



Assessing red drum spawning aggregations and abundance in the Eastern Gulf of Mexico: a multidisciplinary approach

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Many marine fish form spawning aggregations (FSAs) and exhibit meta-population stock structure, affecting reproductive resilience and the optimal spatial scale of management. Red drum use a known FSA site off Tampa Bay (TB FSA site) and another presumed FSA site off Charlotte Harbor (CH FSA site). We studied these sites for 3 years (2012–2014) to assess space use and annual abundance at the TB FSA site using: (i) genetically profiled fish, non-lethally sampled by purse seine ($n = 9087$); (ii) aerial surveys ($n = 37$); and (iii) acoustic telemetry ($n = 122$ fish). Thousands of fish concentrated at the TB FSA site to spawn each year, dispersing afterward to an area of at least ~150 km along the coast and 90 km offshore. Fish acoustically tagged at the TB FSA site showed strong annual spawning site fidelity (91% in 2013 and 85% in 2014) and the straying rate to the CH FSA site to the south was low (6–13%). Annual abundance at the TB FSA site varied, with the estimated abundance in 2013 being four times greater than that estimated for 2014. Similarly, aerial surveys in 2013 sighted 2.5 times as many aggregations as in 2014. However, fine-scale space use, which typically goes unassessed in abundance estimates (short-term surface behaviour and temporary migration), also differed between these years and needs to be integrated into future capture-mark-recapture models.

Keywords: acoustic telemetry, capture-mark-recapture, fish, fisheries management, genetic tracking, movement ecology, population abundance estimation.

Introduction

Fish spawning aggregations (FSAs) occur in a wide range of species (Russell *et al.*, 2012) and are defined as a group of conspecific fish that repeatedly gather in high densities at a specific time and place to spawn, resulting in a mass point source of offspring (Domeier, 2012). This behaviour highlights the importance of spatial structure to population productivity (Berger *et al.*, 2017) and the complexity of spawner–recruit systems (Lowerre-Barbieri *et al.*, 2015, 2017; Sadovy de Mitcheson, 2016). FSAs are important to fisheries

management because: (i) they are highly vulnerable to over-fishing and spatially explicit stressors, comparable to breeding aggregations in seabirds, sea turtles, and whales (Erisman *et al.*, 2015); (ii) the role they play in population structure as well as their contribution to annual reproductive effort (Grüss *et al.*, 2015, 2018); and (iii) their contribution to ecosystem functionality through transfer of nitrogen, phosphorous (Archer *et al.*, 2015), and fatty acids (Fuiman *et al.*, 2015). Marine-protected areas (MPAs) are often proposed to protect FSAs, but the efficacy of this management

approach depends on the movement ecology of the species, as this drives the temporal scale over which individuals remain within the FSA site and when and where they are accessible to fishing outside of the spawning season.

Red drum form spawning aggregations which contribute to an isolation-by-distance (IBD) stock structure (Gold and Turner, 2002), with genetic differentiation increasing over distance. IBD and other meta-population structures are common in marine fishes and have important implications for stock assessments, as optimal management units are often smaller than current stock boundaries (Spies *et al.*, 2015; Kerr *et al.*, 2017). Red drum form an FSA off Tampa Bay (TB), Florida's largest open-water estuary, during their fall spawning season (Murphy and Crabtree, 2001; Winner *et al.*, 2014; Lowerre-Barbieri *et al.*, 2016) and we refer to this area as the TB FSA site. Groups of red drum within this FSA site are referred to as aggregations. However red drum, unlike most aggregating reef fish, are schooling. Thus, multiple aggregations can occur within the TB FSA site and aggregations are not attracted to only one discrete location within the site (Lowerre-Barbieri *et al.*, 2016). Red drum larvae and young juveniles use upper Tampa Bay and rivers as nursery grounds (Peters and McMichael, 1987), with red drum moving down to the mouth of the estuary as they mature, recruiting to the adult population in the fall (Winner *et al.*, 2014). The nearest neighbouring estuary, Charlotte Harbor (CH) is also an important red drum nursery area (Winner *et al.*, 2014). The coastal habitat off this estuary is similar to the TB FSA site and it is a presumed FSA site and we refer to this as the CH FSA site. Spotter planes can be used to detect red drum aggregations as they often swim near the surface (Powers *et al.*, 2012), resulting in a highly effective historic purse seine fishery in the Gulf of Mexico (GOM). Fishing pressure on the adults, combined with recreational fishing pressure on sub-adults within the estuaries, led to over-fishing and the fishery was closed in the mid-1980s to prevent a potential population collapse. Currently, fishing on the adult stock in federal waters remains closed, resulting in a lack of landings data for the GOM adult stock and thus difficulty in estimating stock status. There has not been a Federal stock assessment since 1999 (Porch, 2000), and adult abundance has not been estimated since Nichols (1988) and Mitchell and Henwood (1999).

