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Abstract

Water control structures (WCSs) restrict hydrological connectivity in salt marshes and thereby impede nekton movement within the greater habitat mosaic. Transient fishery species, which spawn outside salt marshes and must get past these barriers to reach spawning areas or salt-marsh nurseries, are especially vulnerable to these structures. Water control structures incorporating slots (narrow vertical openings spanning most of the water column) are thought to improve nekton passage; however, few studies have directly examined nekton passage through WCS slots. Dual-frequency identification sonar (DIDSON) acoustic imaging was used monthly (April–September 2010) on diurnal flood tides to examine nekton movement through 15-cm-wide slots at two identical WCSs located in Louisiana tidal marsh channels. Nekton behavior was compared between these WCSs and a nearby natural salt-marsh creek. Examination of 12 h of subsampled acoustic data revealed large concentrations of salt-marsh nekton at the WCSs ($n = 2{,}970$ individuals total), but passage rates through the slots were low ($\leq 10\%$ of total observed individuals migrated via the slots). Most migrating fish were observed leaving the managed area and swimming against a flood tide. The mean size of migrating individuals (~ 25 cm TL) did not differ in relation to swimming direction (going into versus exiting the managed marsh) and was similar to that reported from other studies examining similar slot widths. Nekton formed congregations in the WCS channel, but no congregations were observed in the natural salt-marsh creek, even though nekton species composition and sizes were similar among sites. The WCSs in our study appear to function as ecological hot spots, where large individuals may encounter enhanced foraging opportunities but also fishing mortality and where smaller individuals may experience greater predation rates.

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Salt-marsh habitats serve as critical nursery areas for numerous fish and natant invertebrate species (nekton), including early life history stages. The value of these nurseries depends on the degree of hydrological connectivity with marine spawning areas (Rozas et al. 2013) and the greater mosaic of integral habitats within coastal and estuarine ecosystems (Peterson 2003; Able 2005; Sheaves 2009). Nekton movement through this habitat mosaic—at both small and large spatial and temporal scales—provides an important pathway for the transfer of energy and nutrients among habitats (Kneib 2000; Allen et al. 2013). Movement of nekton between salt marshes and coastal/ocean habitats (i.e., immigration and emigration) provides an important pathway for the trophic transfer of marsh production to the wider estuary and coastal waters (Weinstein et al. 2000). Much of this production supports valuable coastal fisheries (Deegan et al. 2000). Because nekton usage of habitats is largely species specific and varies according to physical and biological factors (Hoese and Moore 1998; Able and Fahay 2010), the unhindered ability of nekton, particularly juveniles, to locate and use suitable estuarine habitat during critical life history stages will determine their success in reaching adulthood.

Many estuaries are degraded and losing critical habitat due to natural and anthropogenic factors (Peterson and Lowe 2009; Kirwan and Megonigal 2013). Conversion of marsh to open water, erosion of marsh edge habitat, and loss (or drastic reduction) of intertidal and subtidal biogenic reefs all potentially alter the function of estuarine ecosystems for plants and animals alike (e.g., Anthony et al. 2009; Peterson and Lowe 2009). Structural marsh management, which incorporates a combination of levees and water control structures (WCSs) to control marsh hydrology, has often been implemented to mitigate such losses and stabilize marsh habitats (Montague et al. 1987; Rogers et al. 1992). Commonly used WCSs include fixed-crest or variable-crest weirs, gated types, and slotted types (Rogers et al. 1994). By regulating water levels, structural marsh management can establish stable hydrological regimes in the managed area but also may restrict life history connectivity by impeding nekton movement (Rogers et al. 1994; Secor and Rooker 2005; Sheaves 2009). Reduced access from WCSs for transient nekton that must migrate to estuarine nursery habitat from nearshore and offshore spawning areas could negatively affect their recruitment into salt marshes during early life history stages and could subsequently limit the emigration of older juveniles or adults to other coastal habitat types.

Water control structures incorporating slots (narrow vertical openings spanning most of the water column) are thought to improve nekton passage (Herke et al. 1992; Rogers et al. 1992; Rulifson and Wall 2006). Importantly, because slots extend the full height of the WCS and permit flow throughout the water column (when open), they may facilitate passage of the entire nekton assemblage rather than only some species. In riverine systems, vertical slots incorporated into dam fishways

were found to improve passage (Stuart and Mallen-Cooper 1999; Stuart and Berghuis 2002) and provided access for a large portion of the riverine nekton community (Baumgartner et al. 2010, 2012; Thiem et al. 2013).

Most studies comparing managed and unmanaged salt marshes show that transient species are less abundant in managed areas (Knudsen et al. 1989; McGovern and Wenner 1990; Herke et al. 1992, 1996; Rozas and Minello 1999) and suggest that nekton movement into managed areas is restricted by WCSs. Few studies, however, have directly examined salt-marsh nekton passage through WCSs of any type because collecting unbiased data at these structures is a challenge (Rogers et al. 1994; Hoese and Konikoff 1995). For example, traps and nets may alter nekton behavior by interfering with any back-and-forth movement patterns (assuming general undirected movement). Research opportunities also have been limited by an inability to alter the operation of WCSs or manipulate structure designs and by a lack of replication (i.e., identical WCSs within the same marsh system). Consequently, only three studies have directly examined nekton passage through WCS slots in salt marshes. Rogers et al. (1992) and Rulifson and Wall (2006) used traps to compare unidirectional movement of nekton through WCSs with and without slots. During a prior study within the Breton Sound estuary, southeastern Louisiana, we (Kimball et al. 2010) used high-resolution acoustic imaging to examine the effect of WCS slot width on nekton bidirectional movement, providing unique information on fishes that migrated through the slots as well as those that did not; obtaining such information is not possible with traditional direct-capture techniques. Examining the set of individuals that migrate and the set of individuals that do not provides the context necessary to estimate nekton passage efficiency at a given WCS. Although passage efficiency for riverine nekton at structures has received considerable attention (see recent reviews by Roscoe and Hinch 2010; Bunt et al. 2012; and Noonan et al. 2012), information on salt-marsh nekton passage efficiency is nearly absent from the literature (but see Kimball et al. 2010).

Many marshes along the U.S. Gulf of Mexico and Atlantic coasts are currently under some form of structural marsh management (Knudsen et al. 1985; Montague et al. 1987; Cowan et al. 1988; Robinson and Jennings 2012). Due to the importance of such habitats for numerous fishery species, a better understanding of the impacts of WCSs on nekton movement patterns is critical. Such information may help managers improve the design and operation of WCSs to facilitate rather than impair nekton use of salt marshes. Furthermore, efforts to model the impact of reduced hydrological connectivity (i.e., via WCSs) on salt-marsh nekton population dynamics would also likely benefit from such insights (e.g., Neary 2012; Williams et al. 2012).

In an earlier study examining nekton passage through WCS slots, we (Kimball et al. 2010) used acoustic imaging to overcome the limitations of sampling gear that interfere

with nekton movement. Others have also demonstrated the advantages of using this technique (Doehring et al. 2011; Grote et al. 2014). In the present study, we take the next step by incorporating replication and a control in the study design and by using imaging sonar (dual-frequency identification sonar [DIDSON]) to examine nekton movement and behavior at WCS slots. We estimated nekton passage rates through slots by sampling nekton during flood tides at two identical WCSs in a single estuarine system of Louisiana. We also compared the abundance and size of nekton in congregations at these WCSs with those of nekton in a comparable sample volume of an adjacent natural salt-marsh creek (i.e., control) within the same system.

