Recruitment and movement ecology of red drum *Sciaenops ocellatus* differs by natal estuary

Sarah Walters Burnsed[1],*, Susan Lowerre-Barbieri[1,2], Joel Bickford[1],
Erin Hoerl Leone[1]

[1]Florida Fish and Wildlife Conservation Commission, Florida Fish and Wildlife Research Institute, 100 8th Ave. SE,
St. Petersburg, FL 33701, USA
[2]Fisheries and Aquatic Science Program, School of Forest Resources and Conservation, University of Florida,
7922 NW 71st Street, Gainesville, FL 32653, USA

ABSTRACT: Although stock structure is based on reproductive isolation and recruitment to the adult stock is an important parameter for stock assessments, data on the ecological process as individuals move from nursery to adult habitat is rare. As red drum *Sciaenops ocellatus* show delineated estuarine nursery grounds and coastal spawning habitat, we acoustically implanted and monitored subadults in neighboring southwest Florida estuaries Tampa Bay (2012, n = 20) and Charlotte Harbor (2013, n = 20) over 3 yr to evaluate if recruitment and consequent spawning site selection differed between estuaries. To assess estuarine presence, we used a mobile hydrophone survey (Tampa Bay) and estuarine receivers (Charlotte Harbor); recruitment to adult habitat was monitored with nearshore receiver arrays off both estuaries. Tagged fish were of similar size and age but reproductive development, recruitment timing, and spawning habitat post-recruitment varied significantly. Although Charlotte Harbor fish exhibited significantly more advanced gonadal maturity indicators compared to Tampa Bay fish, only 24% were detected in adult habitat the year tagged, with 65% following the next reproductive year. By contrast, 74% of fish from Tampa Bay moved to adult habitat within the same year tagged. Natal homing — returning to the nearshore adult habitat off their estuarine nursery for subsequent reproductive periods — was observed in fish from both estuaries. Differences in recruitment timing and movement patterns of red drum between the 2 estuaries indicates natal estuary drives spawning site selection and consequent movement ecology in ways not previously understood, with potential recreational fishery implications as this species is managed by escapement rates.

KEY WORDS: Red drum · *Sciaenops ocellatus* · Acoustic telemetry · Spatial ecology · Ontogeny · Maturation · Recruitment · Spawning · Natal homing · Tampa Bay · Charlotte Harbor · Florida

1. INTRODUCTION

Spatial connectivity between juvenile and adult habitats and the associated timing of transition between the 2 are key components in understanding the complexities of a species' lifecycle, with these movements influencing how they are most effectively fished and managed (Beck et al. 2001, Gillanders et al. 2003, Dance & Rooker 2015). Species with clearly delineated juvenile and adult habitats provide opportunities to monitor ontogenetic transition with acoustic telemetry, which provides high resolution behavioral data at the individual level in both time and space (Kenworthy et al. 2018). Simultaneous acoustic coverage of both habitats provides a comprehensive accounting method and allows insight into the directionality of the transitional movement to assess if the egression is permanent or fluid. These ontogenetic movement metrics, along with their associated timing with ecological constraints,

can affect the level of connectivity between juvenile and adult life history stages, with direct consequences for spatial management if these movements vary across the distribution and/or management ranges of a given species (Gillanders et al. 2003). Differential use of space following ontogeny, along with behaviors such as spawning site selection, spawning site fidelity, and natal homing, can affect a species' productivity and vulnerability exposure, driving population differentiation and connectivity, which in turn has important implications for stock assessments based on reproductive isolation (Petitgas et al. 2010, 2013, Secor 2015, Allen & Singh 2016, Kerr et al. 2017, Lowerre-Barbieri et al. 2019a).

Consistent, distinct habitat partitioning between adults in Gulf of Mexico coastal waters and juveniles in estuaries (Rooker et al. 2010, Lowerre-Barbieri et al. 2016) makes red drum *Sciaenops ocellatus* an ideal species for examining recruitment timing of subadults to the adult population. Red drum are a popular sport fish in the state of Florida, with an involved regulatory history stemming from intense commercial and recreational pressure in the 1980s (see Winner et al. 2014 for details). As of the last red drum stock assessment in Florida in 2015, escapement rates — the proportion of fish that survive through age 4 relative to fish that would have survived if there was no fishery — exceeded the state's management goal of 40% in all 4 regional management zones for the recreational fishery (Chagaris et al. 2015). Current Florida regulations permit the retention of fish between 457 and 686 mm total length (TL) (Chagaris et al. 2015), generally corresponding to recreationally targeted subadults between ages 1 and 3 (Murphy & Taylor 1990). These estuarine subadults within Tampa Bay, Florida, are known to move from their primary nursery habitats of low salinity backwaters (Peters & McMichael 1987) through areas of the main bay to gather near the mouth of the estuary (Murphy & Taylor 1990, Winner et al. 2014) prior to joining aggregating adults in nearshore coastal waters during the fall (Murphy & Crabtree 2001, Patterson et al. 2004, Winner et al. 2014, Lowerre-Barbieri et al. 2016). As histological indicators indicate that these nearshore aggregations are spawning (Lowerre-Barbieri et al. 2016), subadult transition from the estuary to the nearshore adult aggregations indicates recruitment to the spawning population, which typically occurs by age 5 (Murphy & Taylor 1990) but as early as age 3 or 4 (Murphy & Crabtree 2001, Winner et al. 2014). Adult red drum are highly fecund (up to >3 million eggs batch^{-1}; Wilson & Nieland 1994) and relatively long-lived in the Gulf of Mexico (>30 yr; Winner et al. 2014), with multiple studies indicating natal homing (Patterson et al. 2004, Rooker et al. 2010, Lowerre-Barbieri et al. 2016) despite having high dispersal potential due to their ability to undertake extensive migrations (Overstreet 1983, Pattillo et al. 1997).

Two major estuaries along Florida's Gulf coast, Tampa Bay and Charlotte Harbor, serve as nursery grounds for red drum (Seyoum et al. 2000) and are ecologically and climatically comparable semi-enclosed estuarine systems (Hueter & Manire 1994) given their geographic proximity, comparable dimensions and depth, and shared physical features (Goodwin 1987, 1996) and chemical profiles. Nearshore areas off Tampa Bay have been confirmed as red drum spawning habitat and aerial survey data indicate the nearshore area off Charlotte Harbor likely serves the same purpose (Lowerre-Barbieri et al. 2016). In this study, we acoustically tagged subadult red drum within the estuarine habitats of Tampa Bay (2012) and Charlotte Harbor (2013) and monitored nearshore spawning habitat off each of these estuaries for 3 yr to determine if natal estuary affects recruitment timing or consequent spawning site selection and movement ecology. By graphically and statistically integrating a temporal component to spatial movements through network analyses, we were able to better visualize and interpret the space use and connections of red drum as they recruit to and use nearshore spawning habitats (Jacoby et al. 2012, Stehfest et al. 2013). Using biological data, acoustic telemetry, and network analyses, we specifically tested whether (1) similar-sized fish from each estuary exhibited comparable gonadal development and timing of recruitment to adult habitat, (2) natal estuary affects consequent spawning site selection, and (3) if space use (defined by movement interaction patterns and edge density metrics) differed by natal estuary once fish had recruited to adult habitat.

2. MATERIALS AND METHODS

2.1. Ethics

Although specific permission for sampling was not required due to the research being conducted by the Florida Fish and Wildlife Conservation Commission's Fish and Wildlife Research Institute (FWRI), every effort was made to meet all ethical standards during the acoustic tagging process. No protected species were targeted or inadvertently sampled during this study.

2.2. Study site and period

We conducted this study from 30 August 2012 to 31 December 2015 in nearshore coastal and estuarine waters of central west Florida, USA (Fig. 1). To effectively monitor when subadult red drum recruited from estuarine habitat to the nearshore adult spawning habitat, we captured 20 fish within each estuary and implanted each with an acoustic tag at the beginning of the adult spawning seasons of 2012 (in
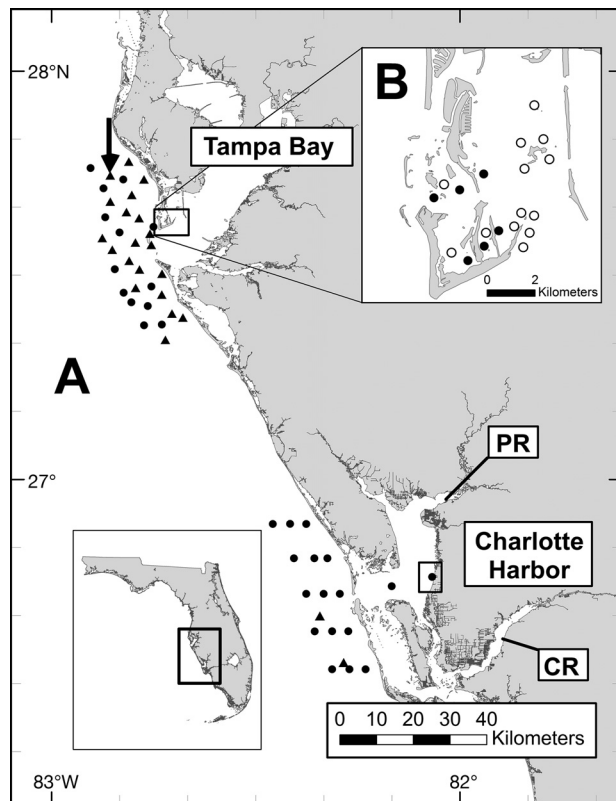