This study is one in a series to improve our understanding of reproductive resilience and abundance of red drum in the Gulf of Mexico. Reproductive resilience is the capacity of a population to maintain the reproductive success needed to result in long-term population stability despite disturbances, including fishing (Lowerre-Barbieri *et al.*, 2015). Reproductive resilience is species specific and greater in species with diverse spatio-temporal spawning activity, as well as other traits in a species' spawner-recruit system (Lowerre-Barbieri *et al.*, 2017). Because FSA dynamics are complex, large and multifaceted data sets and an iterative approach to analysing them is needed. Here we build on Lowerre-Barbieri *et al.* (2016), which confirmed red drum spawn at the TB FSA site and documented a pulse of fish recruiting to the adult population in late fall, leaving the TB FSA site and returning the following year as first-time spawners. In this article, we extend the temporal scale of data used in Lowerre-Barbieri *et al.* (2016) to include 3 years of purse seine sampling and aerial surveys and 4 years of acoustic tracking. In addition, we expand the acoustic tracking data set by integrating detections from mobile platforms and the Integrated Tracking of Acoustic

Animals in the Gulf of Mexico (iTAG) network. Lastly, we genetically profile individuals, non-lethally sampled by purse seine, to develop a mark-recapture database used in a capture-mark-recapture (CMR) model to estimate annual abundance at the TB FSA site.

We used this integrated database to evaluate: (i) large-scale space use; (ii) annual abundance at the TB FSA site; and (iii) if fine-scale space, for which we often do not have data, affected the underlying assumptions of our CMR model. The following hypotheses associated with large-scale space use were assessed: (i) the area and densities of tagged fish will not differ within and outside the reproductive period; (ii) large-scale space use does not vary annually; and (iii) TB FSA site fidelity and straying rates between the TB FSA and CH FSA sites will be close to 50%, the expected rate if spawning site selection is based on habitat suitability and these sites are used interchangeably. We evaluate if annual abundance at the TB FSA site varies in 2013 vs. 2014 based on results of a closed population CMR model. We assess the following processes associated with fine-scale space use that could affect availability to purse seine capture: (i) surface behaviour; (ii) temporary migration to and from the TB FSA site (*sensu* Bird *et al.*, 2014); and (iii) mixing between aggregations.

Methods

Ethics

No specific permission for sampling was required, as sampling was conducted by the Florida Fish and Wildlife Conservation Commission's Fish and Wildlife Research Institute. However, every effort was made to meet all ethical standards (see below the methods used to decrease stress in acoustically tagged fishes). No protected species were sampled.

Study area

This study was conducted in GOM waters off the coast of central, west Florida, using multiple sampling techniques over differing spatial scales (Figure 1a–c). Purse seine sampling, aerial surveys, and acoustic telemetry were conducted from 1 September 2012 to 31 December 2014, with acoustic tracking extended through 2015. The TB FSA site is an area ~60 km along the coast to ~11 km offshore (Figure 1c), where red drum aggregations have been consistently sighted (Murphy and Crabtree, 2001; Winner *et al.*, 2014). An acoustic receiver array (VR2Ws) was designed to monitor sites where aggregations had been previously sighted (Figure 1b) and all purse seine sampling was conducted in the TB FSA site (Figure 1c). A mobile surface receiver (VR100), was deployed from a research vessel on all purse seine sampling dates to evaluate if acoustically tagged fish were within the search area. Aerial surveys included the TB FSA site but were extended along the coast 132 km to the south, to also include the CH FSA site. An acoustic receiver array was deployed at the CH FSA site, but because there was no previous data on aggregation locations, it was deployed in a grid pattern. The spatial scale of acoustic monitoring was increased through the use of an automated underwater vehicle (AUV) deployed to the west of TB FSA site in 2014 (Figure 1b) and through the iTAG (Integrated Tracking of Aquatic Animals in the Gulf of Mexico) network data exchange <http://myfwc.com/research/saltwater/telemetry/itag/>. The iTAG exchange provides members with detection data when their fish are detected on other member's arrays throughout the GOM and