METHODS

Study site.—Our study focused on two WCSs (replicates) and a natural salt-marsh creek (control) located in the southeastern portion of the Calcasieu Lake estuary, Louisiana

(Figure 1). The Mangrove Bayou WCS (29°53′37.36″N, 93°13′52.44″W) and the No-Name Bayou WCS (29°50′17.36″N, 93°19′14.06″W) are identical fixed-crest structures. Each WCS consists of four bays (each 2.4 m wide) with a fixed-crest height of 1.4 m (Figure 2). The far-left bay (as viewed from the managed marsh; see Figure 2) contains three vertical slots (0.15 m wide × 1.2 m high). The remaining three bays have no openings. The WCSs are recessed from the lake shoreline in small canals and are positioned perpendicular to the channel. Canals are about 21 m wide at the WCSs and are lined with rip-rap within 10 m and on both sides of each structure (creating a uniform channel profile). Both WCSs control water exchange between the salt marsh and Calcasieu Lake; during our study, the slots remained fully opened. The natural salt-marsh creek site (hereafter, "marsh creek";
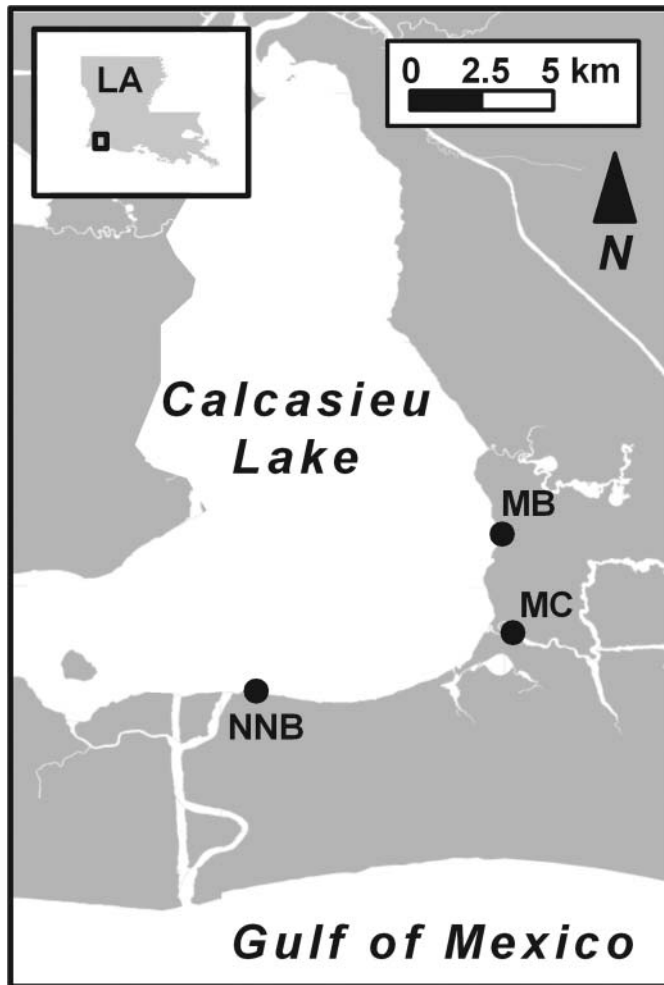
FIGURE 1. Locations of the Mangrove Bayou (MB) and No-Name Bayou (NNB) water control structures and the salt-marsh creek (MC) sample site in the Calcasieu Lake estuary, southwestern Louisiana.
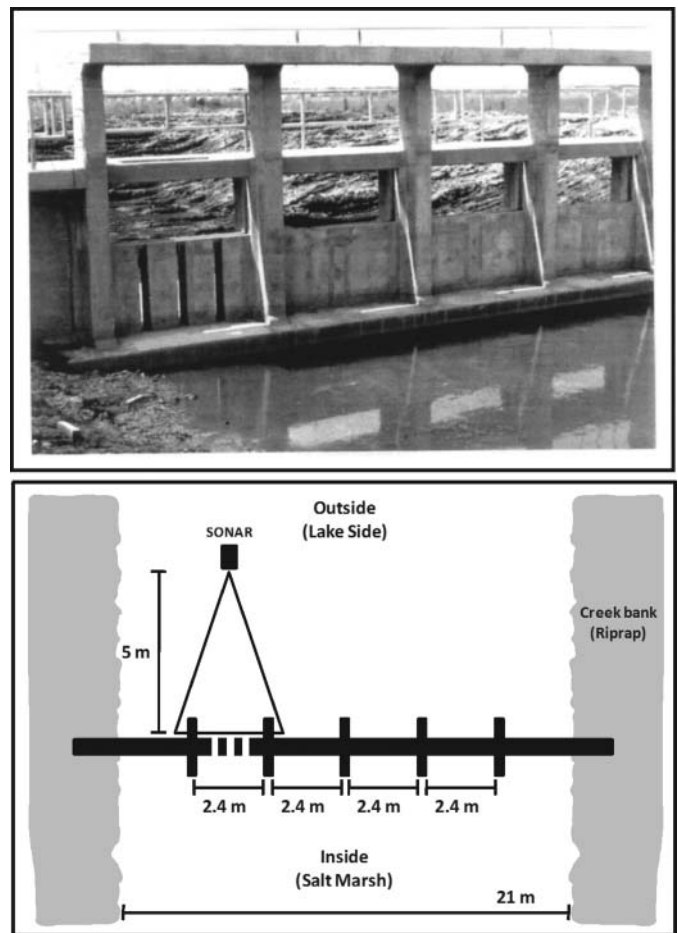
FIGURE 2. Top panel: dewatered view of the No-Name Bayou water control structure (WCS) as seen from the managed marsh (inside), showing the four bays (each 2.4 m wide, with a fixed-crest height of 1.4 m; photo courtesy of Cameron Prairie National Wildlife Refuge, Bell City, Louisiana). The far-left bay contains three vertical slots (0.15 m wide × 1.2 m high). The remaining three bays have no openings. Bottom panel: overhead diagram of the field sampling setup at each WCS, showing the placement of the platform-mounted dual-frequency identification sonar in front of the slotted bay on the lake side (outside).

29°51′33.85″N, 93°13′51.27″W) is located in the managed marsh. The creek at this site is about 25 m wide, with a soft-sediment substrate. The three study sites differed in their approximate water distance from the Gulf of Mexico (Mangrove Bayou WCS: 21.5 km; No-Name Bayou WCS: 10.4 km; marsh creek: 21.4 km).