Fig. 1. Study site, including (A) nearshore receiver arrays, and (B) mobile hydrophone survey sites within the Tampa Bay estuary. (A) Vemco VR2W receivers were deployed at sites where red drum aggregations had been previously located off of Tampa Bay (triangles), with additional receivers (black circles) to ensure relatively even coverage. Arrow: range test location for the VR2W receivers. In nearshore Charlotte Harbor, the initial array (black circles) was based on a grid pattern, as there was no preexisting data on aggregations, and 2 receivers were added within the nearshore array (triangles) in 2013 based on aggregation locations in 2012. Two receivers were deployed within the Charlotte Harbor estuary following subadult tagging in fall 2013. PR: Peace River; CR: Caloosahatchee River. Tagging sites within Charlotte Harbor and Tampa Bay are denoted by rectangles. (B) Within the Tampa Bay estuary, 19 fixed sites were monitored in a mobile hydrophone survey; black circles: sites where subadults were captured, tagged, and released; open circles: sites where subadult schools had been spotted and/ or captured during previous research

Tampa Bay) and 2013 (in Charlotte Harbor). Due to funding and logistical limitations, we staggered tagging over 2 yr. Subsequent movements from each estuarine cohort were tracked during the year they were tagged and for 2 yr post-tagging; Tampa Bay through 31 December 2014 and Charlotte Harbor fish through 31 December 2015.

2.3. Capture, implantation, ageing, and determination of sex and reproductive state

2.3.1. Capture

Subadults predictably aggregate within certain areas of each estuary during early fall. We targeted fish larger than the state of Florida's recreational fishing maximum length limit (686 mm TL) to reduce subsequent harvest mortality of any tagged fish from recreational anglers, as these mixed size-class schools are heavily fished. Schools of subadult red drum were captured in estuarine waters in lower Tampa Bay on 4 dates in 2012 (30 August, 18 September, 25 September, and 10 October; Fig. 1). We collected all fish (except one collected with hook and line on 25 September) by visually locating the schools and capturing them with a 548.6 m long × 2.4 m deep nylon-mesh trammel net. This net consisted of one inside mesh (117.5 mm stretch mesh length, no. 12 twisted nylon twine) and 2 outer mesh walls (356 mm stretch mesh length, no. 18 twisted nylon twine). The net had a 9.5 mm black polypropylene float line with small bullet floats spaced 762 mm on center, and a no. 50 lead core rope along the base of the net. On 6 September 2013, with the help of local fishing guides, we used hook and line gear to capture subadult red drum in the Charlotte Harbor estuary along the eastern wall of the harbor, midway between the Peace and Caloosahatchee Rivers (Fig. 1). We recorded latitude and longitude (GPS coordinates), depth, and salinity at all capture locations, with the exception of Charlotte Harbor, where salinity could not be recorded until later in the month.

2.3.2. Implantation

We measured TL and standard length to the nearest mm for all fish. To determine age, we removed the second anterior dorsal spine and assigned reproductive state for each fish as defined below (see Section 2.3.3). The surgical process followed that of Lowerre-Barbieri et al. (2016); we implanted all fish intra-peri-

toneally with acoustic tags (Vemco, 69 kHz V16-6H). To increase battery life to 1251 d (approximately 3.5 yr), tags were coded with 20–60 s inter-pulse random delays for the first 8 mo and 30–90 s for the following 4 mo before repeating back to the 20–60 s delay again to align the increased frequency with the anticipated fall reproductive period. Surgery times were similar between estuarine tagging groups and ranged from 2:00 to 7:00 min with a mean of 4:36 min for Tampa Bay fish and 4:11 min for fish tagged in Charlotte Harbor. Following implantation, we inserted an external dart tag across the dorsal pterigiophores and immediately released fish at the site of capture. To detect fish after release and confirm short-term survival, we used a Vemco VR100 mobile tracking receiver with an omnidirectional hydrophone.

2.3.3. Ageing and determination of sex and reproductive state

Fish were aged using transverse sections of the second dorsal spine by the Age and Growth Laboratory at FWRI. Spines were removed from the fish, cleaned of excess tissue, and stored frozen until processing for age determination. A total of 3 transverse sections (0.5–0.7 mm) were cut immediately distal of the condyle using a Buehler low-speed Isomet saw equipped with diamond-edged blades. Prepared sections were fixed to microscope slides with a clear mounting medium and viewed under a stereomicroscope at 10–40× magnification using transmitted light. Increment count was determined by enumerating translucent zones. In spines, the wide opaque zones represent the pattern of faster growth and narrow translucent zones represent the pattern of slower growth (Ihde & Chittenden 2003, Allman et al. 2018). Ages were equal to increment counts, although ageing validation using dorsal spines has not been performed for this species.

We determined the sex of implanted fish based on a combination of strip spawning, sex-specific characteristics, and ovarian biopsies. We attempted strip spawning first on all fish by gently applying pressure to the abdomen. Males expressed milt or drummed (a male-specific trait; Holt 2008) and actively spawning females released eggs. We assumed fish that did not demonstrate male characteristics were females, which was confirmed using ovarian biopsies when possible. Fish with urogenital pores too small for biopsy we assumed to be immature females, otherwise biopsies were taken with a catheter composed of a 10 cc syringe equipped with an adapter and

Tygon tubing with an inner diameter of 1.6 mm. We inserted the tubing 10–20 mm into the urogenital pore and then extended the plunger of the syringe to create a vacuum to extract oocytes. All biopsied tissue used for histological analysis was processed in the laboratory as follows: fixed in 10% neutrally buffered formalin for a minimum of 24 h, rinsed in water, and stored in 70% ethanol. Samples were embedded in glycol methacrylate, sectioned to 3–5 μm thickness, stained with periodic acid-Schiff's hematoxylin, and then counterstained with metanil yellow (Quintero-Hunter et al. 1991). We assigned germ cell developmental stages, reproductive state, and reproductive phases based on Lowerre-Barbieri et al. (2009) and Brown-Peterson et al. (2011). The following histological indicators were used in females: primary growth (PG), cortical alveoli (CA), vitellogenic (Vtg1-3), and oocyte maturation (OM) stage oocytes and post ovulatory follicles (POFs). We considered female fish with secondary growth oocytes (SG) to be mature (Lowerre-Barbieri et al. 2011).

2.4. Acoustic monitoring

2.4.1. Overview

We monitored 4 distinct habitats for acoustically tagged fish: (1) within the mouth of the Tampa Bay estuary at release sites of tagged fish, (2) within the Charlotte Harbor estuary at the release site of tagged fish and at an anticipated high-traffic area for fish within the estuary, and in nearshore coastal waters off (3) Tampa Bay and (4) Charlotte Harbor. We categorized detection dates as occurring either during the adult reproductive period (August through December) or a non-reproductive period (January through July) based on Lowerre-Barbieri et al. (2016).

2.4.2. Estuarine habitat

Estuarine monitoring in both Tampa Bay and Charlotte Harbor was not designed or intended to be comprehensive (i.e. account for all tagged animals all the time), but rather to monitor areas with high detection probabilities, including tagging sites, at the lowest cost: manual tracking in the estuary (Tampa Bay) closest to our laboratory and the deployment of 2 stationary receivers in the estuary (Charlotte Harbor) further away. Because of this limited coverage, recruitment was based only on positive detections on nearshore receivers.

At the Tampa Bay tagging sites, we conducted a mobile hydrophone survey using a VR100 over the period 30 August 2012–11 November 2013. We sampled weekly during both annual reproductive periods in 2012 and 2013 and every other week during the 2013 non-reproductive period (January–July). We sampled 19 fixed stations on each trip, 6 of which were the original capture sites and the remaining 13 were locations where subadult red drum had been previously sampled by trammel nets in FWRI's Fisheries Independent Monitoring (FIM) program (Fig. 1). All stations were shallow (average depth: 0.9 m) and some only accessible at high tide. At each station, we lowered the VR100 omnidirectional hydrophone over the side of the boat and left it in the water to listen at 69 kz for a minimum of 2 min. If a tag was detected but not decoded (either due to collisions with other tags or the tag being just outside of range), monitoring continued until the tag could be decoded. Based on prior range testing in this area (Lowerre-Barbieri et al. 2013), we presumed fish to be detectable if they were within 85 m of the hydrophone. We pooled all 19 stations during analysis to generate a presence/absence metric for the entire estuary for each sampling trip.

We monitored estuarine presence within Charlotte Harbor with 2 stationary Vemco VR2W acoustic monitoring receivers, both deployed on 25 September 2013, which was 2.5 wk after fish were tagged within the Charlotte Harbor estuary. We mounted the receivers on 121.9 cm long sand augers with the top of the receiver approximately 0.8 m off the bottom. At the Charlotte Harbor tagging site, we moored one receiver to the bottom of the deepest channel (1.2 m) within 500 m of the tagging site. We moored a second receiver in the middle of Charlotte Harbor near a channel marker in line with the estuary's major inlet (Boca Grande Pass), where we anticipated movement out of the estuary. We could not employ a mobile hydrophone survey in Charlotte Harbor due to funding and logistical limitations.