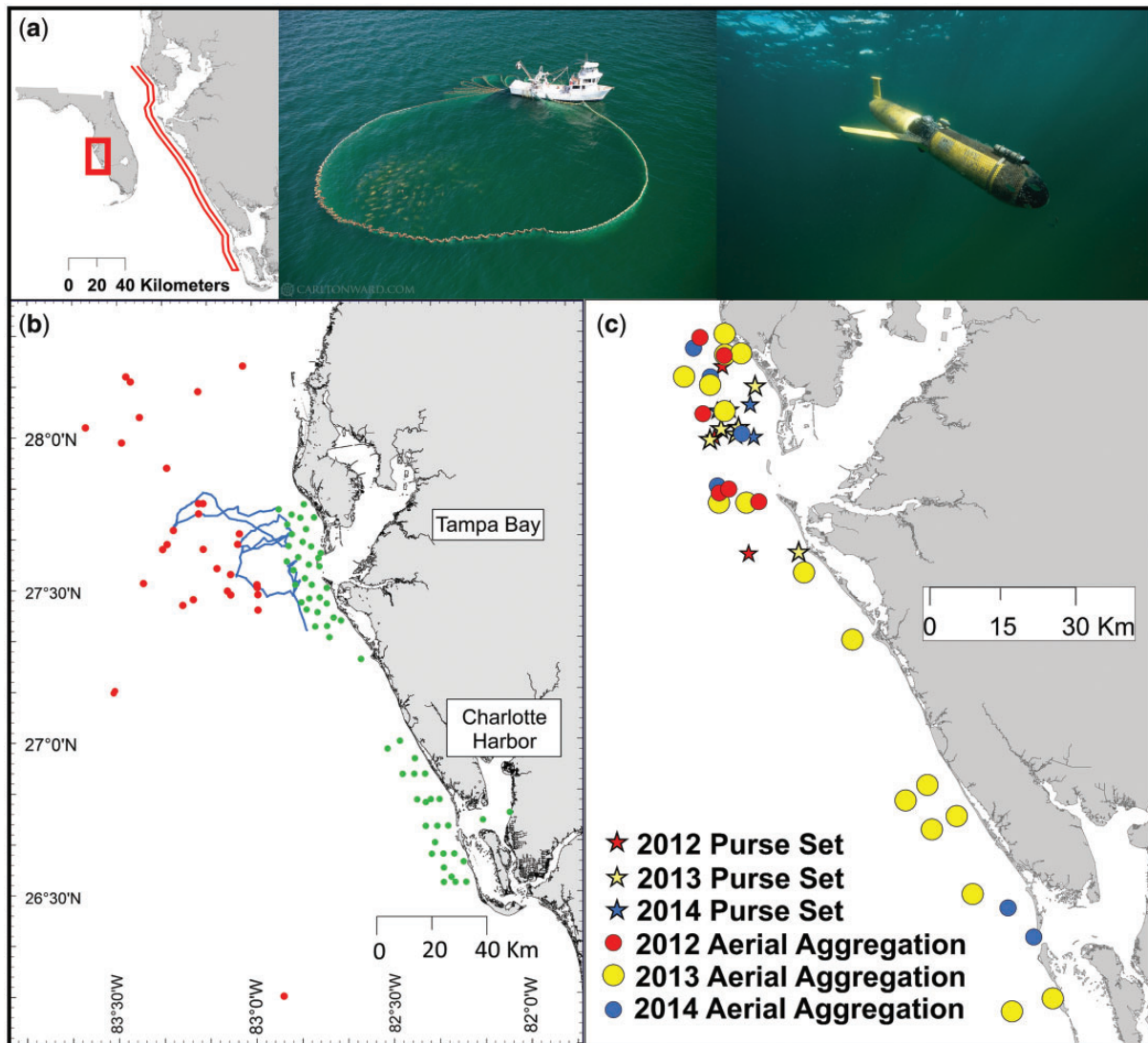


Figure 1. (a) The region of west-central Florida where the study occurred, the path used for aerial surveys, and multiple sampling methods used in this study. (b) Regional detections came from study arrays off Charlotte Harbor and Tampa Bay, as well as offshore opportunistic detections from other study receiver arrays, including artificial reefs monitored by A. Collins, a red snapper study 92 km offshore (furthest west site) monitored by S. Lowerre-Barbieri, and detections from a pilot study using the University of South Florida automated under water vehicle deployed in October 2014 with an acoustic receiver (path indicated). All purse seine sampling occurred within the area monitored by the Tampa Bay study array. (c) The annual number and location of purse seine sets (stars) and the location of red drum aggregations detected in aerial surveys (dots).

for this study it provided data from arrays to the west and north of the FSA site (Figure 1b). We refer to these as opportunistic offshore detections to distinguish them from detections within our study arrays.