Field sampling.—Nekton movement through the WCS slots and in the marsh creek was examined during daytime flood tides monthly in April–September 2010 by using a Sound Metrics DIDSON imaging sonar (www.soundmetrics.com). Limiting our observations to flood tides allowed us to focus on nekton movement from Calcasieu Lake into the managed marsh; in addition, our earlier work showed that nekton passage rates peaked during flood tides (Kimball et al. 2010). The DIDSON collects high-resolution acoustic images (4–21 frames/s) and permits sampling in turbid waters and at night. We used the high-frequency mode (1.8 MHz), which uses 96 beams (0.3° horizontal [H] × 14° vertical [V]) resulting in a total field of view of 29° H × 14° V (see Boswell et al. 2008); this mode is most appropriate for collecting high-resolution data at short ranges (<12 m). The DIDSON was mounted on an adjustable platform, which provided a stable yet portable platform suitable for horizontally aimed acoustic monitoring in shallow (~2 m) estuarine habitats (described by Boswell et al. 2007). The platform-mounted DIDSON was adjusted so as to place the sonar in the center of the water column, and the platform was positioned about 5 m from the slots in the lakeside canal. This position optimized data quality, as it minimized the potentially confounding effect of introducing structure immediately in front of the slot opening, yet it still permitted a view of the entire water column at the slots. For the marsh creek, the platform-mounted DIDSON was also centered in the water column and positioned to acquire a similar field of view (i.e., 5-m viewing range, aimed with the flow of water). Once properly positioned, the platform-mounted DIDSON was left in place to continuously record for 4 h during each daytime flood tide sampling period at each site. Power supply and data acquisition were controlled from the walking platform on top of each WCS (Figure 2) or from the creek bank at the marsh creek site, where the DIDSON interfaced with a laptop computer for real-time viewing and data storage.

Acoustic sampling was supplemented with traditional sampling gears—cast nets to target small individuals (<20 cm) and gill nets for targeting large individuals (>20 cm)—to catalog species presence and migration periods in the study area. Cast nets (4.8-mm monofilament mesh; 2.4-m radius) were used to sample nekton in the canal at each WCS, on both sides (i.e., within 5 m of the WCS in the managed and open marshes), and both upstream and downstream of the DIDSON at the marsh creek (i.e., at the shoreline adjacent to the sonar; and 30 and 60 m upstream and downstream). For each flood tide sampling period, casts (n = 2) were thrown at each station. A single cast at each WCS was missed in April, so the resulting total of 46 casts is slightly less than the balanced total of 48. All 60 casts were collected at the marsh creek. Gill nets (multiple panels of 25-, 51-, and 76-mm monofilament mesh; 1.8 m deep × 15.5 m long) were used to sample nekton at a single location near each WCS (about 10–30 m away; n = 12 sets total). At the marsh creek, gill nets (n = 12 sets total) were set diagonally across the creek and were deployed both upstream and downstream of (about 10–30 m away from) the DIDSON. At each location, gill nets were set for 0.5 h once during each flood tide sampling period.

Environmental and physical variables were measured once during each flood tide in the canal near each WCS and at the platform-mounted DIDSON in the marsh creek. Temperature (°C), salinity, and dissolved oxygen (mg/L) were measured at the surface with a YSI Model 85 handheld meter (Yellow Springs Instruments). Samples were collected at the surface once during flood tide and were analyzed for turbidity (NTU) in the laboratory by using a MicroTPW turbidimeter (HF Scientific). Center-channel water depth (m) was measured on both sides of each WCS every 15 min continuously throughout each sampling period with a HOBO water level logger (Onset Computer), and these data were used to determine maximum and minimum center-channel depths during each flood tide sampling period. Due to the uniform bottom profile of the channel, center-channel water depth was representative of the water depth across the channel in front of the WCSs (on both sides). Water depth at the slots, which was measured from the base of each structure (Figure 2), was about 0.5 m less than the center-channel depth. Center-channel water depth (m) in the marsh creek was measured similarly by using a HOBO water level logger located adjacent to the platform-mounted DIDSON.

Water velocity (m/s) at each site was measured with an Aquadopp (right-angle head) acoustic Doppler current profiler (Nortek USA) in October 2010 to examine potential effects on nekton movement. Sampling of flood tide water velocities was performed in October soon after the completion of nekton sampling so as to avoid possible interference between the DIDSON and the current profiler (e.g., acoustic interference from the profiler near the slots). At the WCSs, the profiler was mounted on the underside of a float on the water's surface and was positioned in the open (lakeside) canal with fixed cables about 2.5 m directly in front of the slots. In this position, the profiler measured water velocities at about 10-cm depth intervals throughout the water column every 5 min for a 1-h period. The float-mounted profiler was positioned in the marsh creek at approximately the same channel position where DIDSON sampling occurred, and velocities were measured by the same methods used for the WCSs.

Data analysis.—The DIDSON data for each 4-h flood tide sampling period were divided into two 2-h blocks. The data were then subsampled by randomly selecting six 5-min segments from the total of twenty-four 5-min segments in each 2-h block. Thus, each flood tide sampling period at each site yielded a combined 1 h (twelve 5-min segments) of DIDSON data for

analysis (total = 3 sites × 6 months = 18 h of subsampled data). Randomly selecting six 5-min segments from each 2-h block made it more likely that the subsampled data would represent the full span of the 4-h sampling period and lessened the possibility of selecting only segments clustered around a single point in time. Subsampled DIDSON data were analyzed by using the Sound Metrics DIDSON software (version 5.25.41). Output data from DIDSON analyses for each flood tide at each WCS were classified into two categories: migrating individuals and congregating individuals. Migrating individuals were defined as nekton that swam through the WCS slots. All 12 h of subsampled data from the WCSs were examined for migrating individuals. Congregating individuals were defined as those that were observed in front of the WCS but did not swim through the slots. Because congregating individuals were relatively abundant and to reduce the possibility of counting individuals multiple times, we randomly selected and examined 12 frames (one from each 5-min segment) for each hour of subsampled data from both WCSs ($n = 144$ frames total). For migrating individuals, the number of individuals and length (TL, cm) of each individual observed per 5-min segment were recorded. For congregating individuals, we recorded the number of individuals and length of each individual observed per frame. Swimming direction (i.e., going into the managed marsh or coming from the managed marsh) was determined for each migrant observed at the WCSs. We also calculated an estimate of the relative percentage of migrants at each WCS during each flood tide as follows: (number of migrating individuals per 5-min segment)/(number of congregating individuals per frame). We examined the subsampled data from the marsh creek ($n = 72$ frames) by following the protocol used for congregating individuals at WCSs; this allowed us to compare the number and size of individuals congregating at each WCS with the number and size of individuals from a natural salt-marsh creek of similar physical characteristics.

