INVITED FEATURE: ACOUSTIC TELEMETRY IN FISHERIES MANAGEMENT

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Assessing reproductive behavior important to fisheries management: a case study with red drum, *Sciaenops ocellatus*

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Abstract. Spawning site selection and reproductive timing affect stock productivity and structure in marine fishes but are poorly understood. Traditionally, stock assessments measure reproductive potential as spawning stock biomass or egg production and do not include other aspects of reproductive behavior. Red drum make an excellent case study to assess these other aspects, as (1) they are highly fecund, pelagic spawners, like most exploited marine fishes; (2) their life cycle is delineated between nursery (estuarine) and adult (coastal and offshore) habitat; and (3) they are managed at these two spatial scales. This study was conducted from August 2012 to December 2013 and integrates data from multiple methods and spatial scales. Aerial surveys were used for large-scale monitoring of aggregations off two known estuarine nursery areas, Tampa Bay and Charlotte Harbor, Florida, USA. Capture-based sampling in Tampa Bay coastal (n = 2581) and estuarine waters (n = 158) was used to assess reproductive state and to confirm coastal spawning. To assess spatial dynamics, we acoustically tagged two population components in the Tampa Bay system, subadults from the estuary (n = 20) and adults from the coastal spawning site (n = 60). Behavioral plasticity was seen in subadult recruitment to coastal habitat, with some subadults maturing and recruiting before or during the spawning season and others (14 of 20 acoustically tagged fish) recruiting at the end of the 2012 spawning season. Both adults and recruited subadults (n = 29) were consequently detected in the Charlotte Harbor array, 132 km to the south. Spawning-site fidelity to the Tampa Bay spawning site occurred at both the population and individual scales. Aggregations consistently occurred in Tampa Bay coastal waters during the spawning season, and approximately two-thirds of tagged adults returned in the 2013 spawning season. A similar proportion of subadults returned to the Tampa Bay spawning site, exhibiting natal homing. However, these first-time spawners arrived later than repeat spawners and were detected over shorter time periods. This study, and others like it, demonstrates how integrating data from individuals tracked over space and time with more traditional population-based sampling is changing our understanding of ecological processes that affect marine fish productivity and our ability to manage for sustainablity.

Key words: acoustic telemetry; Charlottte Harbor, Florida; connectivity; fisheries management; maturation; natal homing; red drum; reproductive behavior; Sciaenops ocellatus; *site fidelity; spatial ecology; spawning; stock structure; Tampa Bay; Florida.*

Introduction

Conserving a stock's future productivity is a fundamental goal of marine fisheries management (Goodyear 1993). In traditional stock assessments, this is accomplished through defining stock boundaries, or the management unit, and then assessing the stock's reproductive potential based on spawning stock biomass (SSB) as a proxy for egg production. Future productivity and stock resilience are estimated with a stock–recruitment relationship. However, highly fecund marine fish typically exhibit poor stock–recruitment relationships, and there is growing awareness that factors in addition to the abundance of mature females and fecundity affect reproductive success (Lowerre-Barbieri et al. 2015). Most marine fish species exhibit some level of breeding population isolation, and this isolation and dispersal amongst sub-populations plays an important role in stock productivity (Spies et al. 2015). In addition, we are learning that spawning site selection and reproductive timing may

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impact productivity as much, or more, than adult stock size (Berkeley et al. 2004, Maunder and Deriso 2013). Because most exploited marine fish are pelagic spawners, releasing huge numbers of small buoyant eggs (Murua and Saborido-Rey 2003) where and when they spawn determines the first environment eggs encounter, including the predator field, environmental factors, and current regime, all of which can impact recruitment success (Jorgensen et al. 2008, Lowerre-Barbieri et al. 2011). In addition, at the individual scale a fish's birth environment may affect its lifetime spatial ecology (Claydon 2004, Ciannelli et al. 2015). This is obvious for fishes exhibiting natal homing, but birth environment can also introduce ecological constraints on the habitats a fish encounters and uses over its lifespan (Ciannelli et al. 2015).

In fisheries science, two common conceptual models used to understand the spatial processes are the metapopulation concept (Levins 1968, Smedbol and Wroblewski 2002) and contingent theory (Kraus and Secor 2004, Cadrin and Secor 2009). Key spatial elements of an individual's life cycle include where an individual is spawned (i.e., the spawning site used by its parents), larval retention area, juvenile nursery habitat, adult feeding habitat, and where that individual spawns, which closes the life cycle and results in either philopatry or allopatry (Smedbol and Stephenson 2001). With acoustic telemetry, it is now possible to begin to follow individuals over space and time to assess reproductive behavior (Dean et al. 2014, Lowerre-Barbieri et al. 2014, Zemeckis et al. 2014) and how movement patterns associated with this behavior can affect fisheries selectivity (Nielsen and Berg 2014, Villegas-Ríos et al. 2014), productivity (Goethel et al. 2011, 2014), and our ability to obtain representative samples to estimate life history parameters, such as length and age at sexual maturation (Gillanders et al. 2003) and spawning frequency (Lowerre-Barbieri et al. 2013).

Red drum, *Sciaenops ocellatus*, in the Gulf of Mexico make an excellent case study for assessing how reproductive behavior affects population structure, as they have clearly delineated estuarine nursery grounds and coastal adult habitat (Rooker et al. 2010). Red drum are moderately long-lived, living to >30 yr (Winner et al. 2014), and highly fecund, producing multiple batches of pelagic eggs (capable of producing >3 million eggs per batch; Wilson and Nieland 1994) during a late-summer/fall spawning season, from August to November (Beckman et al. 1988, Murphy and Crabtree 2001). Adults form large pelagic schools along the United States' Gulf and Atlantic coasts in the fall (Beckman et al. 1988, Murphy and Taylor 1990, Pafford et al. 1990, Ross et al. 1995), spawning primarily in coastal waters off the mouths of estuaries, where the larvae recruit to tidal creeks and rivers (Peters and McMichael 1987, Murphy and Crabtree 2001). In Tampa Bay, Florida's largest open-water estuary, fish recruit to the main estuary at approximately 6 months–1 yr and 150–300 mm total length (TL), remaining until approximately age 3 or 4 (500–800 mm TL), when they seek higher salinity waters at the mouth of the estuary (Winner et al. 2014). This pattern of ontogenetic habitat shifts with recruitment to coastal or offshore adult habitat has been repeatedly reported for red drum throughout their range (Wilson and Nieland 1994, Bacheler et al. 2009, Winner et al. 2014). However, it is not prescriptive, as year-round residents have been documented in the high salinity estuarine environment of Indian River Lagoon, Florida, USA (Reyier et al. 2010).

The population structure of red drum in the Gulf of Mexico follows an isolation-by-distance pattern (Gold et al. 2001). Although the dispersal potential of adult red drum is assumed to be high given their ability to travel long distances (Overstreet 1983), prior research suggests natal homing, with the caveat that movement away from the estuaries is needed to disprove retention as the cause for the observed pattern (Patterson et al. 2004, Rooker et al. 2010). In this study, we integrate data from biotelemetry with more traditional sampling methods, including capture-based sampling and aerial surveys. Our study site includes coastal waters off two of the three major estuaries along Florida's Gulf coast: Tampa Bay and Charlotte Harbor, both of which are red drum nursery grounds (Seyoum et al. 2000). Red drum aggregations are known to occur in the fall in Tampa Bay coastal waters (Murphy and Crabtree 2001, Patterson et al. 2004, Winner et al. 2014), and we hypothesize that these are spawning aggregations and that similar aggregations occur in coastal waters off Charlotte Harbor, 132 km to the south.

We developed a conceptual model of red drum spatial ecology within our study site to test multiple hypotheses (Fig. 1). The model predicts that adults move to Tampa Bay and Charlotte Harbor coastal aggregation sites during late summer/early fall to spawn. Larval retention and nursery habitat are discrete and associated with the estuary adjacent to the aggregation site. Subadults leave their natal estuaries for the first time to recruit to the adjacent aggregation site as they mature. Given the strong schooling instinct of red drum (Porch 2000), first-time spawners are expected to exhibit movements similar to those of repeat spawners. The specific hypotheses tested within this conceptual framework are (1) red drum aggregations occur in the fall in Tampa Bay and Charlotte Harbor coastal waters, (2) length distributions and reproductive state differ between coastal and estuarine fish, with estuarine fish hypothesized to be immature subadults and coastal fish to be adults with a high proportion of spawning capable females, (3) estuarine fish recruit to the spawning population at the beginning of the spawning season in response to the same exogenous cues used by adults for gonadal recrudescence and to move to the spawning grounds, (4) fish will leave the Tampa Bay aggregation site once spawning has ceased but exhibit spawning site fidelity, returning the following spawning season, and (5) estuarine fish recruited to coastal habitat will exhibit movements similar to coastal fish.