Aerial surveys

Aerial surveys were used to identify the number and location of red drum aggregations during the reproductive period in 2012, 2013, and 2014. The assumption was the annual number of aggregations in each FSA site would act as a rough indicator of near-surface abundance (Lohoefer *et al.*, 1987) independent from catchability. Flights followed a specified path and protocol (Lowerre-Barbieri *et al.*, 2016) but in 2012 did not start until 28 September, whereas surveys were conducted from mid-August

through the third week in November in 2013 and 2014 (Table 1). Surveys were conducted during the window of optimum light attenuation, from approximately 09:00 to 13:00 Eastern Standard Time (EST). Aggregation locations were recorded when sighted. Aerial surveys were not designed to estimate the number of fish within an aggregation. However, the number of fish at the surface in the largest aggregation sighted was estimated based on an aerial photo.

Purse seine sampling

Red drum were captured by purse seine and non-lethally sampled at the TB FSA site during the fall spawning season in 2012, 2013, and 2014. The chartered purse boat had an experienced captain and crew, who worked in tandem with a contracted spotter pilot

Table 1. Summary of aerial surveys and number and date range of when red drum aggregations were sighted within our transect.

| Year | No. of Surveys | Survey date range (date range aggregations sighted) | No. of aggregations along survey path | No. of aggregations in TB FSA site |
|------|----------------|---|---------------------------------------|------------------------------------|
| 2012 | 8 | 28 September–19 November (28 September–22 October) | 6 | 6 |
| 2013 | 15 | 19 August–25 November (26 August–18 November) | 17 | 10 |
| 2014 | 14 | 18 August–21 November (25 August–29 September) | 6 | 4 |

(Murphy and Crabtree, 2001; Winner *et al.*, 2014). Each season, purse seine sampling started once aggregations had been sighted in the aerial surveys. Sampling dates were based on availability of fishermen and biologists. On purse seine sampling dates, biologists launched a research vessel from the TB coast by 0900, and the commercial vessel launched from Cortez, just south of Tampa Bay. Biologists on the research vessel searched for red drum aggregation indicators, including fish breaking the surface or the presence of birds (frigates or sea gulls), and/or detections of previously tagged fish on the mobile receiver. This information was communicated to the purse boat captain and spotter plane pilot. If an aggregation was found before the purse boat was at the site, hook and line sampling was conducted and the fish implanted with acoustic tags (see below). After a set was made and the net was pursed, biologists boarded the purse seine and non-lethally sampled as many of the captured fish as possible before sunset (Lowerre-Barbieri *et al.*, 2016) ranging from 109 to 1038 per sampling date. However, the number sampled does not reflect aggregation size because: (i) the net encircled only a portion of the aggregation on any given date; and (ii) frequently, more fish were captured than could be processed in 1 day, with non-sampled fish released at the end of the day (~50–1000 fish). Fish were measured for standard length (SL), total length (TL), fin-clipped for a genetic sample, and assessed for sex and reproductive state (not reported here) before being released.

Genetic tracking

Genetic profiling was used to identify individual red drum and develop a CMR database. Genomic DNA was extracted from fin clips and used to produce multilocus genotype profiles for all captured-and-released red drum based on nine highly variable microsatellite loci. A non-parametric empirical Bayes approach was employed for the joint evaluation and classification of nine categorical relationships, including identity, for all pairs of the sampled pool. Laboratory procedures, classification methods, and ancillary discussion pertaining to error assessment are provided in [Supplementary File S1](#). To eliminate the potential for genetics data-entry error, genotype data were directly imported into a database from post-processed GeneMapper output files, in csv or txt format. The database allowed us to track individuals across sampling events and to develop purse-seine recapture histories. Sex ratio was computed using all genotyped individuals with a sex assignment and evaluated against a null hypothesis of equality using a two-tailed, one proportion Z test. Sex-specific capture data were subjected to two-tailed, two proportion Z tests to examine the possible effect of gender on recapture rate.