Statistical analyses.—Each randomly selected acoustic data unit (i.e., 5-min segment; or frame) was treated as an independent sample in our analyses, in conformance with the procedures used by Kimball et al. (2010). Migrant abundance and relative percentage data were analyzed by using a one-way, randomized complete block (RCB) ANOVA with WCS ($n = 2$; Mangrove Bayou and No-Name Bayou WCSs) as a factor (GLM procedure in SAS version 9.3). Because our study was conducted under similar environmental conditions during a single extended season (summer), season was not a factor of interest; therefore, the data were blocked based on water temperature (as a more ecologically relevant blocking factor than month) to remove unwanted sources of variation (Potvin 2001). Four water temperature groupings were used based on mean monthly temperature observations as follows (Table 1): 22°C (April), 26°C (May), 30°C (June–July), and 29°C (August–September). To quantify variation in the size of migrants, we used a two-way RCB ANOVA with WCS ($n = 2$; Mangrove Bayou and No-Name Bayou WCSs) and direction of movement (going into or coming from the managed marsh) as factors and with water temperature as the blocking factor. For the two-way RCB ANOVA of migrant length, interaction terms were included by using a backward stepwise approach in which nonsignificant interactions were excluded from the model. The abundance and size of individuals observed congregating at the WCSs were compared with those of individuals observed at the marsh creek by using a one-way RCB ANOVA with site ($n = 3$; Mangrove Bayou WCS, No-Name Bayou WCS, and marsh creek) as a factor and with water temperature as the blocking factor. Because some frames at the marsh creek lacked individuals for observation (i.e., July = 5 frames; September = 1 frame), the actual sample size of 210 frames is slightly smaller than the balanced sample size of 216 frames. Prior to analyses, abundance ($\log_{10}[x + 1]$), percentage (arcsine), and length ($\log_{10}$) data were transformed to satisfy the assumptions of ANOVA. Differences in treatment means were examined by using the Tukey–Kramer test for unequal sample sizes (Dunnett 1980; Day and Quinn 1989). We used logit modeling, which is preferred when the response and predictor variables are categorical (Floyd 2001), to independently analyze the effect of WCS

TABLE 1. Mean (SE in parentheses) temperature, salinity, dissolved oxygen (DO), turbidity, and center-channel water depth for each month of nekton sampling (April–September) and water velocity sampling (October) at sites in the Calcasieu Lake estuary, Louisiana. Each variable was measured once per flood tide each month at each sample site (Mangrove Bayou water control structure [WCS], No-Name Bayou WCS, and salt-marsh creek; thus, $n = 3$ per month). Inside water depth was measured only at the two WCSs and was not measured in April.

Environmental variable	Apr	May	Jun	Jul	Aug	Sep	Oct
Temperature (°C)	22.2 (0.7)	26.1 (1.0)	29.8 (0.8)	31.1 (0.9)	29.5 (0.3)	29.0 (0.3)	25.6 (0.8)
Salinity	17.8 (2.0)	23.6 (0.3)	21.3 (0.3)	20.8 (1.9)	23.1 (3.2)	21.4 (0.2)	22.8 (1.1)
DO (mg/L)	6.2 (0.7)	5.7 (0.4)	5.0 (0.3)	3.3 (0.2)	3.4 (0.4)	3.6 (0.4)	5.0 (0.4)
Turbidity (NTU)	4.7 (2.2)	4.0 (2.1)	3.2 (1.0)	1.2 (0.5)	3.2 (0.6)	24.4 (15.8)	1.5 (0.3)
Outside water depth, maximum (m)	1.38 (0.24)	1.40 (0.15)	1.54 (0.20)	1.43 (0.12)	1.55 (0.16)	1.64 (0.14)	1.41 (0.17)
Outside water depth, minimum (m)	1.32 (0.22)	1.32 (0.12)	1.47 (0.18)	1.40 (0.11)	1.49 (0.14)	1.54 (0.10)	1.36 (0.18)
Inside water depth, maximum (m)		1.36 (0.04)	1.46 (0.01)	1.55 (0.04)	1.51 (0.01)	1.64 (0.03)	1.44 (0.04)
Inside water depth, minimum (m)		1.35 (0.05)	1.42 (0.02)	1.54 (0.04)	1.47 (0.01)	1.60 (0.03)	1.44 (0.04)

on swimming direction (LOGISTIC procedure in SAS). The predictor variable was binary (i.e., WCS = Mangrove Bayou or No-Name Bayou).

Data on the species of nekton collected with traditional direct-capture sampling gears (i.e., cast net and gill net) were for descriptive purposes only and therefore were not statistically analyzed. These data were used to inform the analysis and interpretation of acoustic imaging data by providing the abundances and sizes of the nekton species that were present at the WCSs and the marsh creek during the study period.

Environmental and water quality data were examined with descriptive statistics. Water velocity data were examined for each site separately. Mean water velocities were calculated by using all velocity measurements for each 10-cm depth increment and were plotted to create water column velocity profiles (i.e., velocity [m/s] × depth [m]) for the flood tide measurements at each site.

RESULTS

Environmental and water quality characteristics were similar among the three sites in each month (Table 1). Water temperature, salinity, and dissolved oxygen were consistent among sites during each month and followed general trends associated with summertime in northern Gulf of Mexico estuaries. Turbidity was generally low (<5 NTU) during the study period except in September, when turbidity was high at the marsh creek (55.8 NTU). As expected, the inside water depths observed at the WCSs were similar during each sampling event and never exceeded the fixed-crest height (1.4 m). The marsh creek was included in the mean outside water depth calculations, which were also similar during each sampling event. Outside water depths rarely exceeded the fixed-crest height of the WCSs while the DIDSON was deployed (total of 24 h over 6 months) to collect data: only 15% of the total time at No-Name Bayou (June = 3.5 h) and not at all at Mangrove Bayou. Water velocities were low at all three sites; mean water velocities (averaged over all depths) for the two WCSs were similar (Mangrove Bayou: 0.08 m/s; No-Name Bayou: 0.09 m/s), whereas the marsh creek had a slightly lower mean velocity (0.05 m/s). Maximum velocities were up to three times greater at the WCSs (Mangrove Bayou: 0.13 m/s; No-Name Bayou: 0.16 m/s) than at the marsh creek (0.05 m/s).

Congregating Nekton

During 12 h of monitoring with acoustic imaging, 2,970 individuals were observed congregating at the two WCSs (Mangrove Bayou: $n = 1,844$ individuals; No-Name Bayou: $n = 1,126$ individuals; Figure 3B). Although observed in the same discrete time segments, it should be noted that these congregating individuals were observed in 144 image frames rather than from 12 continuous hours of acoustic imaging data (as was done for the migrants). No corrective calculation was
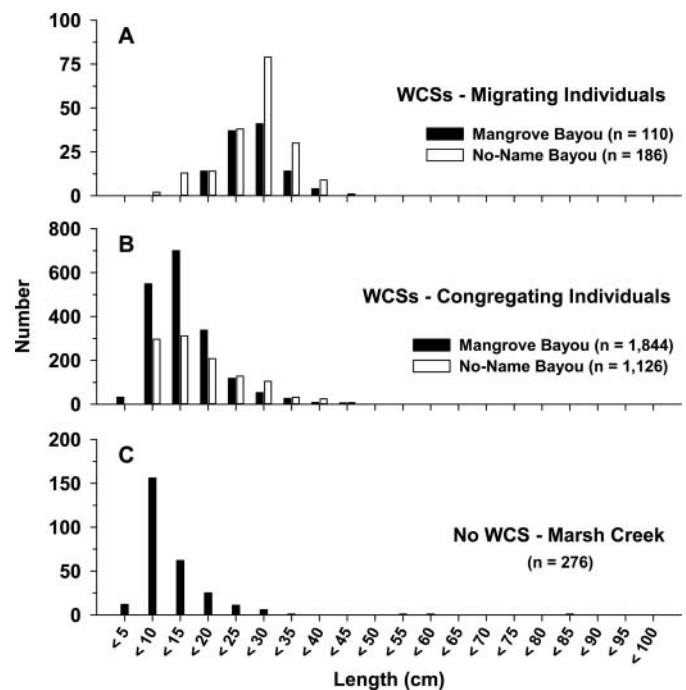