Methods

Ethics

No specific permission for sampling was required, as sampling was conducted by the Florida Fish and Wildlife

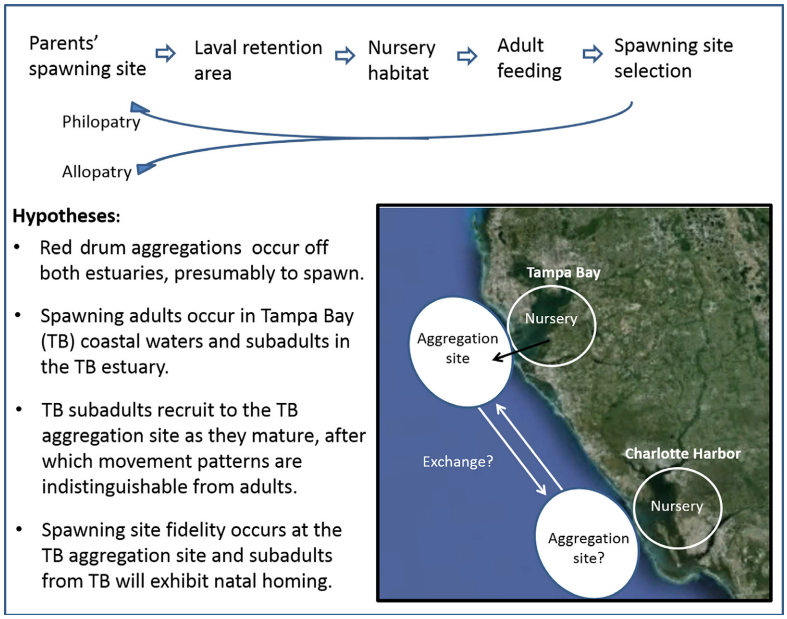

FIG. 1. A conceptual model showing two estuarine nursery habitats (Tampa Bay in the north and Charlotte Harbor to the south) and coastal waters off these estuaries, which were presumed spawning sites. We hypothesized that fish in the Tampa Bay system (aggregation site and subadults recruited from the nursery) would act as a population subunit with few detections in the Charlotte Harbor aggregation site. Detections within the Tampa Bay system were expected to correlate with the spawning season, with fish dispersing over a larger range to forage outside of the spawning season.

Conservation Commission's Fish and Wildlife Research Institute. However, every effort was made to meet all ethical standards (see Implantation of acoustic tags in methods for techniques to decrease stress in acoustically tagged fishes). No protected species were sampled.

Study overview

To test this range of hypotheses, it was necessary to draw on multiple data sources (Table 1) based on collections from several methods and locations (Fig. 2). Aerial surveys were conducted to map the number and location of red drum aggregations during the 2012 and 2013 spawning seasons. These surveys covered from the shoreline to approximately 11 km offshore (Fig. 2B), with a northern border just north of Tampa Bay and a southern border just south of Charlotte Harbor (Fig. 2B). To assess reproductive state and length of red drum in Tampa Bay coastal waters, aggregations were captured by purse seine and nonlethally sampled (Fig. 2B). The results of the nonlethal sampling were ground-truthed by comparing them to results based on sacrificed fish from a prior study that collected red drum by purse seine in coastal Tampa Bay waters (Winner et al. 2014). We acoustically tagged two population components, 60 adults from Tampa Bay coastal waters and 20 subadults from the mouth of the Tampa Bay estuary (Fig. 2, Table 1). For clarity, the terms "subadults" and "adults" are used to distinguish these groups and "recruited subadults" to refer to subadults detected in coastal waters in 2012. In the 2013 spawning season, tagged adults detected in aggregation sites are considered "repeat spawners" and recruited subadults are "first-time spawners". To monitor acoustically tagged fish, we deployed acoustic receiver arrays in Tampa Bay and Charlotte Harbor coastal waters (Fig. 2A) and used a mobile survey within Tampa Bay (Fig. 2C) at sites where subadult red drum schools had been previously captured in the fall (Winner et al. 2014). Depths in acoustic arrays ranged from 3 to 14 m and bottom substrate was predominately sand,

TABLE 1. Data sources for this study by type and location.

Data type	Tampa Bay estuary	Tampa Bay coastal waters	Charlotte Harbor coastal waters
Aerial surveys to detect aggregations	No	Yes	Yes
Fish captured and acoustically tagged	20 subadults	60 adults	…
Acoustic monitoring	Mobile hydrophone survey	Passive receiver array	Passive receiver array
Nonlethal capture-based samples to assess reproductive state and length	Yes	Yes	No
Sacrificed capture-based samples	Yes	Yes	No

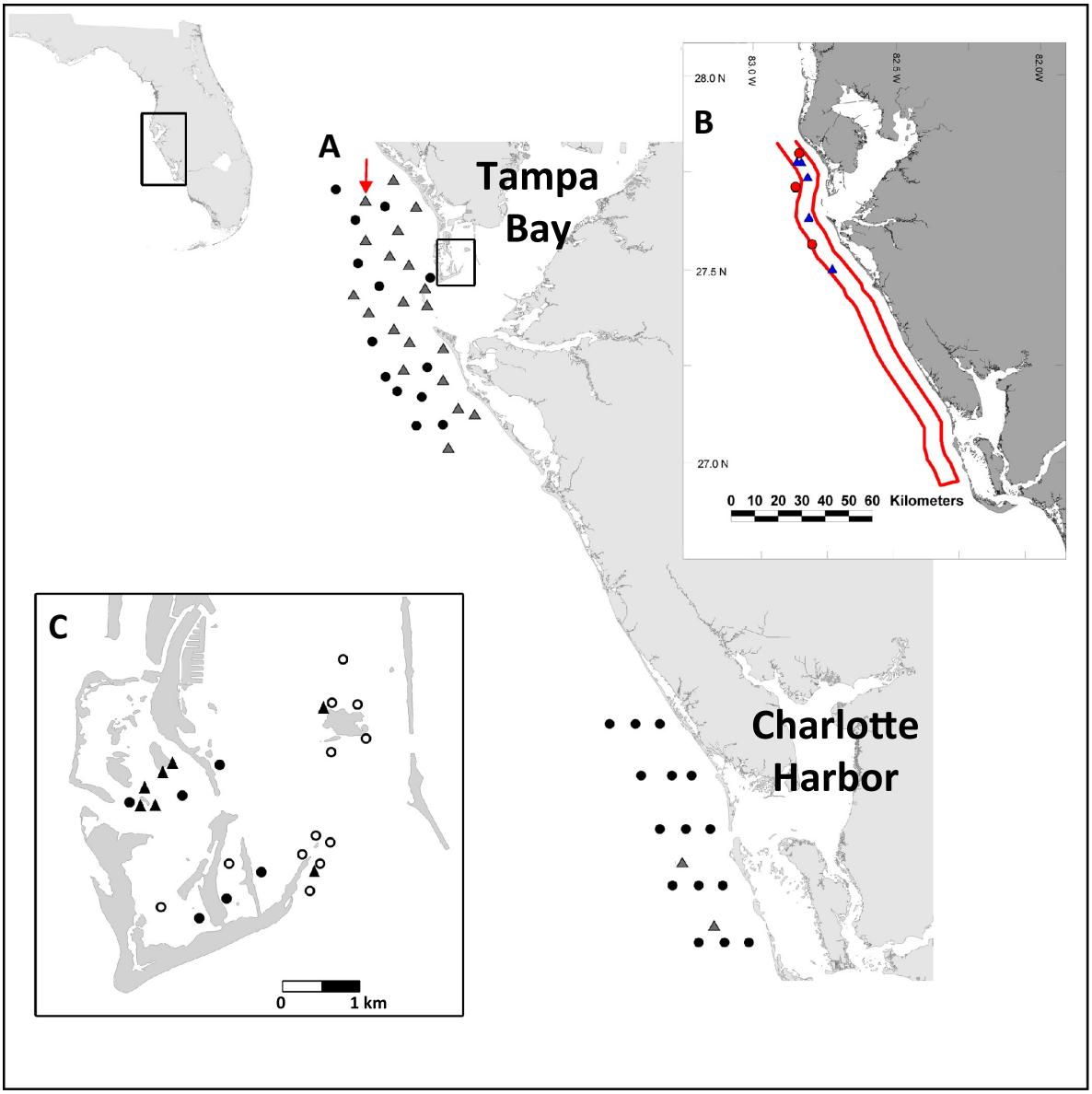

FIG. 2. The study site, including (A) receiver arrays, (B) the aerial transect path and purse seine sample locations, and (C) mobile hydrophone survey sites within Tampa Bay. (A) VR2W receivers were deployed at sites where red drum aggregations had been previously located off of Tampa Bay (triangles), with additional receivers (black dots) to ensure relatively even coverage. The red arrow indicates range test location. In Charlotte Harbor, the initial array (black dots) was based on a grid pattern, as we had no data on aggregations, and two receivers added (triangles) in 2013 based on aggregation locations in 2012. (B) Red lines indicate aerial transect path and purse seine sample locations are indicated with triangles (2007/2008) and dots (2012), which also represent adult tagging locations. (C) Nineteen estuarine sites monitored in a mobile survey; black dots correspond to sites where subadults were captured, tagged, and released and triangles indicate where fish were sampled in 2013.

with a few limestone outcroppings and artificial reefs. Mobile survey depths were much shallower, ranging from 0.4 to 1.6 m, and characterized by seagrass and sand.