CMR model to estimate abundance

We used the Huggins parameterization (Huggins, 1989; White, 2008) of a closed-population CMR model in the program MARK (version 9.0, White and Burnham, 1999) to estimate annual

abundance at the TB FSA site in 2013 and 2014. Abundance could not be estimated in 2012 due to the low recapture rate ($n = 1$). This model allows for modelling of initial capture and recapture probabilities as a function of individual and time-varying covariates. Under this parameterization, initial capture “ p ” and recapture “ c ” probabilities are the only parameters in the model likelihood, and annual abundance is calculated as a derived parameter. Due to relatively low annual recaptures, we included the constraint that initial capture (p) and recapture (c) probabilities were equal (i.e. we assumed there was no behavioural response to the non-lethal purse seine sampling). For each year, we fit 10 candidate models, each representing a different combination of time-varying or constant capture and recapture probabilities and the individual covariates of sex and fish length (TL). To facilitate model fitting, we standardized the continuous covariate, TL, with a mean of zero and standard deviation of one. Due to over dispersion of the global model, i.e. all parameters ($\hat{c} = 3.24$ for 2013 and 2.67 for 2014), we adjusted model rankings using \hat{c} and evaluated relative support for the 10 candidate models using QAICc (Burnham and Anderson, 2002). Lastly, we calculated a model-averaged abundance estimate and unconditional standard error for each year based on QAICc weights associated with the candidate set of models.

Acoustic tracking

One hundred twenty-two fish with a 1:1 sex ratio were intra-peritoneally implanted with acoustic tags (Vemco, 69 kHz V16TP-6H; Vemco, Bedford, Nova Scotia, Canada), and we refer to these fish as “acoustically tagged” or “tracked” fish. Most acoustically tagged fish were adults, captured and released in the TB FSA site in 2012 ($n = 60$) and 2013 ($n = 42$). But we also tracked 20 sub-adults, originally captured, acoustically tagged, and released in estuarine waters in lower Tampa Bay in 2012, which later recruited to adult habitat (Lowerre-Barbieri *et al.*, 2016). Adult tags had temperature and pressure sensors (depth to $68 \text{ m} \pm 3.4 \text{ m}$; water temperature from 0°C to $40^\circ\text{C} \pm 0.5^\circ\text{C}$) but the sub-adults did not. Surgical procedures followed Lowerre-Barbieri *et al.* (2016). Most acoustically tagged fish were captured using net gear, adults in the commercial purse seine (2012, $n = 55$; 2013, $n = 30$) and sub-adults in a trammel ($n = 19$) with the remaining fish captured with hook and line. Sub-adults were tagged over four dates in late summer/fall of 2012. In 2012, adults were tagged over three dates in October. In 2013, adults were tagged over three dates in September. All tags had a random delay of 20–60 s between individual signals (emitted at 69 kHz). Although tags had an expected battery life of 958 days, the realized life span was greater as fish implanted in 2012 continued to be detected during the 2015 spawning season ($n = 15$).

The TB FSA and CH FSA study arrays differed in number of receivers and configuration. The TB array was made up of 33

receivers—20 located at previously identified red drum aggregation sites and 13 to fill in gaps, primarily in the southern area. All receivers at the TB FSA site were deployed by 10 September 2012. The study array at the CH FSA site originally had 15 receivers deployed in an evenly spaced grid in August 2012, with additional receivers later deployed at locations where aggregations were sighted in aerial surveys. Original receiver sites deployed in late summer/fall of 2012 consistently monitored the area except for minimal data gaps due to equipment loss (TB FSA array: one site without data for the 2012 reproductive period and two sites without data for the 2014 non-reproductive period; CH FSA array: one site without data during the 2014 non-reproductive period). Opportunistic detection data used to increase the scale of detection came from: (i) an AUV with a VEMCO VMT-35 transceiver deployed from 10 October 2014 to 31 October 2014 (Figure 1b); (ii) artificial reef sites ($n=27$) used for a study on reef fish led by A. Collins; and (iii) receivers ($n=5$) deployed on natural hard bottom ~92 km offshore for a preliminary red snapper study. Locations where tagged fish had been released were surveyed with the mobile receiver to evaluate if there were stationary tags, presumed to indicate tagging mortality due to stress or predation.