FIGURE 3. Length-frequency distribution for nekton observed with dual-frequency identification sonar at three sites in the Calcasieu Lake estuary: (A) migrating individuals ($n = 296$) at each water control structure (WCS), (B) congregating individuals ($n = 2,970$) at each WCS, and (C) individuals ($n = 276$) at the salt-marsh creek (no WCS). Note that the y-axis scale differs among the panels.

attempted on these congregating nekton data to equalize coverage with the data for migrants. The mean abundance of congregating individuals observed at the Mangrove Bayou WCS was significantly greater than abundance at the No-Name Bayou WCS ($P = 0.0382$; Figure 4A). Congregating nekton displayed similar size distributions at both of the WCSs (Mangrove Bayou: range = 4–155 cm; No-Name Bayou: range = 5–167 cm), with the majority of individuals (Mangrove Bayou: 86%; No-Name Bayou: 72%) ranging between 5 and 20 cm in length (Figure 3B). The mean length of congregating nekton did not differ significantly between the two WCSs ($P = 0.1199$; Figure 4B).

Migrant Abundance, Size, and Swimming Direction

In total, 296 individuals were observed migrating through the slots during 12 h of subsampled acoustic data recorded at the two WCSs; this equates to about 25 migrating individuals per hour. Mean migrant abundance was not significantly different between the two WCSs (Table 2; Figure 5A), although more migrating individuals were observed at No-Name Bayou ($n = 186$ total; 31 migrants/h) than at Mangrove Bayou ($n = 110$ total; 18 migrants/h). More migrants were also observed swimming out from the managed marsh rather than into the managed marsh at both WCSs (Figure 6A), an
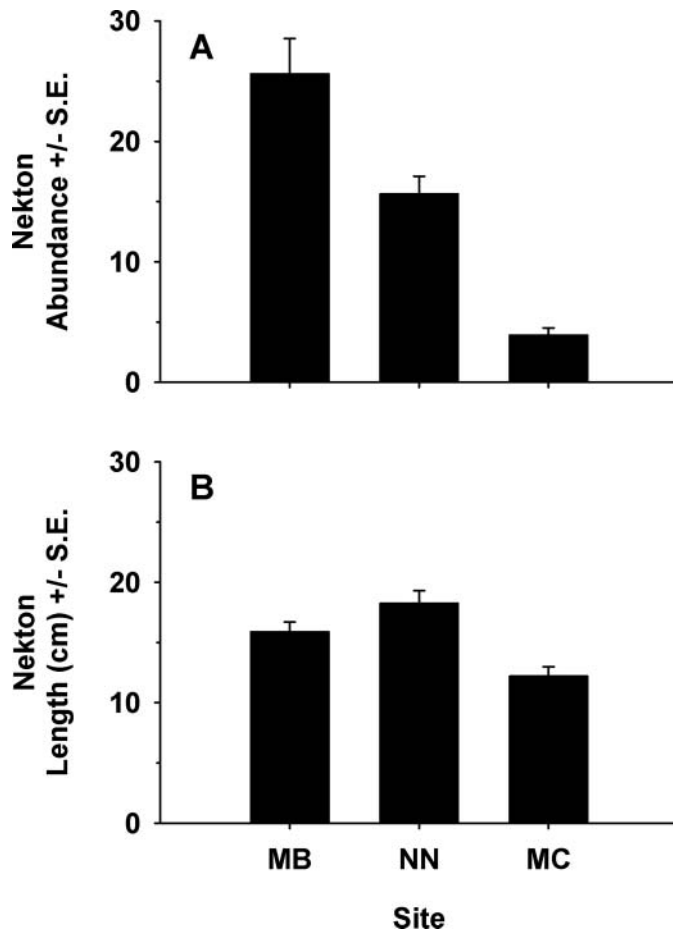
FIGURE 4. Mean (+SE) values of **(A)** nekton abundance (per frame) and **(B)** nekton length (cm TL; per frame) for individuals congregating at each water control structure (WCS; MB = Mangrove Bayou WCS; NN = No-Name Bayou WCS) and individuals in the salt-marsh creek (MC; i.e., no WCS), as observed with dual-frequency identification sonar ($n = 3,246$ individuals total).

indication that the migration patterns of individuals were not influenced by any particular WCS (Wald $\chi^2 = 3.3056$, df = 1, $P = 0.0690$). Migrating individuals ranged in size from 7 to 44 cm, but most migrants (80%) were 20–35 cm in length, and the size distributions were similar for the WCSs (Figure 3A). Mean migrant length ($\sim$25 cm TL) did not vary between WCSs (Table 2; Figure 5C) and did not vary with swimming direction (into or out from the managed marsh; Table 2; Figure 6B). The percentage of migrants was low ($\leq$10% of the observed congregating individuals migrated) at both WCSs (Figure 5B) and did not significantly differ between Mangrove Bayou and No-Name Bayou (Table 2).

Nekton at Water Control Structures versus the Salt-Marsh Creek

Acoustic data revealed that nekton abundance near the WCS slots was three to six times greater than that in comparable sample volumes from the unrestricted marsh creek site ($P < 0.0001$; Table 2; Figures 3B, 3C, 4A), where nekton distributions were likely spread out across the creek. The majority of individuals congregating at WCSs (81%) and observed at the marsh creek (88%) were between 5 and 20 cm in length. Overall size distributions were similar at the WCSs (range = 4–167 cm; Figure 3B) and the marsh creek (range = 4–81 cm; Figure 3C), with some larger individuals (>60 cm) infrequently observed at the WCSs ($n = 23$ individuals combined) and the marsh creek ($n = 1$ individual). Mean nekton length, however, was significantly lower at the marsh creek (mean $\pm$ SE = 12.19 $\pm$ 0.79 cm) than at the WCSs (Mangrove Bayou: 15.89 $\pm$ 0.80 cm; No-Name Bayou: 18.25 $\pm$ 1.05 cm; $P < 0.0001$; Table 2; Figure 4B).

Direct-Capture Sampling

Thirty-six species of nekton comprising 41,367 individuals were collected with cast nets and gill nets during the study period (Table 3). Abundance was greater at the WCSs (Mangrove Bayou: $n = 12,105$ individuals; No-Name Bayou: $n = 24,832$ individuals) than at the marsh creek ($n = 4,520$ individuals). Species richness was greater at the marsh creek

TABLE 2. Randomized complete block (RCB) ANOVA results (*P*-values for *F*-statistics) for the effect of water control structures (WCSs; $n = 2$; Mangrove Bayou WCS and No-Name Bayou WCS) on migrant abundance (per 5-min segment; $n = 144$ total segments), the percentage of migrants ([number of migrating individuals per 5-min segment]/[number of congregating individuals per frame]), and individual migrant length (cm TL; $n = 296$ total individuals) observed with dual-frequency identification sonar. Swimming direction was only included as a factor in the analysis of migrant length; the WCS × swimming direction interaction term was nonsignificant and therefore was excluded from the model. The RCB ANOVA results are also reported for the effect of sample site ($n = 3$; Mangrove Bayou WCS, No-Name Bayou WCS, and salt-marsh creek) on nekton abundance (per frame; $n = 216$ total frames) and nekton length (cm TL, per frame; $n = 210$ total frames). "Nekton" was defined as those individuals observed at the salt-marsh creek as well as those congregating at the WCSs. Factors that were not tested for a given variable were identified as not applicable (na).