Spatial distribution of red drum aggregations in coastal waters

Because aerial surveys are effective at assessing the spatial distribution of red drum aggregations (Powers et al. 2012), we used this method to test the hypothesis that red drum aggregations occurred off Tampa Bay and Charlotte Harbor. Aerial surveys were conducted from 28 September to 19 November in 2012, and 19 August to 25 November in 2013. A Cessna 172 aircraft was flown along a flight path approximately 3.7 km from shore going south and 8 km from shore on the return leg (Fig. 2B). To ensure optimal conditions for spotting aggregations, surveys were flown from approximately 09:00 to 13:00 Eastern Standard Time (EST), the window of optimum light attenuation. The plane was flown at

FIG. 3. Processing stations on the purse seine boat to allow for non-sacrificial sampling in 2012. The stations were made up of holding bins covered with a waterproof tarp and continually filled with seawater, with a ramp that lead to a slide of heavy-duty rubber that ended in a measuring cradle and removable gate. After a fish had been processed, the gate was lifted and the fish returned to the water.

approximately 1500 feet (450 m) and at a speed of 80 kn. Each flight was piloted by a fisheries biologist and had a crew of three biological observers, one who served as photographer. When an aggregation was spotted, the plane circled over it at ~500–700 feet (~150–210 m), and the plane's position was recorded.

Assessing the state–space relationship of population components

Samples from red drum aggregations in Tampa Bay coastal waters were captured by a chartered purse boat with experienced captain and crew working in tandem with a contracted spotter pilot (Murphy and Crabtree 2001, Winner et al. 2014). The purse net was 639.8 m long and 12.2 m deep. In 2012, strikes occurred between 10:00 and 12:15 EST, and the net was pursed in ~1 h, after which biologists boarded the purse boat and set up special processing stations for nonlethal sampling. Stations were made up of holding bins covered with waterproof tarps and filled with pumped seawater, with ramps that led to slides of heavy-duty rubber that ended in measuring cradles and removable gates. After fish were processed, the gate was lifted and fish released (Fig. 3). These fish were not aged because previous samples in this location showed these fish to be older (Winner et al. 2014) than the ages for which nonlethal aging techniques are effective (Bursher and Schull 2009). Fish were measured to the nearest mm for both standard length (SL) and total length (TL), sexed, and an ovarian biopsy taken from females. Additional reproductive state and length data came from 685 sacrificed fish sampled during a previous study (Winner et al. 2014).

Schools of presumed subadult red drum were captured in estuarine waters in lower Tampa Bay in 2012 and 2013 (Fig. 2C) on four dates within the 2012 spawning season (30 August, 18 September, 25 September, and 10 October) and five dates in 2013 (20 August, 27 August, 5 September, 20 September, and 3 October). On 25 September 2012, sampling was conducted with hook and line but all other samples were collected 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 mesh length, #12 twisted nylon twine) and two outer mesh walls (356-mm mesh length, #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 #50 lead core rope along the base of the net. In 2012, a subset of fish were sacrificed for life history analyses (length, age, reproductive development) and 20 fish larger than the State of Florida maximum length limit (685 mm TL) were selected for acoustic tagging. Additional estuarine sampling occurred in 2013, and a representative length range of fish was sacrificed for life history analysis.

Sex determination and reproductive state

Sex of nonlethally sampled fish was based on a combination of strip spawning, sex-specific characteristics, and ovarian biopsies. Strip spawning was attempted on all fish, and males expressed milt or drummed and actively spawning females released eggs. All fish with no male characteristics were assumed to be female, confirmed for most fish by ovarian biopsy and for a few fish based on the presence of ovarian parasites emerging from urogenital pores (Bakenhaster et al. 2014). Fish without male characteristics and urogenital pores too small to be biopsied were assumed to be immature females. Twenty-eight nonlethally sampled females from coastal waters do not have developmental phases due to more females than biopsy vials on 9 October 2012 and several sampling errors ($n = 6$). Fourteen fish were not assigned sex, as they were either accidentally released before sex could be determined or there was a recording error. Biopsies were taken with a catheter composed of a 10 cc (cm^3) syringe equipped with an adapter and Tygon (Saint-Gobain, Courbevoie, France) tubing with an inner diameter of 1.6 mm. The tubing was inserted 10–20 mm into the urogenital pore and the plunger of the syringe extended to create a vacuum to extract oocytes.

Male reproductive state and developmental phase was based on sacrificed fish and assigned based on either histological analysis of gonadal tissue or the gonadosomatic index (GSI), calculated as gonad weight/somatic weight × 100. All gonadal tissue used for histological analysis was processed at 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). Germ cell developmental stages, reproductive state, and reproductive phases were assigned 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). Fish with secondary growth oocytes (SG) were considered mature (Lowerre-Barbieri et al. 2011). Because it was difficult to identify early GVM or late stage POFs in biopsy samples, spawning females were identified based on late OM, ovulation, or fresh POFs in both sacrificed and nonlethal samples. Male histological indicators included the germinal epithelium (continuous or discontinuous), primary spermatocytes, secondary spermatocytes, primary spermatogonia, secondary spermatogonia, spermatids, and spermatozoa. Males that had begun production of spermatozoa had GSIs ranging from 0.05 to 0.29 (n = 11). Thus, males with spermatozoa present or with GSIs greater than 0.30 were considered mature.

Implantation of acoustic tags

Twenty estuarine red drum (10 males and 10 females) were captured in lower Tampa Bay (Fig. 2C) and intraperitoneally implanted with acoustic tags (Vemco, 69 kHz V16TP-6H; Vemco, Bedford, Nova Scotia, Canada). All fish were measured to the nearest mm for total length (TL), had the second anterior spine removed for ageing, and had sex and reproductive state assigned as described previously for nonlethal coastal sampling. No estuarine females had urogenital pores large enough to biopsy and all were assumed to be immature. Three males were developed at the time of implant, as they released small amounts of milt, although it was unclear if they were yet capable of effectively spawning (see *Results*). Because they recruited to adult habitat over the same time period as the remaining subadults, they were analyzed with this group but identified separately in *Results*. To reduce fishing mortality, acoustically tagged fish were selected to be larger than the State of Florida maximum length limit (685.8 mm TL). This resulted in significantly larger (two-tailed t test, n = 74, P < 0.0001, n = 74) acoustically tagged subadults (765 ± 8.3 mm TL) than those sacrificed for life history information in 2012 (636.8 ± 8.6 mm TL). However, sacrificed fish in 2013 encompassed the full size range. To increase battery life to 1251 d (approximately 3.5 yr), tags were coded with two inter-pulse random delays (20/60 s) for the first 8 months and 30/90 s for the following 4 months (120 d). The surgical process for all fish followed that of Lowerre-Barbieri et al. (2013) with the following modifications. No anesthesia was used, as fish were immediately released and Aqui-S (Aqui-S, Lower Hutt, New Zealand) is not approved for food fish in the USA. However, fish were calmed by turning them ventral side up and having their eyes covered with a wet cloth, as this was successful in a preliminary test on five fish. Ambient, surface sea water was flushed over their gills throughout the surgery. Incisions were made along the mid-ventral line to prevent cutting male sonic muscles and a metal spatula was inserted into the incision and under the body wall to limit needle depth, ensuring body organs were not caught in the sutures. All fish had an external dart tag inserted across the pterigiophores of the dorsal fin and were released immediately at the site of capture. The VR100 with an omnidirectional hydrophone was used to detect all fish immediately after release. Surgery times were rounded to the minute and ranged from 2 to 7 min with a mean of 4 min and 36 s.