2.4.3. Nearshore coastal habitat

We monitored recruitment of subadult red drum to adult nearshore coastal habitat and movements along the coast for both Tampa Bay and Charlotte Harbor tagged fish with 2 stationary acoustic receiver arrays (with non-overlapping ranges) deployed off the coasts of Tampa Bay and Charlotte Harbor in early fall 2012, with the most southern nearshore Tampa Bay receiver 104 km from the northern most nearshore Charlotte Harbor receiver (Fig. 1). We observed a detection rate greater than 50% at a range of 399 m in the nearshore Tampa Bay array (Lowerre-Barbieri et al. 2016). The nearshore Tampa Bay array consisted of 33 receivers; 20 located at sites where red drum aggregations were previously identified (Murphy & Crabtree 2001, Winner et al. 2014) and 13 additional receivers to fill in gaps, primarily in the southern portion of this sampling area (Fig. 1). No historical data were available for red drum aggregations in Charlotte Harbor coastal waters, so we deployed 15 receivers in an evenly spaced grid (Fig. 1). We deployed 2 additional receivers in 2013 at aggregation sites identified by aerial surveys during a concurrent adult red drum study in 2012 (Lowerre-Barbieri et al. 2016). We moored VR2W receivers in the nearshore Tampa Bay array using sand augers (121.9 cm long) which were originally held upright with a subsurface buoy. Due to shrimp trawling off Charlotte Harbor, we modified the mooring system for this array to reduce the chance of gear loss by eliminating the subsurface buoy and directly mooring the VR2-W to the sand auger, approximately 0.8 m off the bottom. Because this method did not decrease detection rates, we redeployed the nearshore Tampa Bay receivers with this technique in 2013.

Routine array maintenance included replacing receivers approximately quarterly. A gap in detection would result from pulling a receiver out of the water for maintenance, therefore, divers replaced a previously deployed receiver with another prepared receiver to ensure continuous acoustic coverage. Removed receivers were returned to the lab, downloaded, cleaned of any biofouling, the battery changed, and the outside repainted with antifouling paint if needed. Receivers were deployed at all sites throughout the study period except the southwestern-most receiver in the nearshore Tampa Bay array, which was never relocated after deployment on 7 September 2012. We deployed a replacement receiver at this site on 24 April 2013.

Acoustic telemetry data included tag number and detection date and time. A reference transmitter was used at the start and end of deployments of each receiver to confirm receiver detection times were accurate (Humston et al. 2005, Heupel et al. 2006). We grouped detections into 10 min time bins and filtered them to remove potentially spurious detections based on frequency, such as a tag detected fewer than 5 times on a given date. Because the VR2Ws did not contain overlapping ranges, we assigned fish detections to the location of the individual VR2W.

2.5. Analytical methods

2.5.1. Biological profile comparisons and recruitment timing

To compare the percent of fish that were mature at the time of tagging between estuaries, we grouped all tagged males and females together by estuary and used a chi-squared test. We used a Fisher's exact test to determine if the proportion of fish detected in the nearshore arrays differed by estuary, including only fish that were confirmed to be alive through acoustic detections. Chi-squared and Fisher's exact tests were performed using SAS v.9.4, with $\alpha = 0.05$. We measured recruitment timing as the number of days between the first date an individual fish was detected on any nearshore receiver and the mean arrival date (September 8) of repeat adult spawners to the Tampa Bay nearshore array (Lowerre-Barbieri et al. 2019b). This recruitment metric may be conservative, as nearshore arrays are not comprehensive in coverage and this first acoustic detection may not reflect the original arrival date and location of an individual fish to nearshore habitat. We used a negative binomial model to assess differences in recruitment between estuaries and age classes. We excluded age-1 red drum because only 2 individuals in this age class were tagged; hence, our analysis focused on assessing differences in recruitment (1) between estuaries and (2) between age-2 and age-3 fish. We fit 4 regression models, 3 of which represented a different combination of age and estuary, excluding an interaction term, and one of which was an intercept-only model. For all models, age-2 fish and Charlotte Harbor served as statistical baselines for parameter estimation (i.e. the model intercept). We assessed the relative support for each of the 4 candidate models using Akaike's information criterion with a small-sample bias adjustment (AIC_C; Hurvich & Tsai 1989), where lower AIC_C values indicate a better supported model. We assessed the precision of parameter estimates by calculating standard errors and 95% confidence intervals. Lastly, we assessed goodness-of-fit of all models using a simulation-based, residual analysis approach, implemented in R using the 'DHARMa' package (Hartig 2019). All analyses were conducted using R v.3.5.1 (R Core Team 2018).

2.5.2. Network analysis

Comparing natal estuaries of Tampa Bay and Charlotte Harbor, we used network analyses to visualize subadult recruitment to nearshore adult spawning habitat, examining network use, movement patterns, and connectivity between Tampa Bay and Charlotte Harbor nearshore spawning habitats of subadults, both as new recruits and as repeat spawners. We analyzed the fish tagged in Tampa Bay separately from those tagged in Charlotte Harbor. For each estuary, we developed a spatial network combining detections from all tagged fish. We produced networks by estuary for each reproductive (August–December) and non-reproductive (January–July) period in each year (6 total periods: 3 non-reproductive and 3 reproductive). We selected reproductive periods based on previously identified red drum seasonal movements to and from spawning areas (Lowerre-Barbieri et al. 2016). We developed spatial networks with the package 'igraph' (Csardi & Nepusz 2006) in R v.3.5.0 (R Core Team 2017) based on weighted edge measurements. To calculate a weighted edge, we broke fish movements into sequential steps between pairs of receivers and tallied the total number of observations for each receiver pair during the 2 periods (reproductive and non-reproductive) for each estuary separately. We computed global edge density, which is the proportion of available edges used by fish (Jacoby et al. 2012, Lédée et al. 2015), for each network to compare saturation of movement. This allowed us to compare space use between estuaries and time periods, to understand how much of the available network the fish were using. A large edge density corresponds to greater space use. We expressed the relative importance of each receiver by node size and pathway between receivers by edge weight (line thickness). Receivers with larger node size are visited more frequently and have greater importance to the overall movement pattern. Likewise, thicker edge weights correspond to greater numbers of movements between adjacent receivers, indicating important pathways for fish.

3. RESULTS

3.1. Biological profile of tagged fish

Fish tagged in Tampa Bay and Charlotte Harbor were similar in size (Table 1) and age (Fig. 2) but Charlotte Harbor had a significantly higher percentage (75%) of fish that were mature at the time of tagging ($\chi^2 = 14.55$, n = 40, p < 0.0001) compared to 15% in Tampa Bay. Age range (1–3 yr) and average age (2.1 yr) were identical between the 2 estuaries.

Table 1. Red drum standard length (SL) statistics, tag fates, and recruitment duration (days) by estuary. For those fish that recruited, the recruitment day (RD) range and average are the number of days between the first date an individual was detected on any nearshore receiver and the mean arrival date (September 8) of repeat adult spawners to the Tampa Bay nearshore array (Lowerre-Barbieri et al. 2019b)

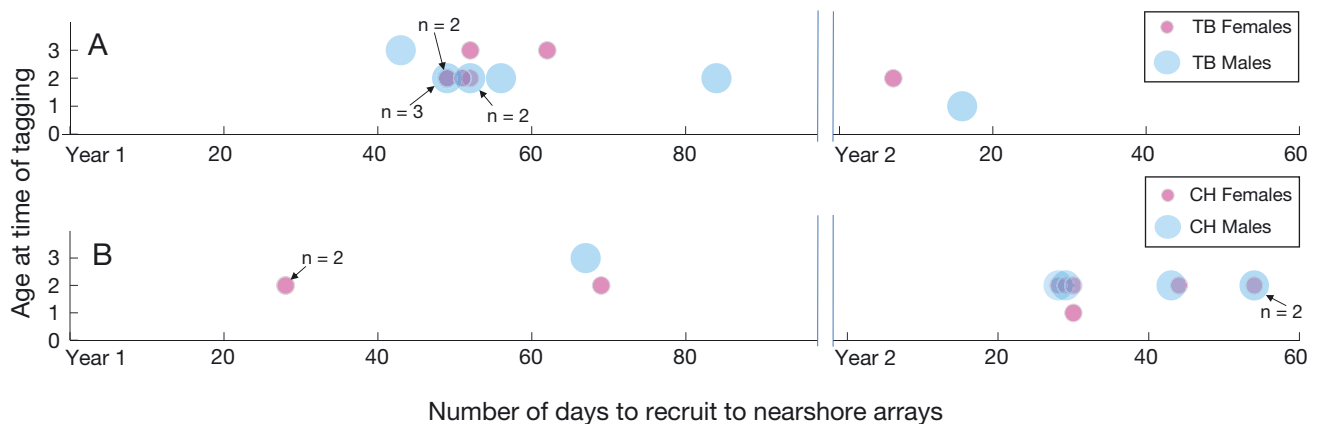| Estuary tagged	SL average (mm)	SL range (mm)	No. of fish never detected	No. of tags recovered	No. of fish detected only in estuary	No. of fish recruited nearshore	RD average (d)	RD range (d)
Tampa Bay	638	597–691	1	0	3	16	94	43–381
Charlotte Harbor	618	592–699	2	1	2	15	309	28–419

Fig. 2. Recruitment timing as measured by the number of days between the first date an individual fish was detected on any nearshore receiver and the mean arrival date (September 8) of repeat adult spawners to the Tampa Bay nearshore array (Lowerre-Barbieri et al. 2019b) according to sex and age at the time of tagging. Only tagged fish detected in the nearshore arrays are included in this figure. Fish tagged in (A) Tampa Bay (TB; n = 16) and (B) Charlotte Harbor (CH; n = 15); pink: females; blue: males. Several instances are indicated when a pair (by n = 2) or triad (n = 3) of fish of the same sex and age were detected on the same day. Note: although the *x*-axis scale for the number of recruitment days is the same for both estuaries, the actual years referenced are offset with Year 1 representing 2012 for (A) fish tagged in Tampa Bay and 2013 for (B) fish tagged in Charlotte Harbor

While there was an equal sex ratio in Tampa Bay, more females (n = 14) than males (n = 6) were tagged in Charlotte Harbor (70:30 ratio). Males (indicated by drumming) tagged in Charlotte Harbor expressed milt more frequently (67%) than males in Tampa Bay (only 30% of drumming fish expressed milt). With the exception of a single fish, females in Charlotte Harbor were confirmed via ovarian biopsy. However, in Tampa Bay, only 1 of the 10 fish classified as female was confirmed (the gonad was observed through the incision site); the remaining 9 were assigned female because they lacked male traits. Urogenital pores in fish from Tampa Bay were too small to enable biopsies—indicating that these females may not have been as sexually developed as those in Charlotte Harbor. Of biopsied females (n = 13) in Charlotte Harbor, 85% were mature, as indicated by the presence of secondary growth oocytes (mean age = 2 yr).