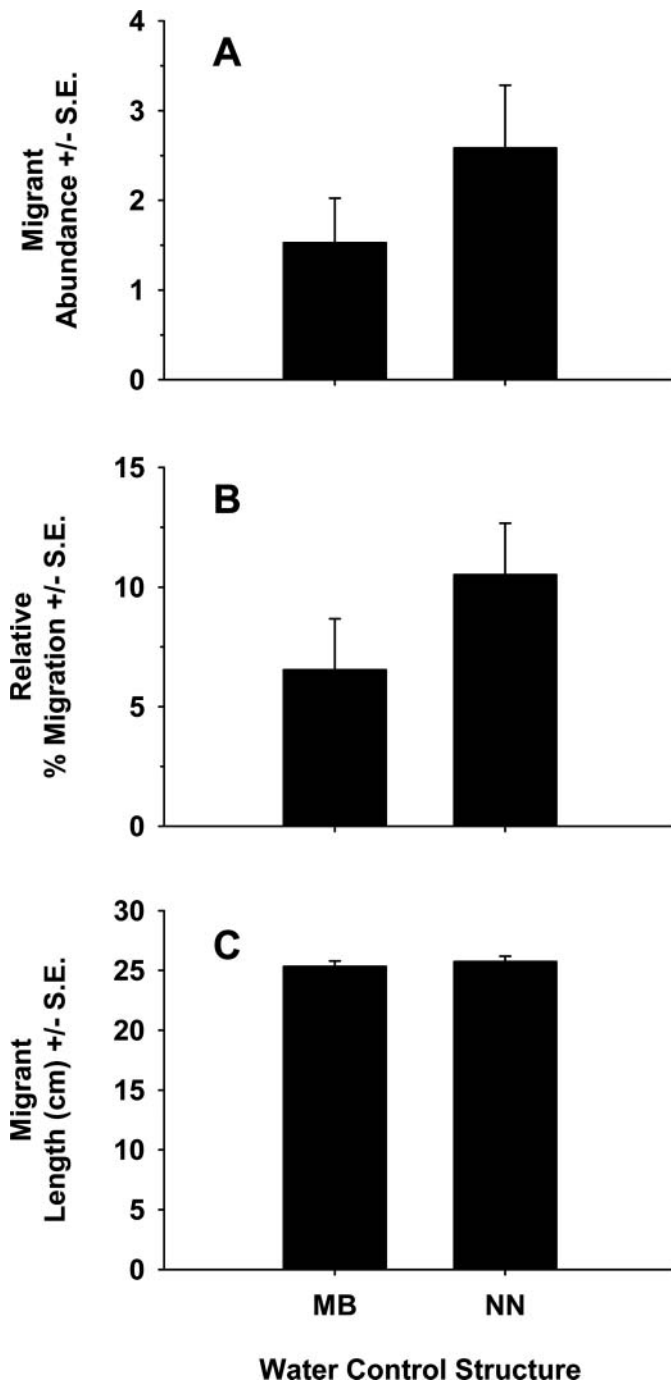| Dependent variable	Error df	WCS (df = 1)	Swimming direction (df = 1)	Site (df = 2)
Migrant abundance	139	0.1205	na	na
Migrant percentage	139	0.0862	na	na
Migrant length	290	0.8409	0.4105	na
Nekton abundance	210	na	na	<0.0001
Nekton length	204	na	na	<0.0001

FIGURE 5. Mean (+SE) **(A)** migrant abundance (per 5-min segment), **(B)** relative percentage of migrants (i.e., [number of migrating individuals per 5-min segment]/[number of congregating individuals per frame]), and **(C)** migrant length (cm TL; per 5-min segment), as observed with dual-frequency identification sonar at the Mangrove Bayou (MB) and No-Name Bayou (NN) water control structures ($n = 296$ migrants total).

FIGURE 6. Mean (+SE) **(A)** migrant abundance (per 5-min segment) and **(B)** migrant length (cm TL; per 5-min segment), as observed with dual-frequency identification sonar at the Mangrove Bayou (MB) and No-Name Bayou (NN) water control structures ($n = 296$ migrants total). Migrants are classified based on swimming direction (inside = individuals going into the managed salt marsh; outside = individuals coming from the managed marsh).

were collected in the cast nets (41,299 individuals in cast nets; 68 individuals in gill nets). Gill-net samples consisted primarily of large individuals (15–45 cm; 76%), whereas cast-net samples were mostly small individuals (<15 cm; 96%). The small nekton (<15 cm) we collected were primarily composed of Gulf Menhaden (66%), Atlantic Croakers (16%), and Spot (9%). Larger individuals (>15 cm) were generally less abundant and consisted mostly of Hardhead Catfish, Gizzard Shad, Spotted Seatrout, Striped Mullet, and Black Drum.

DISCUSSION

Passage rates through the WCS slots in our study area were low (i.e., ≤10% of congregating individuals). These passage rate estimates are likely valid because congregating individuals were enumerated from a single frame, which avoided the abundance overestimation that would have been caused by

($n = 30$ species) than at the Mangrove Bayou WCS ($n = 22$ species) and No-Name Bayou WCS ($n = 27$ species). Twice as many species were collected in cast nets ($n = 31$ species) as in gill nets ($n = 15$ species), and almost all individuals
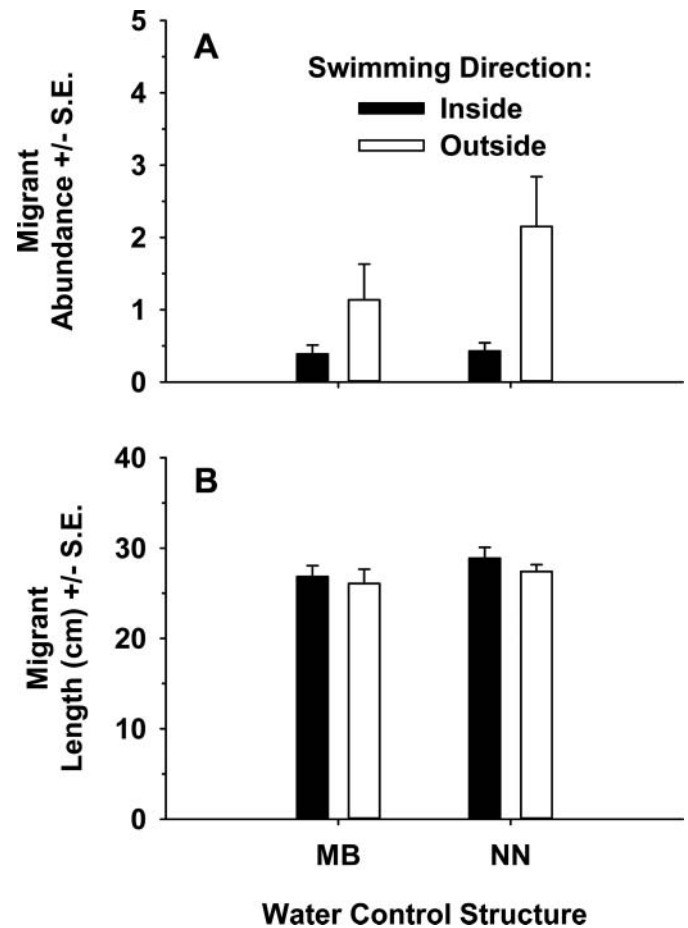
TABLE 3. Total number of individuals collected (per month) and mean length (mm; SE in parentheses) for each species sampled with cast nets (n = 106 casts) and gill nets (n = 24 sets) at the three sites combined (Mangrove Bayou and No-Name Bayou water control structures and the salt-marsh creek). Fish and invertebrates were measured in terms of TL (*), FL (#), or carapace width (§).