Sixty adult red drum (30 females and 30 males) were captured, intra-peritoneally implanted with acoustic tags (Vemco, 69 KHz V16TP-6H; Vemco, Bedford, Nova Scotia, Canada) and released within the Tampa Bay (TB) array. These fish were primarily captured by purse seine in 2012 (5 October, n = 7; 9 October, n = 38; and 17 October 2012, n = 10), with five fish sampled by hook and line on 17 October. The surgical process, tag inter-pulse delays, and release protocol were all the same as described previously for the subadults, with the exception that spines were not removed for age analyses and all females were biopsied. Surgery times ranged from 2 to 9 min with a mean surgery time of 4 min and 13 s.

Acoustic monitoring

Overview.— Three habitats were monitored for acoustically tagged fish: within the mouth of the Tampa Bay estuary, and in Tampa Bay and Charlotte Harbor coastal waters (Fig. 2). Detection dates were categorized in two ways. Most detections were assessed in terms of within (26 August–18 November; see *Results*) or outside of the spawning season, but a larger time frame was needed to assess first and last detection dates and periods of high or low detections. This was because fish moved to the spawning grounds before the spawning season and remained in this area for a short time afterwards. Thus, we developed a reproductive period, August–December, and a non-reproductive period, January–July.

Estuarine habitat.— A mobile hydrophone survey using a VR100 (Vemco, Bedford, Nova Scotia, Canada) was conducted within the mouth of Tampa Bay (Fig. 2C) over the period 30 August 2012–December 2013. Sampling was weekly during both reproductive periods and every other week in the non-reproductive period. Nineteen fixed stations were sampled on each trip, six of which were the original capture sites (Fig. 2C). The remaining 13 stations were locations where subadult red drum had been previously sampled by trammel nets in the Florida Fish and Wildlife Research Institute's Fisheries Independent Monitoring (FIM) program. All stations were shallow (average depth = 0.9 m) and some accessible only at high tide. At each station, the omnidirectional hydrophone of the VR100 was lowered over the side of the boat and left in the water to listen at 69 kz for a period of 2 min. Based on prior range testing in this area (Lowerre-Barbieri et al. 2013), fish were presumed to be detectable if they were within 85 m of the hydrophone.

Coastal habitat.— Two acoustic receiver arrays were deployed in coastal aggregation sites off Tampa Bay (TB array) and Charlotte Harbor (CH array; Fig. 2A). This passive tracking method is useful to determine site fidelity

and spatial and temporal behavior difficult to assess with more traditional tagging methods (Heupel et al. 2006, Lowerre-Barbieri et al. 2013), with the advantage of continuously detecting any fish within the tag's expected range. A detection rate of more than 50% was observed at a range of 399 m in a preliminary deployment of five receivers and a sentinel tag (5 September 2010–21 January 2011) within the area the TB array was later deployed (Fig. 2A). Data recorded by each receiver included tag number and detection date and time. The Tampa Bay array was made up of 33 receivers (VR2W; Vemco, Bedford, Nova Scotia, Canada), 20 located at sites where aggregations were previously identified, and 13 to fill in gaps, primarily in the southern portion of this sampling area (Fig. 2A). Because there was no prior data on red drum aggregations in Charlotte Harbor coastal waters, 15 receivers were deployed in an evenly spaced grid. An additional 10 receivers were held in reserve to be deployed at aggregation sites identified in aerial surveys, with two of these deployed in 2013. VR2W receivers in the TB array were moored at the appropriate GPS location using sand augers (121.9 cm long) and originally held upright with a subsurface buoy. Due to shrimp trawling off Charlotte Harbor, the mooring system was modified for this array to reduce the chance of gear loss by eliminating the subsurface buoy and directly mooring the VR2W to the sand auger, approximately 0.8 m above the substrate. Because this method did not decrease detection rates, receivers in the TB array were deployed this way in 2013.

Routine array maintenance included replacing receivers approximately quarterly. Removed receivers were returned to the lab, downloaded, cleaned of any biofouling, the battery changed, and the outside repainted with antifouling paint, as needed. All sites had receivers deployed throughout the study period except the southwesternmost receiver in the TB array, which was never relocated. A replacement receiver was deployed at this site on 24 April 2013.

Data analysis

As a first step to assess the spatial distribution of spawning within the study site, we evaluated the number, temporal pattern of occurrence, and location of red drum aggregations detected in aerial surveys in 2012 and 2013. To evaluate if population components used coastal and estuarine habitat differently, we assessed the proportion of mature and spawning capable fish in Tampa Bay estuarine and coastal samples. Significant differences in fish length with sampling location (estuarine vs. coastal samples) were analyzed using two-tailed *t* tests. All averages are presented as mean ± SD. To assess potential first-time spawners in coastal waters, the coastal population was broken into two size classes. Small adults (those comparable in length to immature fish sampled in the estuary) were compared to larger adults in terms of sex ratio and proportion of spawning capable females. Differences were tested with a chi-square test, as were differences in the proportion of small adults over time.

Telemetry data were filtered to remove potential spurious detections ($n = 1$), which were defined as fish detected only on a single date with fewer than five detections. An additional two confirmed adult mortalities were removed from the data set as well as detections on the date of implantation, as they may reflect abnormalities in behavior due to the stress of implantation. Adult detection dates were assessed over the period after which all fish had been implanted (17 October 2012) and continued through 31 December 2013. Detection rates were assessed over three periods: the 2012 reproductive period, the 2013 nonreproductive period, and the 2013 reproductive period. Because adult fish were not all implanted until mid-October, the 2012 reproductive period did not include the full spawning season. The number of days detected (DD), the total period of detection (TP), and the residence index (RI) were calculated separately for each period and habitat (Tampa Bay estuarine, Tampa Bay coastal, and Charlotte Harbor coastal). TP was estimated as the number of days from first detection to last detection and RI was calculated as the ratio of DD to TP (March et al. 2010, Palmer et al. 2011). RIs were calculated only for fish detected on more than five dates in any given period. The number of unique fish detected within a week was calculated as the weekly detection rate. These rates were calculated separately for the two population components and for each habitat. Consecutive week numbers were assigned throughout the study period. The first week subadults were detected in coastal arrays was considered their recruitment week. Once in adult habitat, these fish were referred to as "recruited subadults".

Spawning site fidelity to the Tampa Bay aggregation site was assessed separately for repeat spawners and first-time spawners (i.e., recruited subadults). We used adjusted spawning site fidelity estimates based on the proportion of observed fish in the TB array in the 2013 spawning season divided by the number of fish tagged in 2012 and expected to be alive (Robichaud and Rose 2001, Zemeckis et al. 2014). Adjusted spawning site fidelity rates for tagged individuals were calculated as

$$\mathrm{SSF}_{i,j} = \frac{\#\text{observed}}{(\#\text{tagged})(1 - A - T)},$$

where the number observed is the number of fish detected in the TB array in the 2013 spawning season, and A is the annual proportion of deaths calculated as $A = 1 - \exp(-M)$. Because there is no fishery for adult red drum, fishing mortality (F) was not expected to affect survivorship and an M of 0.20 was used (Porch 2000). Given the spatial ecology reported for red drum (Bachelor et al. 2009, Winner et al. 2014), subadults captured in Tampa Bay were assumed to have been spawned in the Tampa Bay aggregation site and to have resided only in the Tampa Bay nursery grounds. Thus, natal homing was assumed in recruited subadults that were detected in the TB array in the 2013 spawning season.

To evaluate if red drum reside in coastal waters off Tampa Bay and Charlotte Harbor year-round or move to these areas primarily to spawn, we assessed the presence in these areas within and outside of the spawning season.