3.2. Tagging site profiles and tag accounting

We caught, tagged, and released fish in shallow water (0.6–1.2 m). The average salinity across sites in Tampa Bay was 28.03 ppt and ranged between 26.0 and 30.70 ppt while salinity at the Charlotte Harbor tagging site was much lower (13.1 ppt). We detected 90% of acoustically tagged fish in at least 1 of the 4 monitored habitats. One Tampa Bay fish was never detected, and in Charlotte Harbor 2 fish were never detected and another lost its tag or died (tag was recovered 3 wk later at the tagging site; Table 1); these 4 fish were removed from further analyses. The proportion of tagged fish detected in the nearshore arrays did not differ significantly between the 2 estuaries (Fisher's exact test, p = 0.3496), with 84% of Tampa Bay fish and 88% of Charlotte Harbor fish detected in nearshore adult habitat.
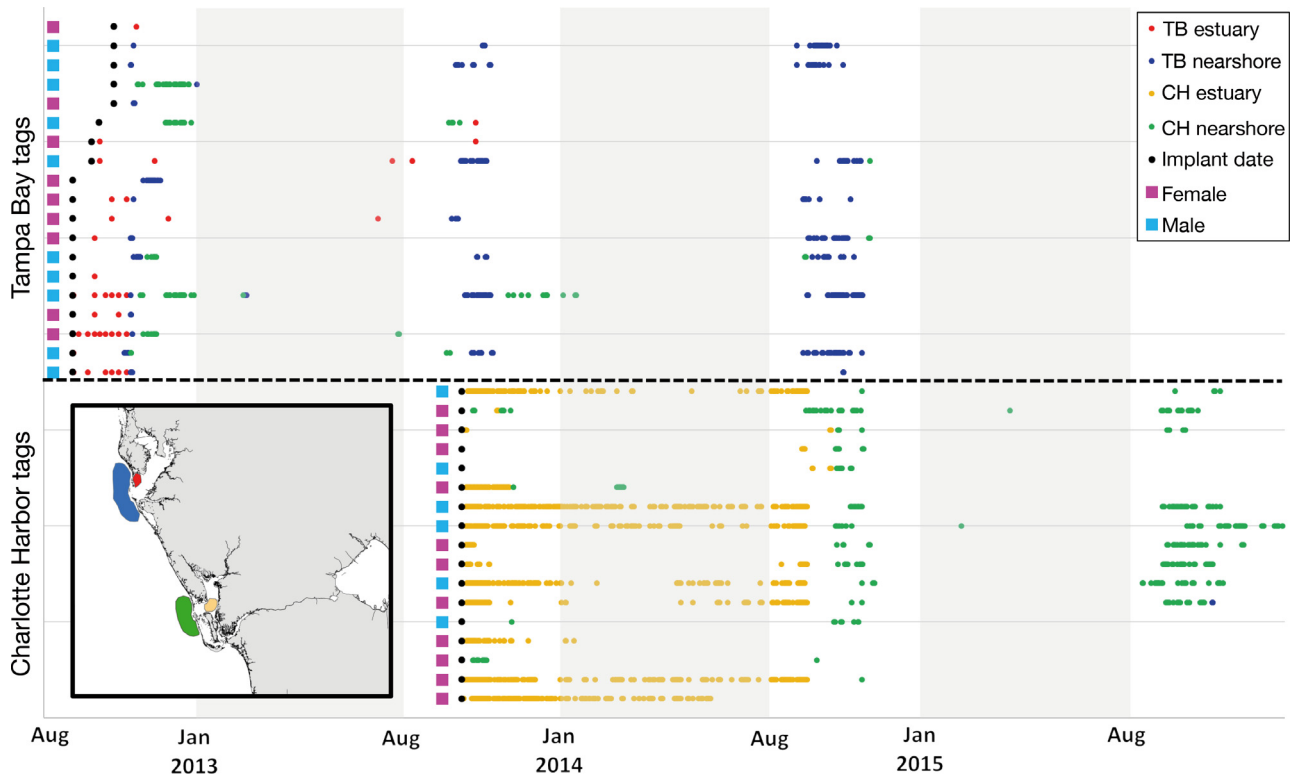
Fig. 3. Individual daily detections of acoustically tagged red drum by habitat. Fish above the dashed line: tagged in Tampa Bay; fish below: tagged in Charlotte Harbor. Detections within Tampa Bay habitats are either within the estuary detected by the mobile hydrophone survey (red dots) or within the nearshore array (blue dots). Detections within Charlotte Harbor habitats are either within the estuary at either of the 2 stationary receivers (yellow dots) or within the nearshore array (green dots). Vertical gray sections: non-reproductive period (January–July); vertical white sections: reproductive period (August–December); black dots: date tagged. Gender is demarked by a blue (male) or pink (female) box proceeding each tagging date

3.3. Estuarine detections and time of recruitment

Although highly variable at the individual level, fish that recruited to nearshore habitat did so significantly earlier in Tampa Bay than in Charlotte Harbor. On average, Tampa Bay fish (n = 16) took 94 d to recruit to nearshore habitat while Charlotte Harbor recruitment took over triple the amount of time, 309 d (n = 15; Table 1, Fig. 2). In total, 14 fish in Tampa Bay were detected in the nearshore habitat within their tagging year, whereas only 4 Charlotte Harbor fish were detected in nearshore habitat during the year tagged (Fig. 3), driving the large disparity in average recruitment time. For fish that recruited in the same year as they were tagged, recruitment time was similar between the 2 estuaries: 54 d in Tampa Bay and 48 d in Charlotte Harbor. Within both estuaries, the fish that did not recruit in the year they were tagged did so in the following year (Fig. 3), recruiting earlier in the reproductive season than fish from the same estuary did the year prior and with a larger disparity between estuaries (Fig. 2). While estuary significantly

affected recruitment timing to nearshore habitat, age did not. Model selection results based on AIC_C indicated equivalent support for 2 models (Table 2). The best approximating model contained only estuary and was 1.17 times (0.54/0.46) more plausible than the second-best approximating model that contained age and estuary (Table 2). There was no support for the model that contained only age, nor was there sup-

Table 2. Model description, number of parameters (*K*), Akaike's information criterion values (AIC_C, ΔAIC_C), and Akaike weights (*w*) for the candidate set of negative binomial regression models relating red drum age class (ages 2 and 3) and estuary (Tampa Bay and Charlotte Harbor) to the number of days between the recruitment time of individuals and the average recruitment time

Model	K	AIC_C	ΔAIC_C	w
Estuary	3	348.30	0.00	0.54
Age + estuary	4	348.64	0.34	0.46
Age	3	362.47	14.18	0.00
Null	2	365.06	16.76	0.00

port for the intercept-only model (Table 2). Because of their equivalent support, we chose to base inference on the more general, second-best approximating model that contained age and estuary. Based on this model, the rate ratio (exponentiated parameter estimate) associated with the parameter estimate for estuary indicated that the expected number of recruitment days was, on average, 3.64 times (1/0.28) lower in Tampa Bay compared to Charlotte Harbor (Table 3). Similarly, the rate ratio associated with the parameter estimate for age indicated that the expected number of recruitment days was, on average, 1.94 times (1/0.52) lower for age-3 fish compared to age-2 fish; however, this relationship was considered imprecise as the 95% confidence interval overlapped zero (Table 3). Lastly, the simulation-based assessment of residuals from each of the 4 candidate models indicated that all models provided an adequate fit to the observed data.

There was poor agreement between gonadal development and spatial indicators of maturity in Charlotte Harbor fish. Only 25% of the males which produced milt (n = 4) recruited to nearshore habitat in the year they were tagged. Recruitment may be more age-driven, as the 1 recruited fish was age 3 and the other 3 males were age 2 (Fig. 2). Similarly, of the 7 females with yolked oocytes at the time of tagging, only 1 fish (age 2) recruited that same year. The other 2 females to recruit during their tagging year (also age 2) did not exhibit histological maturity traits. Tampa Bay fish were not able to be biopsied, so maturity traits could not be assessed for females, and the low number of males with milt that recruited (n = 2) was too few to determine any maturity movement trends.