Acoustic telemetry data included: tag number, detection date and time, location where the detection was made, and for adults, estimated depth. To ensure synchronized time stamps across receivers, a hand-held transmitter was used to produce a known-time detection on all receivers prior to deployment and download (Humston *et al.*, 2005; Heupel *et al.*, 2006). Detections were grouped into 10 min time bins. Given the distance between receivers in the FSA arrays (mean = 3729 m; range: 2021–5115 m) and realistic swimming speeds, fish were not expected to be detected on more than one receiver within the study arrays in this time bin and this was confirmed. Fish location was assigned as the location of the receiver, but with the recognition that results from range testing (Lowerre-Barbieri *et al.*, 2016) indicated the fish could be up to 400 m away from this location. Five “fates” were assigned to each acoustically tagged fish: (i) dead (an assumption based on stationarity); (ii) never detected; (iii) ghost (only detected on one date and less than five detections on that date), (iv) detected only the date the fish was acoustically tagged; and (v) alive.

Telemetry data was used to assess large-scale and fine-scale space use associated with specific time periods. Large-scale space use analysis was based on detections from all monitored habitats and tracking data sources and included: defining the detection areas and densities within and outside the reproductive period; annual detection histories; and spawning site fidelity and straying rates. The reproductive period was defined as August through December (Lowerre-Barbieri *et al.*, 2016) and kernel densities were estimated to evaluate differences in space use within and outside the 2013 and 2014 reproductive periods. To ensure that a small number of high site fidelity fish did not drive the observed patterns, only unique fish detected per receiver per month were used. To assess variability in large-scale annual space use and potential skip spawning (Rideout and Tomkiewicz, 2011; Gillanders *et al.*, 2015; Fowler *et al.*, 2016), we calculated the proportion of fish with discontinuous annual detection histories, defined as fish exhibiting a break in annual detections, i.e. fish not detected anywhere over at least a year but detected in a consequent year. These analyses are based on the four complete years of detection data (2013 through 2015).

Spawning site fidelity and straying rates of acoustically tagged fish were estimated over a core spawning period. In multiple batch spawners individual spawning periods are often shorter than population spawning seasons and asynchronous (Wright and Trippel, 2009; Lowerre-Barbieri *et al.*, 2011). The red drum population spawning season is 26 August–18 November (Lowerre-Barbieri *et al.*, 2016) and fish often moved through the CH FSA site to reach the TB FSA site. To evaluate straying we needed a criterion to categorize spatio-temporal detection histories expected to correlate with spawning. To do so we defined a core spawning period based on mean arrival and departure dates at the TB FSA site. Straying was defined as fish detected only in the CH FSA site on more than one date during the core spawning period, although potentially detected in the TB FSA site after this time period. Potential straying was defined as fish detected in both the CH FSA and TB FSA within the core spawning period on more than one date in either or both sites.

Annual spawning site fidelity estimates (SSF) were calculated for 2013 and 2014 and based on only fish recruiting after the year they were tagged and the core spawning period in contrast to Lowerre-Barbieri *et al.* (2016), which included fish in the year they were tagged and used the more extended population spawning season. Annual observed SSF was calculated as:

$$SSF_t = \frac{\# \text{observed in TB FSA}(t)}{\# \text{detected overall}(t)}$$

where the number observed equals the number of tagged fish detected at the TB FSA site in the core spawning period in year t and the number detected represents the number of fish detected anywhere (i.e. in study arrays, on the mobile receiver, or in the opportunistic detection region) within year t . This method assumes undetected fish have died outside of the monitored area.

We also calculated annual adjusted spawning site fidelities (Robichaud and Rose, 2002; Zemeckis *et al.*, 2014) separately for 2013 and 2014

$$SSF_t = \frac{\# \text{observed in TB FSA}(t)}{(\# \text{tagged})(t-1)(1-A-T)}$$

where the number observed is the number of fish detected in the TB array in the core spawning period in year t , the number tagged is the number of tagged fish released in year $t-1$, and A is the annual proportion of deaths due to mortality. Because there is no adult fishery, mortality was calculated as $A = 1 - \exp(-M)$ with an M of 0.20 (Porch, 2000). T is observed tag-induced mortality for the year $t-1$. For sub-adults, the number recruited to adult habitat was used rather than the number tagged. In 2014, to account for multiple years of mortality on fish acoustically tagged in 2012, the denominator was calculated as

$$(\# \text{tagged})(t-2)(1-A-T_{t-2})(1-A) + (\# \text{tagged})t-1(1-A-T_{t-1})$$

This method assumes undetected fish in a given year are due to a combination of mortality and fish moving out of the region, assuming a constant detection probability across years.