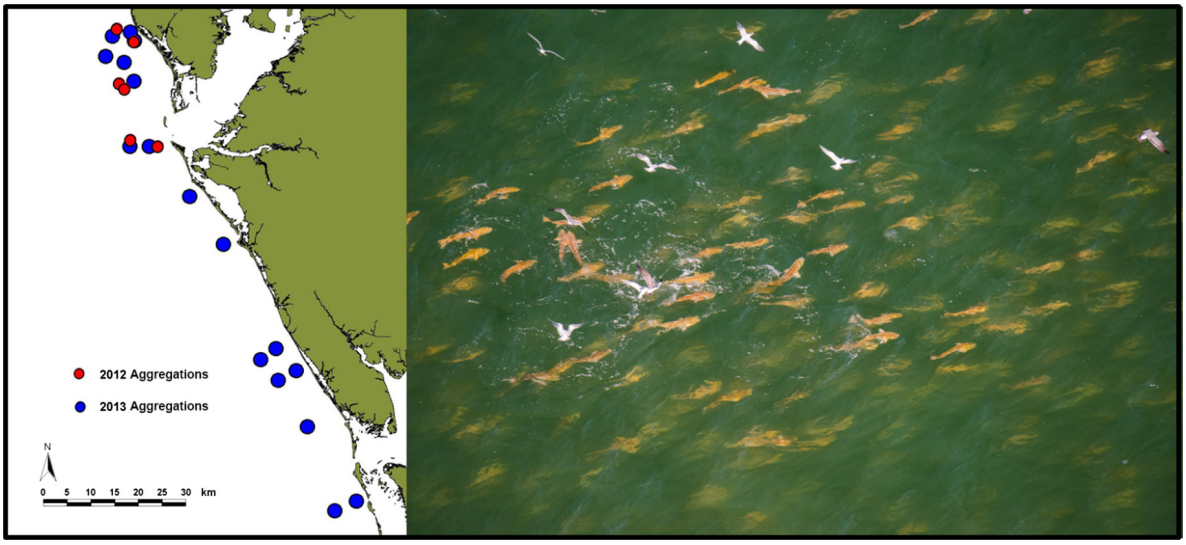

FIG. 4. Red drum aggregations detected in aerial surveys in 2012 (red) and 2013 (blue). In 2012, aggregations were detected over the period of 28 September–22 October. In 2013, aggregations were detected over the period of 26 August–18 November. An aerial photograph of a red drum aggregation breaking the surface. Photo credit: Carlton Ward.

This was modeled using generalized linear models (GLMs; PROC GENMOD in SAS), a binomial distribution, and a logit-link function. Fish not present were categorized as 0 and fish present were categorized as 1. The model included explanatory variables of spawning season and array location (TB or CH), as well as an interaction effect between these two variables. All statistical analyses were performed using SAS version 9.3 and an alpha level of 0.05.

RESULTS

Spatial distribution of red drum aggregations

We hypothesized that red drum aggregations would occur in coastal waters off both Tampa Bay and Charlotte Harbor estuaries. In 2012, all aggregations detected in aerial surveys were located in Tampa Bay coastal waters (n = 6), but two additional aggregations were detected off Charlotte Harbor by other methods. One aggregation was detected in a flight dedicated to scouting Charlotte Harbor coastal waters, and the other was reported by a trusted local fishing guide who caught and photographed fish from the school. The 2012 aerial surveys detected red drum aggregations off Tampa Bay from 28 September–22 October in 2012, with typically just one aggregation spotted per flight. However, on 28 September 2012, two separate aggregations were observed. In 2013, red drum aggregations were detected in aerial surveys off both estuaries (Fig. 4), with a total of 17 aggregations detected from 26 August to 18 November, and these dates were considered representative of the spawning season. Aggregations were fairly evenly distributed off Charlotte Harbor (n = 7) and Tampa Bay (n = 9), with a maximum of three aggregations sited per date.

Assessing the state–space relationship of population components

Fish sampled in Tampa Bay coastal waters were adults and virtually all spawning capable (i.e., had yolked oocytes or spawning indicators). Nonlethal samples (n = 1878) were taken from aggregations on three dates in 2012, from 5 October to 17 October (Fig. 2B). Samples from sacrificed fish from a previous study (n = 703) came from two dates in 2007 (17 September and 26 September) and three dates in 2008 (15 September, 2 October, and 7 October). More than 99% of sacrificed males were mature (n = 397). Similarly, more than 99% of females were mature in both studies (n = 1103) and 97% of those assessed histologically were spawning capable (sacrificed females, n = 288; nonlethally sampled females, n = 797). Approximately half of the spawning capable females (47%) were actively spawning with late OM oocytes or fresh POFs. The mean size of fish sampled in coastal waters was 907.3 ± 62.1 SD mm TL (n = 2581).

In contrast, most fish sampled in the estuary were subadults. The mean length of estuarine fish (695.0 mm TL ± 98.7) was significantly smaller than that of coastal fish (log-transformed TL; two-tailed t test, n = 2739, $P < 0.0001$). In 2012, estuarine fish (both those tagged and those sacrificed) ranged in length from 489 to 842 mm TL, with a mean length of 671.4 mm TL ± 79.8 SD (n = 74). However, in 2013 larger fish were also sampled within Tampa Bay (range: 481–971 mm TL, n = 84). Most estuarine females were immature (86%, n = 71), including all females sampled in 2012 (n = 16 sacrificed, 10 tagged) and 78% of those in sacrificed samples from 2013 (n = 45). However, ten adult females were sampled in the estuary in 2013, seven of which had fully yolked oocytes

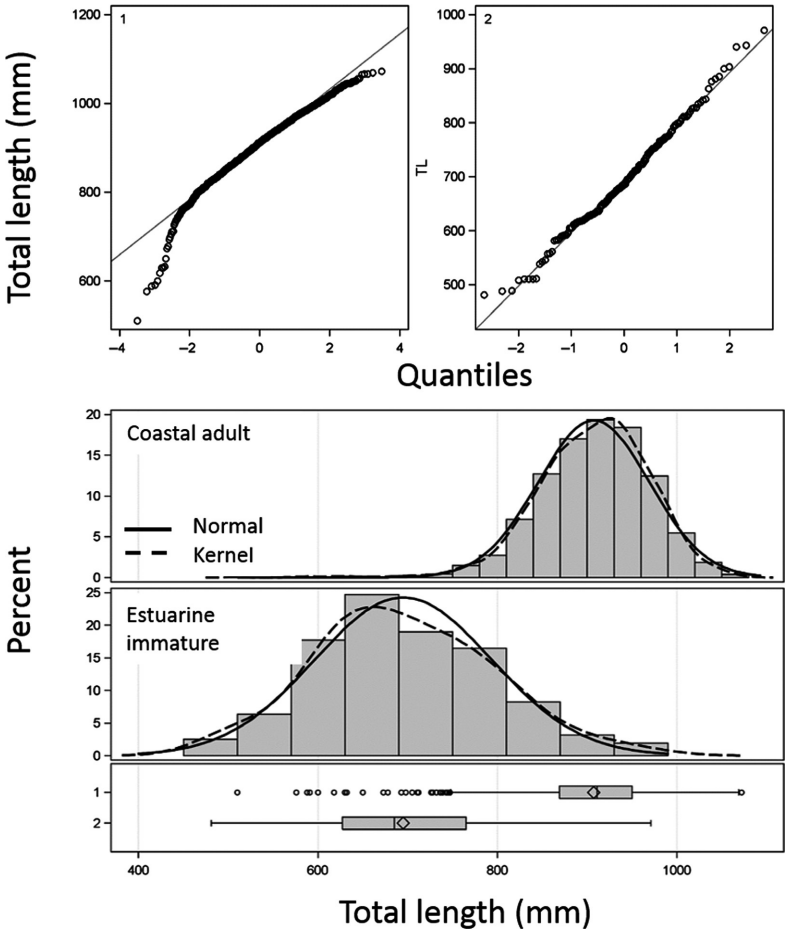

FIG. 5. Length distributions of adults from Tampa Bay coastal waters and immature fish from within Tampa Bay. In the box plots, mean is denoted by a diamond and median with a vertical line. The ends of the boxes represent the 25th and 75th percentiles and the whiskers are the minimum and maximum data points. Dots represent outliers. (bottom) QQ plots (top) show that coastal adult samples (left) had more small fish than expected in a normal distribution. Immature fish (right) were approximately normally distributed.

and were spawning capable. These females had a mean TL of 869.7 mm ± 61.0 and a mean age of 5.2 yr ± 1.8. It was difficult to distinguish between male subadults and adults. Most of the males from sacrificed samples in 2012 had some level of development (spermatocytes or spermatids, n = 22) and 11 males had spermatozoa and discontinuous germinal epitheliums (length range 630–742 mm TL). However, GSIs were quite low (mean = 0.063, SD = 0.04) with a maximum of 0.29 making it unclear whether these fish could effectively spawn with such low reserves of milt. In the 2013 sacrificed samples from the estuary, six males had GSIs >0.3 (mean length = 836.7 mm TL ± 74.0, mean age = 5.7 yr ± 4.8). Three of these fish were clearly adults as they had GSIs >1.0 (range 1.4–4.8).