Schooling synchrony associated with egression from the estuary was documented in Charlotte Har-

bor at the tagging site but could not be assessed in Tampa Bay due to depth limitations preventing stationary receivers at the tagging sites. Of the 15 Charlotte Harbor fish to recruit to nearshore habitats, 67% shared their last inshore detection at the tagging site receiver in synchrony with at least 1 other fish. All 10 of these fish left the estuary during the second reproductive period. Transition time from the estuarine tagging site after the last detection to the first detection in the Charlotte Harbor nearshore array varied from 6–57 d with an average of 36 d. Nearly all of the 10 fish shared a nearshore recruitment metric (receiver or date or both) with another fish, but the same schooling partners were not observed when fish arrived in the nearshore habitat as when fish departed the estuarine tagging site.

Once a fish recruited to the nearshore, its return to the estuary was rare; the majority of recruited fish (28/31, 90%) exhibited apparent unidirectional movement, with 3 exceptions. It is important to note our ability to monitor the estuary for fish returning after recruitment to the nearshore arrays was limited to predominately areas within the vicinity where fish were tagged. In Tampa Bay, 9 fish (56%, n = 16) were detected within the estuary prior to recruitment to the nearshore during the mobile hydrophone survey and only 2 fish returned to estuarian habitat after recruiting. The first was a male tagged in mid-September 2012 that recruited to the nearshore on 1 December 2012, nearly 1 mo later than any of the 14 fish that recruited that year, likely a result of being first detected in the nearshore Charlotte Harbor array (Fig. 3). Nearly 11 mo after recruitment, and during the middle of the second reproductive period in 2013, this fish was detected back within the Tampa Bay estuary during the mobile hydrophone survey and was not detected again for the duration of the study (Fig. 3). The second Tampa Bay fish to return to the estuary after recruitment was reported by an angler fishing near an inlet off a pier 6.1 km to the north of the northernmost mobile hydrophone survey site. Extensive movements were recorded for this male fish on both nearshore arrays before and after its recapture; notably being the only fish detected on nearshore arrays outside of the reproductive periods in multiple years (Fig. 3). The third fish to demonstrate a brief estuarine return was a Charlotte Harbor female that recruited to Charlotte Harbor nearshore habitat exactly 1 mo

Table 3. Parameter estimates, SE, 95% CI (lower and upper), and rate ratios (RR) for the best- and second-best approximating negative binomial regression models relating red drum age (age 2 and age 3) and estuary (Tampa Bay and Charlotte Harbor) to the number of days between the recruitment time of individuals and the average recruitment time

Parameter	Estimate	SE	Lower CI	Upper CI	RR
Best approximating model					
Intercept (Charlotte Harbor)	5.71	0.19	5.36	6.11	
Tampa Bay	−1.40	0.27	−1.93	−0.87	0.25
Theta (overdispersion)	1.96	0.49			
Second-best approximating model					
Intercept (Charlotte Harbor)	5.73	0.19	5.38	6.11	
Age 3	−0.66	0.38	−1.39	0.18	0.52
Tampa Bay	−1.29	0.26	−1.82	−0.76	0.28
Theta (overdispersion)	2.11	0.53			

after being tagged. This fish was not initially detected within the estuary prior to recruitment, but 3 wk following nearshore recruitment, the fish was detected on the receiver moored in the middle of Charlotte Harbor nearly continuously over a 50 h time frame starting on 30 October 2013. Multiple detections of this fish followed on the nearshore Charlotte Harbor array for the remainder of the 2013 reproductive period as well as throughout the following 2 reproductive periods (Fig. 3).

3.4. Nearshore spatial patterns

Movement data within the nearshore arrays during the first and second reproductive periods revealed distinct differences in use of space and array connectivity between Tampa Bay and Charlotte Harbor fish. During the first reproductive period, Tampa Bay fish exhibited greater movement complexity compared to Charlotte Harbor fish, resulting in a higher value of edge density by using more of the available network (Fig. 4). Even though fish from both estuaries used the nearshore
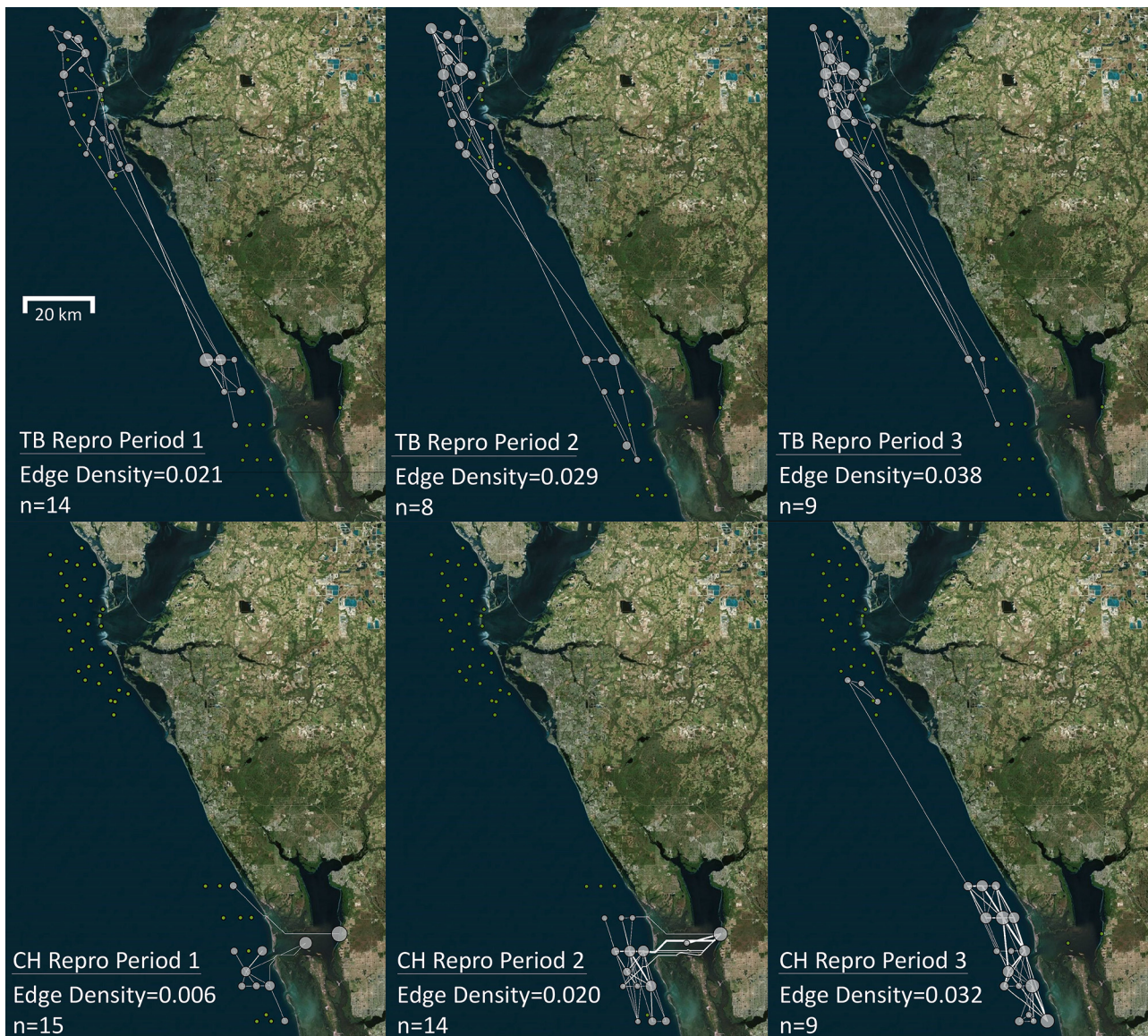

Fig. 4. Network analysis during 3 consecutive reproductive periods (August–December) for fish tagged in Tampa Bay (TB; top row, first reproductive period is 2012) and Charlotte Harbor (CH; bottom row, first reproductive period is 2013). Visited receivers are indicated by gray dots (nodes) and unvisited receivers by green dots (nodes). Detection frequency and relative importance of each receiver indicated by node size. Edge weight (line thickness) is proportional to the interaction frequency between connected receivers (i.e. more frequent interactions are depicted by thicker edge weight). Number of fish included in the analysis is reported (n) as well as the edge density metric, with a large edge density corresponding to greater space use

Charlotte Harbor array during their first respective reproductive periods, their movements were concentrated in different parts of the array. The Tampa Bay fish (n = 6) made significantly longer movements to reach the nearshore Charlotte Harbor array and were primarily detected on the most northern receivers of the nearshore Charlotte Harbor array during the end of the reproductive period. In contrast, during the earlier portion of the reproductive period, the Charlotte Harbor recruits (n = 4) were detected predominantly at the middle and southern receivers, in line with natural egression out of Charlotte Harbor through the most major estuarine inlet (Fig. 4). The Charlotte Harbor estuarine receiver at the tagging site was used by the largest number of fish in that estuary for the first 2 reproductive periods (Fig. 4), driven by the high site fidelity the fish had to the tagging site in conjunction with the delayed recruitment of the majority of tagged fish until the second reproductive period (Fig. 3). The prominence of the recruitment path from this estuarine tagging site receiver to the nearshore Charlotte Harbor array in the second reproductive period is evident in the edge weight graphic along with the expanded range of movement within the nearshore Charlotte Harbor array (Fig. 4). While the number of fish tracked from the Tampa Bay estuary decreased during the second reproductive period, the edge density increased (Fig. 4). The 6 returning fish, along with the final 2 recruits that joined them in the Tampa Bay nearshore habitat, exhibited similar movement patterns as the 14 Tampa Bay recruits did the previous reproductive period, but with an increase in space use and movements between receivers along with a slightly expanded range further south into the nearshore Charlotte Harbor array (Fig. 4).