Species	Cast net							Gill net						
	Apr	May	Jun	Jul	Aug	Sep	Length	Apr	May	Jun	Jul	Aug	Sep	Length
Diamond Killifish *Adinia xenica**	0	1	0	0	0	0	29.0 (0.0)							
Striped Anchovy *Anchoa hepsetus*#	0	0	1	106	0	1	58.3 (1.2)							
Bay Anchovy *Anchoa mitchilli*#	31	23	235	299	120	44	43.0 (0.6)							
Sheepshead *Archosargus probatocephalus**	0	0	0	1	0	0	220.0 (0.0)							
Hardhead Catfish *Ariopsis felis*#								0	0	6	1	4	0	243.2 (19.4)
Alligator Gar *Atractosteus spatula**								0	0	0	0	1	0	947.0 (0.0)
Silver Perch *Bairdiella chrysoura**	0	0	0	0	4	0	86.3 (3.6)	1	0	0	0	0	0	150.0 (0.0)
Gulf Menhaden *Brevoortia patronus*#	10,456	3,221	7,296	6,175	5	16	47.0 (0.5)	0	1	0	0	1	2	142.4 (8.2)
Blue crab *Callinectes sapidus*§	11	2	2	1	0	0	23.8 (6.6)							
Crevalle Jack *Caranx hippos*#	0	0	0	1	2	0	118.7 (17.2)	0	0	0	0	1	0	142.0 (0.0)
Atlantic Spadefish *Chaetodipterus faber**								0	0	0	0	1	0	121.0 (0.0)
Atlantic Bumper *Chloroscombrus chrysurus*#	0	0	0	36	0	0	46.7 (1.0)							
Bay Whiff *Citharichthys spilopterus**	0	1	1	0	0	0	54.0 (1.0)							
Sand Seatrout *Cynoscion arenarius**	0	0	0	5	0	0	153.2 (4.0)							
Spotted Seatrout *Cynoscion nebulosus**								1	1	0	0	1	3	332.8 (40.5)
Sheepshead Minnow *Cyprinodon variegatus**	1	0	2	0	0	0	34.0 (1.0)							
Gizzard Shad *Dorosoma cepedianum*#	0	2	0	1	0	0	198.0 (51.1)	3	2	2	1	4	1	312.0 (13.4)
Ladyfish *Elops saurus*#	0	0	0	9	0	2	223.8 (12.9)							
Northern brown shrimp *Farfantepenaeus aztecus**	0	114	106	6	1	2	65.0 (1.5)							
Gulf killifish *Fundulus grandis**	5	17	1	0	0	0	55.8 (2.2)							
Darter Goby *Ctenogobius boleosoma**	0	1	0	0	0	0	50.0 (0.0)							
Naked Goby *Gobiosoma bosc**	1	1	0	0	0	0	46.0 (1.0)							
Scaled Sardine *Harengula jaguana*#	0	0	0	164	5	235	51.7 (2.6)							
Pinfish *Lagodon rhomboides*#	0	3	9	2	4	1	74.7 (6.3)							
Spot *Leiostomus xanthurus**	248	2,569	211	193	276	9	89.3 (2.1)	0	0	0	0	4	0	174.5 (21.8)
White shrimp *Litopenaeus setiferus**	0	1	0	3	10	10	58.5 (6.5)	0	0	1	0	1	7	131.0 (4.4)
Inland Silverside *Menidia beryllina*#	927	288	9	10	6	0	65.0 (0.9)							
Atlantic Croaker *Micropogonias undulatus**	3,378	2,837	31	40	163	1	68.1 (1.1)	1	0	0	0	0	0	182.0 (0.0)
Striped Mullet *Mugil cephalus*#	14	5	127	7	30	10	164.0 (6.0)	2	1	0	1	2	0	202.0 (6.8)
White Mullet *Mugil curema*#	0	0	406	32	13	9	104.8 (2.1)							
Leatherjack *Oligoplites saurus*#	0	0	0	28	69	4	92.7 (1.8)							
Daggerblade grass shrimp *Palaemonetes pugio**	95	422	12	0	3	0	31.6 (0.3)							
Southern Flounder *Paralichthys lethostigma**	0	1	0	0	0	0	940.0 (0.0)							
Black Drum *Pogonias cromis**	0	1	0	0	0	0	217.0 (0.0)	5	1	0	0	0	0	292.0 (3.0)
Red Drum *Sciaenops ocellatus**								0	1	0	1	0	0	304.2 (22.5)
Atlantic Needlefish *Strongylura marina**	2	0	0	0	0	0	360.0 (40.0)	0	1	0	1	0	0	417.5 (27.5)
Total	15,169	9,508	8,450	7,119	711	342		13	8	9	5	20	13	

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counting individuals multiple times. Comparing the number of migrants observed over a continuous period (e.g., 5 min) with discrete "snapshot" estimates of congregating individuals observed at longer time intervals (e.g., 1 frame per 5 min) likely provides the best estimate of passage efficiency. During our previous study (Kimball et al. 2010), we may have underestimated the passage rate (<5%) at a slotted WCS by using continuously observed data from both congregating and migrating individuals.

Water control structures appear to attract and concentrate salt-marsh nekton. Congregating individuals were often observed swimming in a circular pattern or remaining stationary (oriented into the current) near the slots—behaviors also observed in congregating nekton at another salt-marsh WCS (Kimball et al. 2010). In contrast, individuals in the salt-marsh creek displayed primarily random, nondirectional swimming behavior and remained in the DIDSON field of view for only a short time. The congregating nekton was much more abundant (3–6×) at the WCSs than at the salt-marsh creek site even though the assemblages were similar in species composition, dominant species, and individual sizes. High nekton densities at WCSs may indicate ecological hot spots at these critical bottlenecks, where processes such as predation and foraging are enhanced or intensified relative to those in other habitats within the estuary (Sheaves 2009). This concept has already been advanced for structures (e.g., dams) in riverine ecosystems (McLaughlin et al. 2013) and is likely applicable for structures in estuarine ecosystems as well (Sheaves 2009). For some individuals, WCSs appear to be used primarily as a foraging site rather than as an access point for entering or exiting managed marshes, which may account for the low passage rates observed here and elsewhere (Kimball et al. 2010). Turbulence created by water exchange at the slots may concentrate food for planktivores, and the abundance of forage fish (e.g., Gulf Menhaden; Kimball et al. 2010; present study) that are drawn to this food source may in turn attract piscivorous fishes to WCSs. Humans (fishers) take advantage of these nekton aggregations and often target both game fishes (e.g., Spotted Seatrout and Red Drum) and their prey (e.g., penaeid shrimps and blue crabs) at WCSs. The effect of such fishing pressure on these species' populations due to WCS placement in managed marshes is not known. Nekton diet and feeding habits have been examined at structures in rivers, where large nekton aggregations increase competition among predators and lead some species to alter their feeding strategies (Baumgartner 2007). Our lack of understanding about the effect of WCSs on nekton trophic interactions in managed salt marshes warrants further study.

