall 2006; Teodosio and Garel 2015; Wright et al. 2016) or $\geq$ 150 cm s^{-1} (e.g., Stevens 2006; Eberhardt et al. 2011) observed at some WCSs. Considering the swimming performances observed in our study, and that some fishes swim against the current when transiting openings through WCSs (Kimball et al. 2010, 2015, 2017), these higher flow conditions would preclude passage for all but the largest juveniles of these species. Our results suggest that openings in WCSs purported to facilitate fish passage may only do so under low-flow conditions of limited duration; such favorable conditions for fish passage would be dictated largely by site-specific tidal and weather conditions. Further complicating this issue, because fishes often delay passage or display milling or congregating behavior at a structure prior to transiting the opening, even when individuals are physically capable of swimming through openings in a structure (e.g., openings are sufficiently sized and velocities are favorable), flow conditions may be just one aspect influencing a fish's behavioral response to encountering WCSs in salt marshes (Wright et al. 2016; Kimball et al. 2017). Predation may also be a factor at WCSs because large piscivorous predators frequent these structures, which provide ambush sites, and milling fishes may be especially vulnerable to predators (Kimball et al. 2015, 2017). Together with documenting the swimming ability of other estuarine fishes, future research should aim to document and understand the complex hydrodynamics associated with WCSs typically used in managed marsh systems. The possible effects of turbidity and predation on successful passage at these structures also requires attention. Collectively, this information would likely contribute to more effective and efficient design, operation, and management of WCSs in salt marshes and help mitigate the impact of marsh management practices on fishery resources.

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