Movements of fish from both estuaries were most similar during the last monitored reproductive period. As all recruited fish had moved nearshore by the conclusion of the second reproductive period, nearshore detections in the third reproductive period were from fish (n = 19) exhibiting natal homing, with special consideration of 4 fish which were also detected in the neighboring array (Fig. 3). These additional detections on neighboring arrays were either first or last detections within the reproductive period, likely capturing transition to or from natal arrays, as the majority of detections for all 4 fish occurred within the nearshore array corresponding to the natal estuary (Figs. 3 & 4). The most dramatic changes in node sizes and edge weights between the third reproductive period and the 2 prior periods occurred in the nearshore Charlotte Harbor array, indicating returning fish modified their use of the nearshore space

following recruitment to expand their range and movements (Fig. 4). Although the same number of Tampa Bay fish (n = 3) were present in the nearshore Charlotte Harbor array during this reproductive period as the prior reproductive period (different individuals), the overall amount of space used within the nearshore Charlotte Harbor array was reduced while the amount of connections between the 2 arrays increased (Fig. 4). Only one fish from Charlotte Harbor visited the nearshore Tampa Bay array, which was for 2 d in October 2015 (Fig. 4). Although Tampa Bay fish initially displayed greater space use during the first reproductive period compared to Charlotte Harbor fish, as the number of recruited Charlotte Harbor fish approached that of Tampa Bay, fish from both estuaries displayed an increase in space use and movement over time, and ended the third reproductive period with similar metrics of edge density (Fig. 4).

4. DISCUSSION

Spatial and temporal movement data of acoustically tagged red drum demonstrate the power of telemetry to capture transitions from nursery to spawning habitat that would otherwise be missed using biological data collection methods alone (Gillanders et al. 2003). While red drum habitat has been well documented for both subadults (Adams & Tremain 2000, Dresser & Kneib 2007, Bacheler et al. 2009, Kenworthy et al. 2018) and adults (Beckman et al. 1988, Murphy & Taylor 1990, Ross et al. 1995, Murphy & Crabtree 2001, Powers et al. 2012), few studies have linked the 2 habitats through multiple life history stages (Winner et al. 2014). Using telemetry to capture the specific ontogenetic shift from juvenile to adult habitat is relatively novel (Lowerre-Barbieri et al. 2016) and this study is the first to our knowledge to compare whether that transition differs between estuaries. Large juveniles have previously been found to move into the estuarine shoreline habitats of Tampa Bay between the ages of 6 mo and 1 yr, and remained there until age 3 or 4, but these movements were inferred from changes in relative abundance and progression of size- or age-classes among separate habitats (Winner et al. 2014). Similarly, biological data from North Carolina red drum indicate subadults join the adult population in coastal waters after maturity at age 3 or 4 (Ross et al. 1995), a pattern further supported by conventional and acoustic tagging within the same area showing age 3 to be the age when the last remaining estuarine red drum move to the coast (Bacheler et al. 2009). Tele-

metry detections from this study suggest a slightly earlier recruitment age to nearshore adult habitat, as we observed tagged fish recruiting out of the estuary by age 2 or 3. Although most fish sampled in Tampa Bay coastal waters have been 4 yr or older, fish as young as age 2 have been detected (Winner et al. 2014). As older and larger fish can have more extended spawning seasons that begin earlier than those of younger and smaller counterparts (Wright & Trippel 2009) and since degree of maturity varied at the time of tagging in this study with fish recruiting to the nearshore later in the spawning season, the extent to which these tagged fish contributed to the spawn is likely relatively small. Tagged fish from both estuaries demonstrated increased movement complexity over time, indicating spawning space use may evolve with maturity, potentially a social inter-action effect with the school of more experienced animals (Lowerre-Barbieri et al. 2016).

Differences in the recruitment timing of tagged subadult red drum between 2 neighboring estuaries observed in this study indicate that the mechanism which signals transition from nursery habitat to adult habitat is not driven simply by a size, age, or even maturity threshold. Nearly all Tampa Bay tagged fish recruited within the same year of being tagged and few showed signs of advanced maturity. Conversely, Charlotte Harbor fish of the same age did not recruit until the year following tagging despite having more progressed signs of advanced maturity. During the 2nd reproductive period, the majority of Charlotte Harbor fish demonstrated relatively consistent site fidelity to the tagging site, adding to growing evidence of subadult red drum demonstrating high residency at specific sites (Dresser & Kneib 2007, Bacheler et al. 2009, Kenworthy et al. 2018). Delayed recruitment by Charlotte Harbor fish could be due, in part, to the greater distance of the tagging site from the nearshore habitat compared to the distance in Tampa Bay. Charlotte Harbor fish had to move 3 times the distance as Tampa Bay fish to reach the nearshore habitat, yet fish from both estuaries who recruited in the year they were tagged had similar mean recruitment times post-tagging (54 d in Tampa Bay and 48 d in Charlotte Harbor). Since fish were tagged in different years and in different areas, annual variability in environmental cues cannot be ruled out. However, as water temperature and rain-fall for 2012 and 2013 showed similar patterns for both areas between years and sites (using the US Geological Society's National Water Information System; https://nwis.waterdata.usgs.gov/nwis), there do not appear to be any major differences.

Red drum are known to experience variation in juvenile recruitment, as documented by the persist-ence of strong year-class strength through ontogeny to adulthood (Ross et al. 1995, Rooker et al. 1998, Scharf 2000, Murphy & Crabtree 2001, Winner et al. 2014). Additionally, red drum have been shown to demonstrate individual behavioral plasticity in rela-tion to recruitment to adult habitat (Lowerre-Barbieri et al. 2016) but it is unknown if there is behavioral plasticity on a cohort level associated with recruit-ment cycles or if there is a density-dependent effect on recruitment timing. Annual indices of abundance of riverine young-of-the-year red drum in Tampa Bay and Charlotte Harbor show similar patterns of rela-tively low, but stable, recruitment following peaks in 2003 and 2004 (Tampa Bay) and in 2002 and 2003 along with a smaller increase in 2010 (Charlotte Har-bor) (FWC-FIM 2013), indicating that although tag-ging occurred in different years, it is unlikely the year-long delay of Charlotte Harbor fish to recruit to adult habitat was an effect of year-class strength. The mechanism driving egression out of the estuary has been hypothesized to be tied to subadults encounter-ing adults and becoming integrated into the spawn-ing school in nearshore Tampa Bay (Lowerre-Barbieri et al. 2016), but this concept is unlikely to apply in Charlotte Harbor where the geographic delineation between subadult and adult habitat is much larger. As the apparent rate of return of adult red drum to the estuary was shown to be low in this study (3 individuals) and to areas proximate to the estuarine mouth, it follows that subadults in higher saline areas adjacent to nearshore waters would have increased opportunity to encounter these returning adults or possibly cues from the nearshore aggregations, resulting in earlier recruitment to the adult population as seen in Tampa Bay fish.

Delayed recruitment by Charlotte Harbor fish potentially elevates their mortality rate, since expo-sure to the recreational fishery is higher within the confines of the estuary compared to the open near-shore environment. Although fish tagged in this study were outside of the legal limits of a slot fish, their longer residence within the estuary increases the opportunity for catch-and-release fishing and the associated post-release stress or post-release mortal-ity (5.6%; Flaherty et al. 2013) coupled with illegal harvest, as experienced by the residential adults in the Indian River Lagoon (Reyier et al. 2011). We specifically targeted certain areas within both Tampa Bay and Charlotte Harbor for tagging and monitoring due to their annual predictability of hosting large schools of subadult red drum — knowledge shared

by anglers and guides who anticipate and plan to fish at these locations. Although most (86%) tagged fish in both Tampa Bay and Charlotte Harbor successfully recruited to the nearshore, it is unknown if the 5 fish detected within the estuary but not detected on the nearshore arrays simply did not recruit, recruited without detection (especially in Charlotte Harbor where fish could recruit to the south of the array by transitioning along the intracoastal), or potentially did not escape the estuary due to fishing pressures. Professional guides in both estuaries have voiced concerns about the escalating fishing pressure on these subadult schools as the angler population has swelled and there has been a perceived decline in the number of fish and reduced cohesiveness of the remaining schools (DMFM 2016). Current Florida management for red drum divides the state into 4 regions: northern and southern on each coast (Chagaris et al. 2015). Smaller scale management units, such as by estuary, may be more biologically appropriate for red drum given the difference in recruitment timing, but enforcement challenges at this small scale may prove to be impractical. Increased estuarine-time raises risk to fishing pressure, plus other local-scale effects such as freshwater inflow and water quality, as they could influence the population dynamics of a fishery shown to have local production (Rooker et al. 2010). Although the latest state-level stock assessment did not raise concerns over management benchmarks of escapement rates (Chagaris et al. 2015), continued monitoring of the subadult and young-of-the-year classes will be necessary to ensure that increased fishing pressure or ecosystem stressors (most recently, a protracted red tide bloom of *Karenia brevis* affecting both Tampa Bay and Charlotte Harbor from September 2017 to January 2019; Weisberg et al. 2019) are not detrimental to recruitment.