The size of fish observed migrating through WCSs in this region has been consistent in studies of salt marshes and does not appear to be related to slot size. Migrating fish in our study were similar in size to those migrating through a WCS with 15-cm slots (majority of fish = 15–35 cm TL; mean ∼ 30 cm TL) located at a salt marsh within Breton Sound estuary (Kimball et al. 2010). Rogers et al. (1992) and Rulifson and Wall (2006) evaluated smaller slot widths (i.e., 10 cm and 4 cm, respectively), but neither study reported the size of migrating nekton. A slot width of 15 cm reportedly limited the migration of large (>100-cm) fish through a dam fishway within a large river of northeastern Australia (Stuart and Berghuis 2002). It is unlikely that slot width limited nekton passage in our study, however, as few individuals (congregating or migrating) larger than 60 cm were observed. Furthermore, increasing the slot width to 45 cm (Stuart and Mallen-Cooper 1999) or 60 cm (Kimball et al. 2010) did not increase passage rates or the size of migrating individuals.

Most of the migrating fish in our study were observed leaving the managed area and swimming against a flood tide. Water velocities at the WCS slots were too low (<0.2 m/s) to limit the migration of most nekton and only exceeded the swimming capabilities of larvae and small (e.g., <3 cm) juveniles (e.g., Mitchell 1989; Luckenbach and Orth 1992; Faria et al. 2009). Individuals migrating out of managed marshes have been reported to be larger than those leaving unmanaged marshes (e.g., penaeid shrimps; Knudsen et al. 1989, 1996), ostensibly due to emigration impedance (resulting in long retention times), reduced predation, or decreased competition in managed marshes (Hoese and Konikoff 1995). Although we observed a similar pattern at another salt marsh (Kimball et al. 2010), some emigrating individuals may have exited the marsh undetected by passing through large flap gates (open only during ebb tide) that could not be monitored. In our study, the similar size of migrants swimming in both directions suggests that salt-marsh nekton—at least the size range of migrants we observed—do not experience long retention times and may transit WCS slots in a more routine, frequent manner.

In addition to examining bidirectional nekton passage, acoustic imaging allowed us to simultaneously observe migrating and congregating individuals at the two WCSs. Without data collected simultaneously from both migrants and congregating individuals, it would be difficult to interpret and compare results from nekton passage studies based on other metrics (e.g., number of migrating individuals per hour). For instance, migrants were observed at a rate of 25 individuals/h in our study, which is consistent with the only other study examining unhindered bidirectional passage of nekton through WCS slots (passage rate = 24 individuals/h; Kimball et al. 2010). Nekton passage rates reported from the only other studies to directly examine movement through slots in a salt marsh were well below (2 individuals/h; Rulifson and Wall 2006) and above (248 individuals/h; Rogers et al. 1992) the rates we observed, but those two studies only assessed nekton passage in one direction. Focusing on passage in a single direction (e.g., upstream or downstream) may be appropriate for riverine nekton exhibiting strong migrational cues (e.g., salmonids); however, salt-marsh nekton at WCSs do not swim unidirectionally most of the time.

Exceptions occur for emigrating life history stages of some nekton species (e.g., penaeid shrimps; Knudsen et al. 1985, 1989, 1996) and for individuals migrating in response to environmental cues (e.g., cold front passage; Herke and Rogers 1984). Observations of such phenomena are more likely to occur with approaches that involve near-continuous (e.g., daily) sampling efforts or that target a single species during critical life history periods (e.g., offshore spawning migration) rather than with efforts focusing on the entire nekton assemblage during specific seasons (e.g., Kimball et al. 2010) or tide stages (present study).

The use of imaging sonars allows a comprehensive examination of nekton movement and behavior at salt-marsh WCSs, but it has some limitations (Kimball et al. 2010; Doehring et al. 2011). Species identification with acoustic imaging is limited to large fishes (e.g., tunas and groupers; Frias-Torres and Luo 2009; Han et al. 2009) or fishes that display unique swimming behaviors (e.g., eels; Mueller et al. 2008; Doehring et al. 2011). Most fishery species recruit to marsh nursery areas as larvae or postlarvae, which are too small to be detected by these acoustic devices. Consequently, we could not examine the effects of WCSs on recruitment processes in our study. Small individuals (<3 cm) of some locally abundant invertebrate species (e.g., penaeid shrimps; Knudsen et al. 1989, 1996) were probably underrepresented in our study, whereas some small juvenile fishes were only identifiable because they formed distinctive schools (e.g., Gulf Menhaden and mullets *Mugil* spp.; Kimball et al. 2010; Doehring et al. 2011). Because WCSs may inhibit immigration into managed marshes (Herke et al. 1992), future work should examine this topic and determine whether WCSs restrict immigration enough to affect fishery production from managed areas. For a more in-depth examination of nekton behavior and species-specific movement patterns at salt-marsh WCSs, techniques other than imaging sonars will be required. For example, PIT technology can be used to collect species-specific data on juvenile fishes (e.g., 12-mm PIT tags; Bass et al. 2012). Currently, a sonar unit is only capable of projecting in one dimension (horizontal or vertical); thus, three-dimensional observation of nekton would require the use of two sonar units simultaneously (K. M. Boswell, unpublished data). In our study, the DIDSON unit was aimed horizontally, so we were unable to determine the position of individuals in the water column. Such information may reveal the depth preferences of migrating nekton at WCSs (e.g., top, middle, and bottom of the slot opening).

Although restricting hydrological connectivity with anthropogenic barriers is known to influence nekton community structure and habitat function in salt marshes (e.g., Rozas and Minello 1999; Rozas et al. 2013), the effects of these barriers on the population dynamics of salt-marsh nekton, particularly transient species, are unknown. To improve our understanding in this area, numerical simulation models would be useful for predicting the effects of WCSs on nekton populations and fishery production from managed marshes. Such models have been used successfully to estimate the effects of spatial configuration and flooding patterns in salt marshes on penaeid shrimp production (Roth et al. 2008). Our estimates of nekton passage efficiency (Kimball et al. 2010 and present study) could be used in such models to estimate the production from managed marshes that is exported to the wider estuary. This type of approach may be an important tool for assessing the effects of levees and storm surge barriers that are currently proposed for coastal states such as Louisiana (CPRA 2012), where large proportions of salt-marsh habitat are already under some form of management (Cowan et al. 1988).

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