The adult coastal population had more small fish (≤850 mm TL, comparable to the size fish sampled in the estuary) than expected in a normal distribution (Fig. 5). The length distribution of immature estuarine fish was approximately normal, but the adult coastal population included a long left-handed tail. Fish ≤850 mm TL presumably represent first-time spawners, recently recruited from the estuary and their relative abundance significantly increased as the season progressed (χ^2 = 64.90, P < 0.0001, df = 2), from 9.6% on 5 October to 27.2% on 17 October 2012. However, within the coastal population, small adults (≤850 mm TL) had a greater number of males and fewer spawning capable females than large adults (>850 mm TL). Only 84% of small females were spawning capable (n = 116) compared to >99% of large females and this difference was significant (χ^2 = 69.52, P < 0.0001, df = 2). The sex ratio of small adults was 1.8:1 males to females compared to 1.2:1 for large adults and these differences were also significant (χ^2 = 11.86, P < 0.0006, df = 1).

Shifts in state space

Subadult recruitment to the spawning population prior to or within the spawning season was supported by capture-based sampling but not by the movement patterns of most acoustically tagged fish. Subadults captured and released in the estuary were detected (n = 12) within the estuary in

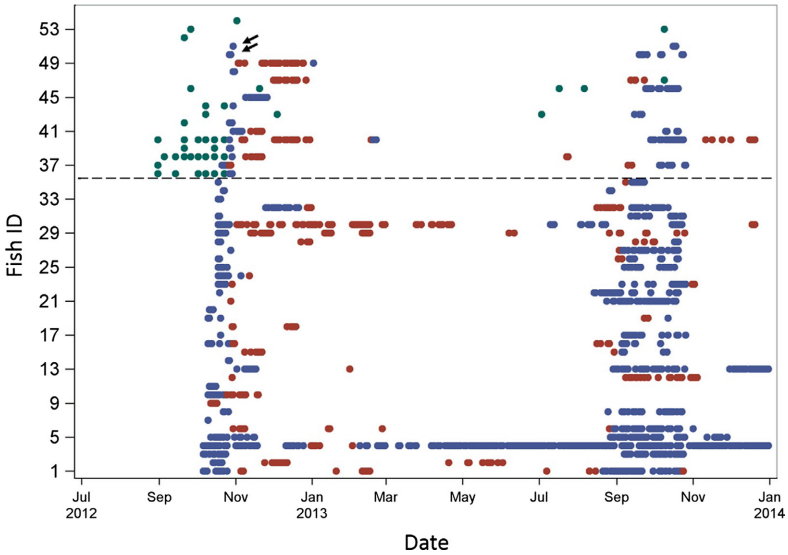

FIG. 6. Daily detections by individual and habitat. Fish above the dashed line are fish that were originally subadults captured and tagged in Tampa Bay. Arrows indicate males that had milt at the time of implant. Those below the dashed line are adults captured and tagged from Tampa Bay coastal waters. Estuarine detections during the mobile hydrophone survey are indicated in green, while detections within coastal acoustic arrays are in blue (Tampa Bay) and red (Charlotte Harbor).

2012 and had a mean TP of 26.4 d. No fish were detected in the estuarine mobile survey from 4 December 2012 to 3 July 2013. Most tagged subadults moved to coastal waters in late fall 2012 (n = 14). Twelve of these were first detected in the TB array with a mean first date of detection of 28 October 2012 (range: 21 October–9 November). This included two of the males that were developed and released milt on the date they were tagged (10 October 2012). Although these fish were mature based on gonadal development, their movement patterns were similar to the other acoustically tagged subadults, recruiting to adult coastal habitat on 27 October and 30 October 2012 (Fig. 6).

Subadults that recruited at the end of the 2012 spawning season had a wide range of lengths and included 2 and 3-yr-olds. In addition, these fish came from multiple implant schools and dates (Fig. 7). The mean age of 2012 recruited subadults was 2.21 yr ± 0.43 and mean TL was 767 mm ± 35.1 (Fig. 7), similar to the length and age range of all tagged subadults. However, the youngest fish tagged (age 1) and a 1-yr-old (at implant) exhibited the expected recruitment pattern and were not detected in the TB array until early in the 2013 spawning season. These two fish were detected in the estuarine mobile array in 2012 and then again in July 2013. They were first detected in the TB array on 15 September and 24 September 2013. The smallest fish (age 2, TL = 695 mm TL) was detected in the estuary in 2012 and 2013 but never detected in the coastal arrays.

Coastal waters off Tampa Bay were used as spawning grounds but rarely for overwintering. Red drum aggregations occurred within the spawning season in TB coastal waters in all years studied (2007, 2008, 2012, and 2013), and these aggregations included actively spawning females. At the individual scale, red drum occurred in this habitat almost exclusively during the reproductive period, moving elsewhere in between spawning seasons. A total of 41 acoustically tagged red drum (29 adults and 12 subadults) were detected in the TB array in the 2012 reproductive period and only four during the 2013 nonreproductive period (two adults and two subadults).

Although most acoustically tagged fish moved south, evidenced by detections in the CH array after leaving the TB spawning site, overwintering habitat varied. A total of 23 (17 adults, six recruited subadults) fish were detected in the CH array in 2012. The mean date of adult first detection was 11 November 2012 (range: 12 October–31 December) and the mean date for recruited subadult first detection was 9 November 2012 (range: 27 October–1 December). However, residence rates in the CH array during the nonreproductive period were very low for subadults and varied for adults, suggesting some fish overwintered there and some moved to other locations (Fig. 6). Adults exhibited a mean TP of 79.3 ± 64.8 d and mean DD of 10.9 ± 11.2 d (n = 7). Recruited subadults exhibited a different pattern with only two fish detected during this period on one or two dates. Four fish returned to the TB array within the 2013 nonreproductive period (two adults, two recruited subadults), one of which then used this area to overwinter (fish ID 4, TP = 173 d, DD = 104 d). In contrast, the other adult simply returned to the spawning site a little early (first detected 10 July 2013) and the two recruited subadults were detected in the winter months on only a few days (2 January 2013 and 19–21 February 2013).

Spawning site selection and fidelity

Most fish detected in the 2013 spawning season returned to the Tampa Bay spawning site but some fish apparently

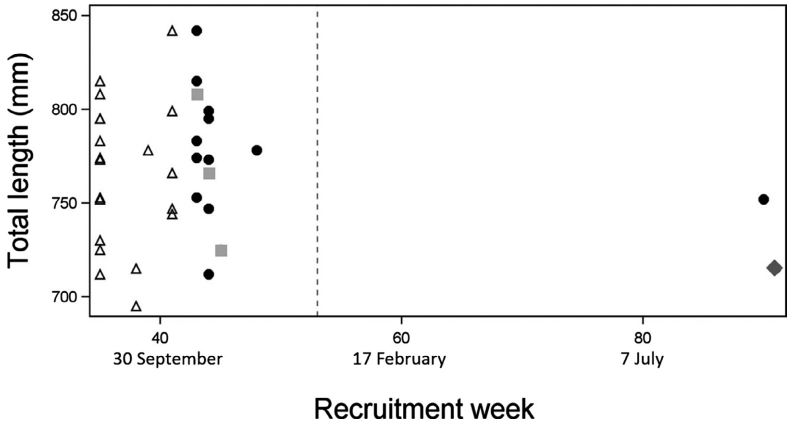

FIG. 7. Subadults tagged in the estuary by implant week (triangles), recruitment week, length (total length, mm), and age at time of implant (diamond, 1-yr-olds; circles, 2-yr-olds; squares; 3-yr-olds).

spawned in Charlotte Harbor coastal waters. A total of 33 fish (25 adults and 8 subadults) were detected during the 2013 spawning season in coastal waters and 91% of these (23 adults and 7 subadults) were detected in the TB array. These adults were considered repeat spawners and recruited subadults were considered first-time spawners. Four of these fish (three repeat spawners and one first-time spawner) had TPs of 5 d or less and could have been simply moving through the area. For the remaining fish, the first date of detection in the TB array was 26 August and the last date was 15 October 2013. Repeat spawners had a mean TP of 47.2 ± 19.1 d and a mean DD of 20.3 ± 11.3 d within the spawning season (n = 20), whereas first-time spawners exhibited less time on the spawning grounds, with a mean TP of 21.7 ± 10.9 d. However, detection rates during this time were similar to repeat spawners (first-time spawner mean RI = 0.45 ± 0.18, repeat spawner RI = 0.45 ± 0.19). In contrast, three fish were detected in the 2013 spawning season only in the CH array (two repeat spawners and one first-time spawner) and were first detected in late August or early September. Of these fish, the repeat spawners had a mean TP of 59.5 ± 2.1 d, similar to that seen in the TB array, but with a lower DD of 13.5 ± 9.2 d. The one first-time spawner had a TP of 12 d and a DD of 4 d. Two fish may have spawned off both Charlotte Harbor and Tampa Bay as they were detected in both arrays for extended periods (one repeat spawner and one first-time spawner). The adult was detected for 16 d in the TB array and for 12 d in the CH array. Similarly, the subadult was detected 19 d in the TB array and 8 d in the CH array.