The sexual development disparity between fish of similar size and age in Tampa Bay and Charlotte Harbor coupled with the delayed movement of the more developed Charlotte Harbor fish to the nearshore habitat raises possibilities of red drum spawning within Charlotte Harbor or that secondary growth oocytes are poor indicators of functional maturity. Spawning in Florida primarily occurs in proximity to inlets, bay mouths, or nearshore areas (Murphy & Taylor 1990, Lowerre-Barbieri et al. 2016) but has also been reported to a lesser degree within estuaries, particularly within areas of the Indian River Lagoon where high salinity provides an environment more typical of marine rather than estuarine waters (Murphy & Taylor 1990, Johnson & Funicelli 1991,

Reyier et al. 2011). Of the 13 biopsied Charlotte Harbor females, 11 were mature at the time of tagging in fall 2013 and only 2 of these mature fish moved offshore during the first reproductive period. The majority of the remaining mature females, along with a similar proportion of mature males at the time of tagging (as indicated by milt release) were detected at the tagging site until their movement offshore the following reproductive period, indicating that gonadal development is not indicative of functional maturity or that fish potentially spawn within the estuary. Spawning at the actual tagging site is unlikely due to salinity limitations preventing successful hatching and larval survival, as optimal salinity for hatching success (30 ppt; Holt et al. 1981) is over double the value measured at the tagging site. However, because fish were not accounted for comprehensively at the tagging site during the first reproductive period and could potentially move undetected to more salinity-appropriate areas of the harbor to spawn, and because it was not possible to determine if these physiologically mature fish were functionally mature, spawning within the estuarine system in what would presumably be their first year of maturity is a possibility that should not be negated and merits further study. Fish ultimately recruited to the nearshore adult habitat during the reproductive period the year following tagging and (with the exception of one fish) did not return to the estuary, indicating the predominate spawning habitat is in nearshore waters and estuarine spawning, if occurring, is likely on a small level and involves younger and inexperienced fish. Histological assessments of subadults sacrificed in the Tampa Bay estuary at the time when Tampa Bay fish in this study were tagged indicate the majority of females of a similar size were immature, and although males had some level of spermatogenesis, milt reserves were low, indicating a delay of functional maturity (Lowerre-Barbieri et al. 2016). Conversely, virtually all females caught in red drum nearshore aggregations that were of the same size as tagged fish were mature, indicating a strong locational effect on reproductive state (Lowerre-Barbieri et al. 2016).

Natal-site philopatry by fish tagged in both estuaries was demonstrated by their return in subsequent reproductive periods to nearshore spawning habitat in proximity to the estuary where they were originally tagged. Lowerre-Barbieri et al. (2016) first reported that two-thirds of the Tampa Bay subadults return to natal areas, and Charlotte Harbor subadults in this study exhibited an even higher rate of natal homing with close to 75% returning to Charlotte

Harbor nearshore waters. Movements of both groups of fish away from the nearshore areas outside of the spawning season, and their return during reproductive periods, helps strengthen the case for philopatry as opposed to retention (Patterson et al. 2004, Rooker et al. 2010). Charlotte Harbor fish exhibited nearly exclusive site fidelity to nearshore natal habitat, with only one fish moving to the nearshore Tampa Bay array during the last reproductive period. Tampa Bay fish, however, demonstrated increased mixing, with detections on the Charlotte Harbor nearshore array during all reproductive periods — a pattern also shared by acoustically tagged adult red drum in nearshore Tampa Bay waters (Lowerre-Barbieri et al. 2019b). Red drum population structure in the Gulf of Mexico follows an isolation-by-distance pattern with the highest probability of gene exchange occurring between adjacent estuaries and bays (Gold et al. 2001). As Tampa Bay and Charlotte Harbor are neighboring estuaries, both with robust red drum nurseries (Seyoum et al. 2000) and nearshore spawning aggregations (Murphy & Crabtree 2001, Patterson et al. 2004, Winner et al. 2014, Lowerre-Barbieri et al. 2016), use of both areas as spawning habitat within a given reproductive period would increase connectivity rates between habitats and potentially serve to increase resiliency to temporal stressors (fishing pressure) or spatial disturbances such as red tide (Gold et al. 2001, Thorrold et al. 2001, Lowerre-Barbieri et al. 2017).

We sought to evaluate effects of natal estuary on a variety of factors associated with recruitment and subsequent reproductive behaviors of red drum, and our results demonstrated estuarine-specific demographics and behavioral ecology. Because of the size and scope of the area used by this species, acoustic tracking of individuals both within the estuary and in the nearshore environment involved porous acoustic coverage as it was not possible to continuously monitor all potential habitat. Our recruitment assessment to adult habitat is therefore potentially conservative and, conversely, we may have missed instances of fish moving back into the estuaries. Imperfect detections, however, did not prevent our ability to determine that recruitment and movement ecology differs by natal estuary. The year-long delay to recruit by Charlotte Harbor fish merits further study to determine if this was merely an effect of the tagging site or is an estuarine-wide behavior. This extended estuarine residence and consequently longer exposure to the fishery may eventually result in a localized effect on the population, given that our data demonstrate natal homing is prevalent with the primary source to replenish the adult population locally entrained in the most proximate estuary. Similarly, although Tampa Bay fish in this study recruited more quickly, all tagged fish were caught and released at the mouth of the estuary and further work to target fish in other areas of the estuary would help evaluate if the estuarine mouth site is a primary or secondary source for recruits to the spawning population. Additional work to further elucidate the level of connectivity between red drum subadult and adult populations will only improve the efficacy of management conservation of this iconic species (Gillanders et al. 2003), especially in light of increasing ecosystem challenges associated with coastal development (Halpern et al. 2008), as experienced by the central west coast of Florida.

LITERATURE CITED

Adams DH, Tremain DM (2000) Association of large juvenile red drum, *Sciaenops ocellatus*, with an estuarine creek on the Atlantic coast of Florida. Environ Biol Fishes 58: 183–194

Allen AM, Singh NJ (2016) Linking movement ecology with wildlife management and conservation. Front Ecol Evol 3:155

Allman RJ, Patterson WF, Fioramonti CL, Pacicco AE (2018) Factors affecting estimates of size at age and growth in grey triggerfish *Balistes capriscus* from the northern Gulf of Mexico. J Fish Biol 92:386–398

Bacheler N, Paramore L, Burdick S, Buckel J, Hightower J (2009) Variation in movement patterns of red drum (*Sciaenops ocellatus*) inferred from conventional tagging and ultrasonic telemetry. Fish Bull 107:405–418

Beck MW, Heck KL Jr, Able KW, Childers DL and others (2001) The identification, conservation, and management of estuarine and marine nurseries for fish and invertebrates. Bioscience 51:633–641

Beckman DW, Wilson CA, Stanley AL (1988) Age and growth of red drum, *Sciaenops ocellatus*, from offshore waters of the northern Gulf of Mexico. Fish Bull 87:17–28

Brown-Peterson N, Wyanski D, Saborido-Rey F, Macewicz B, Lowerre-Barbieri S (2011) A standardized terminology for describing reproductive development in fishes. Mar Coast Fish 3:52–70

Chagaris D, Mahmoudi B, Murphy M (2015) The 2015 stock assessment of red drum, *Sciaenops ocellatus*, in Florida. Publication No. IHR2015-003. Florida Fish and Wildlife Conservation Commission, Tallahassee, FL

Csardi G, Nepusz T (2006) The igraph software package for complex network research. InterJournal Complex Syst 1695:1–9

Dance MA, Rooker JR (2015) Habitat- and bay-scale connectivity of sympatric fishes in an estuarine nursery. Estuar Coast Shelf Sci 167:447–457

DMFM (Division of Marine Fisheries Management) (2016) Red drum stakeholder engagement review and discussion public hearing, April 13, 2016. Florida Fish and Wildlife Conservation Commission, Jupiter, FL

Dresser BK, Kneib RT (2007) Site fidelity and movement patterns of wild subadult red drum, *Sciaenops ocellatus* (Linnaeus), within a salt marsh-dominated estuarine landscape. Fish Manag Ecol 14:183–190

Flaherty KE, Winner BL, Vecchio JL, Switzer TS (2013) Spatial and size distribution of red drum caught and released in Tampa Bay, Florida, and factors associated with post-release hooking mortality. Gulf Caribb Res 25:29–41

FWC-FIM (Fish and Wildlife Conservation Commission-Fisheries Independent Monitoring) (2013) Fisheries-Independent Monitoring Program 2013 annual data summary report. Florida Fish and Wildlife Research Institute, St Petersburg, FL

Gillanders BM, Able KW, Brown JA, Eggleston DB, Sheridan PF (2003) Evidence of connectivity between juvenile and adult habitats for mobile marine fauna: an important component of nurseries. Mar Ecol Prog Ser 247:281–295

Gold JR, Burridge CP, Turner TF (2001) A modified stepping-stone model of population structure in red drum, *Sciaenops ocellatus* (Sciaenidae), from the northern Gulf of Mexico. Genetica 111:305–317

Goodwin CR (1987) Tidal-flow, circulation, and flushing changes caused by dredge and fill in Tampa Bay, Florida. US Geological Survey, Water-Supply Paper No. 2282. US Geological Survey. https://pubs.er.usgs.gov/publication/wsp2282

Goodwin CR (1996) Simulation of tidal-flow, circulation, and flushing of the Charlotte Harbor estuarine system, Florida. US Geological Survey, Water Resources Investigations Report No. 93–4153. US Geological Survey. https://pubs.er.usgs.gov/publication/wri934153