Spawning site fidelity to the Tampa Bay spawning grounds was exhibited at both the population and individual scales. Red drum aggregations were detected during the spawning season in this area during all years studied and adjusted site fidelity rates to the Tampa Bay spawning site were 63% for first-time spawners and 61% for repeat spawners. However, adults had a much higher proportion of fish with unknown fates (i.e., fish never detected). Forty percent of adults were never detected compared to 5% of the subadults. Surgery times were similar for both groups and undetected adult surgery times did not differ significantly from those which were detected (two-tailed t test, n = 58, P = 0.63). However, 91% of non-detected fish were implanted on 9 October 2012.

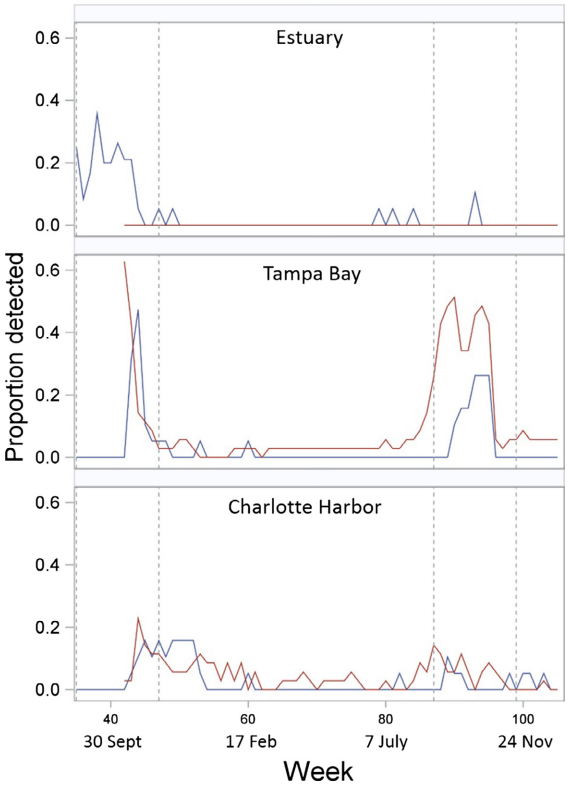

FIG. 8. Weekly detection rates, calculated as the proportion of fish detected within a given week out of those detected during the study period by fish type (blue represents fish that were tagged as subadults within Tampa Bay and red represents adults tagged in Tampa Bay coastal waters) and habitat type. Adults were implanted in mid-October 2012 after the subadults. The first date of the reference week is below week number. The dashed lines indicate the spawning season (26 August–18 November).

Spatial dynamics

Most subadults recruited to coastal waters at the time that adults were beginning to move away from the spawning grounds at the end of the 2012 spawning season (Fig. 8). Weekly detection rates were low for both population components in all three habitats during the nonreproductive period, although a few fish were detected in July in the estuarine mobile survey and on the Tampa Bay spawning grounds. Weekly detection rates in the CH array did not exhibit a seasonal pattern, although the highest detection rates occurred fairly soon after fish had moved away from the Tampa Bay spawning grounds. Adult daily detections were significantly greater during the spawning season (binomial regression, $n = 1051$ events, $P < 0.0001$) and in the TB array ($P < 0.0001$), with a significant interaction ($P < 0.0001$). The same general pattern was seen in recruited subadults (binomial regression, $n = 190$ events, $P < 0.0001$ for main effects and the interaction).

Discussion

Spatial distribution of red drum aggregations

Understanding drivers of spawning site selection and the relationship between spawning sites and foraging habitat has important implications for understanding metapopulation structure and spawning migrations (Claydon et al. 2012, Bauer et al. 2013). In this study, red drum aggregations occurred during the fall spawning season off both Tampa Bay and Charlotte Harbor, although few aggregations were observed off Charlotte Harbor in 2012, and none in the aerial surveys. Red drum aggregations have been previously reported in Tampa Bay coastal waters during their spawning season (Murphy and Crabtree 2001, Winner et al. 2014) and occasionally in the spring (Murphy and Crabtree 2001). Although these aggregations can be made up of thousands of fish, their behavior is somewhat different than that commonly associated with reef fish spawning aggregations (Domeier and Colin 1997, Claydon 2004). Red drum have a strong schooling instinct and are often seen feeding on baitfish at the surface of the water (S. K. Lowerre-Barbieri, *unpublished data*). Baitfish schools move through this area in spring and fall and red drum feeding on these baitfish may play a role in movements and our ability to site aggregations near the surface. However, the presence of red drum aggregations and detections in the TB array during the spawning season indicates reproductive behavior is the primary driver of movement to Tampa Bay coastal waters.

Both the Tampa Bay and Charlotte Harbor aggregation sites provide an area to release eggs close to estuarine nursery grounds, as well as foraging habitat to provide the energy needed for an income breeder to produce multiple batches of eggs. However, very few aggregations were seen off Charlotte Harbor in 2012, when a red tide occurred in this area, documented in our aerial surveys from 3 October to 5 November. The difference in aggregation prevalence off Charlotte Harbor over the two spawning seasons suggests local conditions may affect spawning site selection. Similar red tide effects on spawning aggregations have been reported for two other sciaenids (Lowerre-Barbieri et al. 2013, Walters et al. 2013).

Assessing the state–space relationship of population components

Maturation is the reproductive parameter most used in traditional stock assessment models of marine fishes, as it is needed to estimate SSB (Lowerre-Barbieri 2009) and also the trait expected to have the greatest impact on fitness (Stearns 1992). However, it is a complex physiological process, which is not yet fully understood, driven by endogenous cues, linking an individual's growth and reproductive systems, and exogenous cues, which link an individual with its environment (Okuzawa 2002). In addition, there is a spatial component as fish shift from nursery to spawning habitat (Gillanders et al. 2003), which can only be studied and integrated into our understanding with the ability to track individuals over space and time. In our study, most estuarine females were immature and virtually all coastal females were mature, including fish of similar size to those which were immature in the estuary. The strong effect of sampling location on reproductive state found in this study has important implications for estimates of maturity used in stock assessments, highlighting the need to sample locations where adults and subadults mix or from both adult and subadult habitat for samples representative of the population (Tomkiewicz et al. 1998).

Our study also highlights the need to differentiate between maturation indicators and functional maturity. Most males sampled in the estuary would be considered mature (Brown-Peterson et al. 2011), given that they had some level of spermatogenesis and several acoustically tagged males released small amounts of milt. The greater gonadal development of estuarine males compared to females suggests a lower energetic threshold for gonadal development in males linked to the lower energetic cost of spermatogenesis versus oogenesis (Schärer and Robertson 1999). However, the low milt reserves of these males and their movement patterns, which were similar to immature females suggests these males were not yet ready to spawn, i.e., functionally mature.

Shifts in state space

Although we hypothesized that subadults would recruit to the Tampa Bay spawning site prior to or early in the spawning season as they matured, most acoustically tagged subadults recruited at the end of the spawning season indicating individual plasticity in this behavior. Some subadults clearly do recruit early in the spawning season, based on the large number of small adults in Tampa Bay coastal waters and recruitment of two tagged subadults to Tampa Bay coastal waters in September 2013. However, our acoustic tracking data suggests the

more common pattern may be for subadults to recruit at the end of the spawning season. Although all tracking data will be potentially biased by the location and time that fish were captured and the size and age at implant, increases in the abundance of small adults over the spawning season were also seen in coastal samples. This plasticity in the timing of recruitment to adult habitat suggests that, at least for some fish, there is a cue to recruit to adult habitat that is not linked to reproductive development or the exogenous cues which initiate it. Adult red drum have been shown to move into estuarine and coastal habitats after spawning in Georgia (Lowerre-Barbieri et al. 2008) and we documented a few adults within Tampa Bay. Given the strong schooling instinct of red drum, it is possible that subadults may move to adult habitat after encountering adults in the estuary and then following them when they return to coastal waters, similar to reports that reef fish spawning-site selection may be learned by following the behavior of older fish (Colin 1996).