Halpern BS, McLeod KL, Rosenberg AA, Crowder LB (2008) Managing for cumulative impacts in ecosystem-based management through ocean zoning. Ocean Coast Manage 51:203–211

Hartig F (2019) DHARMa: Residual diagnostics for hierarchical (multi-level/mixed) regression models. R package version 0.2.4. https://CRAN.R-project.org/package=DHARMa

Heupel MR, Semmens JM, Hobday AJ (2006) Automated acoustic tracking of aquatic animals: scales, design and deployment of listening station arrays. Mar Freshw Res 57:1–13

Holt SA (2008) Distribution of red drum spawning sites identified by a towed hydrophone array. Trans Am Fish Soc 137:551–561

Holt J, Godbout R, Arnold C (1981) Effects of temperature and salinity on egg hatching and larval survival of red drum *Sciaenops ocellatus.* Fish Bull 79:569–573

Hueter RE, Manire CA (1994) Bycatch and catch-release mortality of small sharks in the Gulf coast nursery grounds of Tampa Bay and Charlotte Harbor. Mote Marine Technical Report No. 368. Final report to NOAA/NMFS/MARFIN, Project NA17FF0378-01. Mote Marine Laboratory, Sarasota, FL

Humston R, Ault J, Larkin MF, Luo J (2005) Movements and site fidelity of the bonefish *Albula vulpes* in the northern Florida Keys determined by acoustic telemetry. Mar Ecol Prog Ser 291:237–248

Hurvich CM, Tsai C (1989) Regression and time series model selection in small samples. Biometrika 76:297–307

Ihde TF, Chittenden ME (2003) Validation of presumed annual marks on sectioned otoliths of spotted seatrout, *Cynoscion nebulosus*, in the Chesapeake Bay region. Bull Mar Sci 72:77–87

Jacoby DMP, Brooks EJ, Croft DP, Sims DW (2012) Developing a deeper understanding of animal movements and spatial dynamics through novel application of network analyses. Methods Ecol Evol 3:574–583

Johnson DR, Funicelli NA (1991) Spawning of red drum in Mosquito Lagoon, east-central Florida. Estuaries 14:74–79

Kenworthy MD, Grabowski JH, Layman CA, Sherwood GD and others (2018) Movement ecology of a mobile predatory fish reveals limited habitat linkages within a temperate estuarine seascape. Can J Fish Aquat Sci 75:1990–1998

Kerr LA, Hintzen NT, Cadrin SX, Clausen LW and others (2017) Lessons learned from practical approaches to reconcile mismatches between biological population structure and stock units of marine fish. ICES J Mar Sci 74:1708–1722

Lédée EJ, Heupel MR, Tobin AJ, Knip DM, Simpfendorfer CA (2015) A comparison between traditional kernel-based methods and network analysis: an example from two nearshore shark species. Anim Behav 103:17–28

Lowerre-Barbieri SK, Henderson N, Llopiz J, Walters S, Bickford J, Muller R (2009) Defining a spawning population (spotted seatrout *Cynoscion nebulosus*) over temporal, spatial, and demographic scales. Mar Ecol Prog Ser 394:231–245

Lowerre-Barbieri S, Ganias K, Saborido-Rey F, Murua H, Hunter J (2011) Reproductive timing in marine fishes: variability, temporal scales, and methods. Mar Coast Fish 3:71–91

Lowerre-Barbieri SK, Walters S, Bickford J, Cooper W, Muller R (2013) Site fidelity and reproductive timing at a spotted seatrout spawning aggregation site: individual versus population scale behavior. Mar Ecol Prog Ser 481:181–197

Lowerre-Barbieri SK, Walters Burnsed SL, Bickford JW (2016) Assessing reproductive behavior important to fisheries management: a case study with red drum, *Sciaenops ocellatus.* Ecol Appl 26:979–995

Lowerre-Barbieri S, DeCelles G, Pepin P, Catalán IA and others (2017) Reproductive resilience: a paradigm shift in understanding spawner-recruit systems in exploited marine fish. Fish Fish 18:285–312

Lowerre-Barbieri SK, Kays R, Thorson JT, Wikelski M (2019a) The ocean's movescape: fisheries management in the bio-logging decade (2018–2028). ICES J Mar Sci 76:477–488

Lowerre-Barbieri SK, Tringali MD, Shea CP, Walters Burnsed S, Bickford J, Murphy M, Porch C (2019b) Assessing red drum spawning aggregations and abundance in the eastern Gulf of Mexico: a multidisciplinary approach. ICES J Mar Sci 76:516–552

Murphy MD, Crabtree RE (2001) Changes in the age structure of nearshore adult red drum off west-central Florida related to recruitment and fishing mortality. N Am J Fish Manage 21:671–678

Murphy MD, Taylor RG (1990) Reproduction, growth, and mortality of red drum *Sciaenops ocellatus* in Florida waters. Fish Bull 88:531–542

Overstreet RM (1983) Aspects of the biology of the red drum, *Sciaenops ocellatus*, in Mississippi. Gulf Res Rep 7(Suppl 1):45–68

Patterson H, McBride R, Julien N (2004) Population structure of red drum (*Sciaenops ocellatus*) as determined by otolith chemistry. Mar Biol 144:855–862

Pattillo MA, Czapla TE, Nelson DM, Monaco ME (1997) Distribution and abundance of fishes and invertebrates in Gulf of Mexico estuaries, Vol 2: species life history summaries. NOAA's Estuarine Living Marine Resources (ELMR) Report No. 11. NOAA/NOS Strategic Environmental Assessments Division, Silver Spring, MD

Peters KM, McMichael RH Jr (1987) Early life history of the red drum, *Sciaenops ocellatus* (Pisces: Sciaenidae), in Tampa Bay, Florida. Estuaries 10:92–107

Petitgas P, Secor DH, McQuinn I, Huse G, Lo N (2010) Stock collapses and their recovery: mechanisms that establish and maintain life-cycle closure in space and time. ICES J Mar Sci 67:1841–1848

Petitgas P, Rijnsdorp AD, Dickey-Collas M, Engelhard GH and others (2013) Impacts of climate change on the complex life cycles of fish. Fish Oceanogr 22:121–139

Powers SP, Hightower CL, Drymon JM, Johnson MW (2012) Age composition and distribution of red drum (*Sciaenops ocellatus*) in offshore waters of the north central Gulf of Mexico: an evaluation of a stock under a federal harvest moratorium. Fish Bull 110:283–292

Quintero-Hunter I, Grier H, Muscato M (1991) Enhancement of histological detail using metanil yellow as counterstain in periodic acid Schiff's hematoxylin staining of glycol methacrylate tissue sections. Biotech Histochem 66:169–172

R Core Team (2017) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna

R Core Team (2018) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna

Reyier EA, Lowers RH, Scheidt DM, Adams DH (2011) Movement patterns of adult red drum, *Sciaenops ocellatus*, in shallow Florida lagoons as inferred through autonomous acoustic telemetry. Environ Biol Fishes 90:343–360

Rooker JR, Holt SA, Holt GJ, Fuiman LA (1999) Spatial and temporal variability in growth, mortality, and recruitment potential of postsettlement red drum, *Sciaenops ocellatus*, in a subtropical estuary. Fish Bull 97: 581–590

Rooker JR, Stunz GW, Holt SA, Minello TJ (2010) Population connectivity of red drum in the northern Gulf of Mexico. Mar Ecol Prog Ser 407:187–196

Ross JL, Stevens TM, Vaughan DS (1995) Age, growth, mortality, and reproductive biology of red drums in North Carolina waters. Trans Am Fish Soc 124:37–54

Scharf FS (2000) Patterns in abundance, growth, and mortality of juvenile red drum across estuaries on the Texas coast with implications for recruitment and stock enhancement. Trans Am Fish Soc 129:1207–1222

Secor DH (2015) Migration ecology of marine fishes. Johns Hopkins University Press, Baltimore, MD

Seyoum S, Tringali MD, Bert TM, McElroy D, Stokes R (2000) An analysis of genetic population structure in red drum, *Sciaenops ocellatus*, based on mtDNA control region sequences. Fish Bull 98:127–138

Stehfest KM, Patterson TA, Dagorn L, Holland KN, Itano D, Semmens JM (2013) Network analysis of acoustic tracking data reveals the structure and stability of fish aggregations in the ocean. Anim Behav 85:839–848

Thorrold SR, Latkoczy C, Swart PK, Jones CM (2001) Natal homing in a marine fish metapopulation. Science 291: 297–299

Weisberg RH, Liu Y, Lembke C, Hu C, Hubbard K, Garrett M (2019) The coastal ocean circulation influence on the 2018 West Florida Shelf *K. brevis* red tide bloom. J Geophys Res C Oceans 124:2501–2512

Wilson C, Nieland DL (1994) Reproductive biology of red drum, *Sciaenaps oscellatus*, from the neritic waters of the northern Gulf of Mexico. Fish Bull 92:841–850

Winner BL, Flaherty-Walia KE, Switzer TS, Vecchio JL (2014) Multidecadal evidence of recovery of nearshore red drum stocks off west-central Florida and connectivity with inshore nurseries. N Am J Fish Manage 34:780–794

Wright PJ, Trippel EA (2009) Fishery-induced demographic changes in the timing of spawning: consequences for reproductive success. Fish Fish 10:283–304