In our study, all tagged red drum, adults and recruited subadults, appeared to leave the Tampa Bay spawning site, as there was a lack of detections near the end of the 2012 reproductive period and most of these fish were later detected in the CH array. However, it is important to recognize that neither array nor the mobile hydrophone survey had overlapping ranges between receivers or sampling sites. Thus, monitoring of all three sites was permeable, as demonstrated by fish detected in the CH array without first being detected in the TB array (two subadults and six adults) and potentially affected by different detection probabilities. Because of this, the lack of detection on any given date cannot be considered valid data. However, differences in detection rates over time in a given array should be representative of seasonal fish presence or absence patterns. Thus, the lower detection rates within the nonreproductive period suggest red drum concentrate in large numbers in relatively small spawning sites during the spawning season but move to other locations to forage or overwinter once spawning is completed. The ability for red drum to cover large distances has been documented as individual red drum have been recaptured farther than 700 km from where they were originally tagged (Overstreet 1983). Although we had no means to acoustically monitor such great distances, our tagged red drum were detected in both of our arrays, which were approximately 132 km apart. In addition, they were detected on another project's receivers, deployed at offshore wrecks ~32.2 km west of our TB array in 24.4 to 36.6 m deep (A. Collins, *unpublished data*), demonstrating the wide range of habitats these fish use.

Spawning site selection and fidelity

Spawning site selection and fidelity are poorly understood in marine fishes (Rowe and Hutchings 2003), even though they are the underlying behavior driving stock structure. Spawning site selection is not random, inferring a level of fitness associated with this trait (Ciannelli et al. 2015, Lowerre-Barbieri et al. 2015). Yet what drives spawning site selection is rarely understood (Sadovy et al. 1996) and considered a major challenge in marine ecology today (Leis et al. 2011, Bauer et al. 2013). Several hypotheses have been put forth to explain spawning site selection, including natal homing and learned behavior through "spawning groups" formed at first maturity or by following the behavior of older fish (Colin 1996, Adams et al. 2009).

Spawning site fidelity is a mechanism that contributes to the formation and maintenance of metapopulation structure, reducing reproductive connectivity between spawning sites and delaying recolonization of fished out spawning sites (Zemeckis et al. 2014). Spawning site fidelity is commonly assumed to occur at the lifetime scale. However, it simply reflects consistent spawning-site selection over time and for iteroparous, multiple-batch spawners, it occurs over several temporal scales: lifetime, annual, and interannual (Lowerre-Barbieri et al. 2014). At the interannual scale (i.e., within the spawning season), it will affect our ability to estimate spawning frequency, which when studied at the individual scale often differs from estimates based on population scale data (Bijoux et al. 2013, Lowerre-Barbieri et al. 2013). Because red drum spawn off estuarine nursery grounds, first-time spawners, recruiting during the spawning season, would have a high probability of spawning on their natal spawning grounds but not necessarily return to spawn in consequent years.

However, spawning site fidelity was similar in both adult and first-time spawners (recruited subadults), with roughly two-thirds of the fish returning to the Tampa Bay spawning grounds. These site fidelity rates are similar to those observed in Atlantic cod in the Gulf of Maine, where it has been recognized that inclusion of the metapopulation structure in stock assessments and fishery management plans would help prevent continued declines in spawning diversity and help promote the rebuilding of the stock (Zemeckis et al. 2014). However, in this study, a relatively large number of acoustically tagged adults were never detected (n = 23), potentially due to delayed mortality after the implantation process. The highest proportion of undetected fish came from an implantation date when fish were moved from the purse seine to the hold of another boat to be held for surgery. These same fish were not detected the following year; and relocation rates of additional fish implanted in 2013, when they were taken directly from the purse net to surgery, were higher (S. K. Lowerre-Barbieri, *unpublished data*). However, only two tags were recovered from mortalities in the area covered by the TB array, and thus, it cannot be ruled out that these fish simply left the areas being monitored, highlighting a key limitation to passive acoustic receiver arrays.

Although spawning site fidelity was similar in adults and first-time spawners, the time of arrival on the spawning grounds in 2013 differed, with first-time spawners arriving later than adults and thus presumably having shorter spawning seasons. This pattern of older, larger fish spawning sooner and for longer durations than younger fish is increasingly being reported in a range of species (Wright and Trippel 2009) and has important

implications for fisheries management, given that fisheries often cause age truncation (Pecquerie et al. 2009, Wright and Trippel 2009). We have hypothesized that subadults recruit to adult habitat after encountering adults and then become integrated into these schools. The small adults sampled in the adult aggregations seem to support this hypothesis. However, the later arrival times on the Tampa Bay spawning grounds in 2013 of first-time spawners suggests recruited subadults may not have remained within larger adult schools, and further research on school fidelity is needed to better understand these processes.

Movement patterns indicated several behavioral contingents associated with spawning site selection. Spawning site fidelity was the most common pattern observed, but two other patterns were also observed, and they occurred in both sexes and population components. Several fish, all of which were first detected in the TB array in the 2012 reproductive period, were detected in the 2013 spawning season within the CH array or in both arrays. This potential mixing with other spawning populations, as well as possible spawning at multiple sites within a spawning season, may be the equivalent of a spatial bet-hedging strategy similar to the temporal pattern of producing multiple batches of eggs.

Natal homing was suggested by the return to the Tampa Bay spawning grounds in 2013 by roughly two-thirds of recruited subadults. Natal homing has important implications for fisheries management as it suggests a positive feedback loop between selecting a site with high potential for reproductive success and passing this advantage on to your offspring. This, in turn, would result in spatially explicit population productivity and the potential for relatively small hot spots to impact abundance at a much larger spatial scale. Previous research, based on otolith chemistry, has also indicated red drum adults from a given spawning site originated from estuarine nurseries in the same region (Patterson et al. 2004, Rooker et al. 2010). However, the question was raised whether red drum were simply retained in an area close to their natal estuary or whether fish in fact moved away from the area and returned to spawn. In this study, we were able to confirm that fish moved away from the Tampa Bay spawning grounds but returned the following year. Thus, although the range of adult red drum may be quite large, in the spawning season, they will be concentrated in relatively small and consistently used spawning sites. This pattern of spatial ecology can make species more vulnerable to overfishing (Cadrin and Secor 2009).

Conclusions

Reproductive resilience in marine fishes has been defined as "the reproductive capacity of a population to maintain the level of reproductive success needed to result in long-term population stability, despite disturbances such as environmental perturbations and fishing" (Lowerre-Barbieri et al. 2015). Reproductive success occurs at the individual scale and large differences amongst individuals are common with important consequences for population dynamics (Clutton-Brock and Sheldon 2010). Although this idea is well-integrated into ecology, it is only now being integrated into the understanding of marine fish population dynamics (Pecquerie et al. 2009). Traditionally, fisheries data has come from sacrificed fish, with the need to assume that the patterns of many individuals sampled at one place and time are comparable to individual behavior. However, telemetry allows us to follow individuals over space and time giving us insight into spatial reproductive behavior (which affects a fish's vulnerability to fishing as well as its reproductive success) such as shifts in habitat usage (Chin et al. 2013), spawning site selection (Lowerre-Barbieri et al. 2014, Ciannelli et al. 2015), and spawning site migrations and fidelity (Robichaud and Rose 2001, 2003, Svedäng et al. 2007, Adams et al. 2011, Lowerre-Barbieri et al. 2013). However, telemetry, like any other sampling method, has its own limitations including not being able to contextualize individual movements with larger population attributes, such as reproductive state. In this study, we used a novel approach to collect nonlethal capture-based data which was comparable to that from sacrificed fish. In addition, we were able to use aerial surveys to repeatedly assess aggregation presence at a large spatial scale. Integrating telemetry data with these other data types allowed us to assess individual movements in the context of population spawning behavior. Such an approach will be needed for fisheries management in the 21st century as we begin to assess how fishing affects long-term productivity in ways other than simple abundance, such as changes in population structure (Cadrin and Secor 2009), fisheries-induced evolution (Ciannelli et al. 2015), and energetics (Kawabata et al. 2015).

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Data Availability

Data associated with this paper have been deposited in Dryad: http://dx.doi.org/10.5061/dryad.47bs5