Fine-scale space was evaluated in terms of vertical movements, temporary migration, and mixing among aggregations over short time periods. Because vertical movement during annual fishing periods affects the efficacy of both the aerial surveys and purse

seine sampling we used depth results from acoustically tagged fish to evaluate surface behaviour. The annual fishing period was defined as all days from the first to the last purse seine sampling date in a given year. Daily mean minimum depth during the diel period of purse seine and aerial survey sampling (9:00–13:00 EST) over the core spawning period was used as an indicator of annual surface behaviour, the assumption being that although depth data was not available for a large number of fish, the collective behaviour of red drum, i.e. if one fish comes to the surface to feed it will be accompanied by others would make this a good indicator. Annual mean minimum depth was calculated and compared for significance with an ANOVA and Tukey's *post-hoc* pairwise test.

To evaluate the effect of short-term movements on availability to capture in 2013 and 2014, we compared daily red drum aerial survey and purse seine sampling with high density concentration areas of acoustically tagged fish over the reproductive period. Kernel density estimates for the 2013 and 2014 reproductive periods were based on hourly detections of individual fish. We also calculated the mean location of acoustically tagged fish on each purse seine sampling date and difference between these within the annual fishing period. To evaluate the effect of short-term movements on availability to capture in 2013 and 2014, we assessed results at daily and weekly scales. The location of sighted aggregations and successful purse sampling were compared with high density detection areas of acoustically tagged fish in the reproductive period. We also calculated the mean location of acoustically tagged fish on each purse seine sampling date and the difference between these within the annual fishing period.

Availability to capture, due to temporary migration, was evaluated at the annual fishing period scale and weekly within the annual fishing periods. Significance of annual differences was tested with a chi-squared test. Proportions were calculated as the number of fish detected within the TB FSA site divided by the number of fish detected anywhere in that year for fish not implanted in the year assessed, i.e. for 2013, only detections from fish tagged in 2012 were used. Significance between mean weekly proportion of fish detected was tested with a *t*-test. Mixing amongst aggregations was evaluated based on the tag-recapture data and by assessing the horizontal movement of three acoustically tagged fish recaptured at the same time by the purse seine. All averages are presented as mean \pm SE and an alpha of <0.05 was considered significant. The remains of one fish were recovered after an apparent shark attack and removed from the data set after confirming the genetic profile indicated it was a fish sampled earlier that day.

Results

Red drum were successfully sampled by aerial surveys, purse seine, and genetic and acoustic tracking. Aggregations occurred in the TB FSA site annually (Figure 2a–c) and were sighted at the presumed CH FSA site in 2013 and 2014. However, the behaviour and number of fish in an aggregation varied, from relatively small groups of fish feeding on baitfish (Figure 2d), to aggregations with large numbers of fish at the surface (Figure 2e), or others which were partly or completely subsurface (Figure 2f). Aggregations were often observed swimming rapidly and always accompanied by sharks of various species. The largest observed aggregation was estimated to have roughly 10 000 fish at the surface. The annual number and location of sighted aggregations differed with year (Figure 1c and Figure 3c and d). In 2012,

aggregations ($n=6$) were detected only in the TB FSA site. Whereas, in 2013 ($n=17$) and 2014 ($n=6$) they were observed in both the TB FSA site and the CH FSA site (Table 1). Throughout the study, 9087 red drum from 13 aggregations were non-lethally sampled for length, sex, reproductive state, and a fin clip for genetic analysis. Fish size (TL) was similar across years: 901 mm TL (576–1064 mm TL) in 2012; 909 mm TL (571–1099 mm TL) in 2013; and 903 mm TL (579–1069 mm TL) in 2014. A total of 87 fish (45 females: 42 males) were acoustically tracked over multiple dates, including 35 adults implanted in 2012; 36 adults implanted in 2013 and 16 sub-adults which recruited to adult habitat. Thirty-five acoustically tagged fish were not included in further analyses because: (i) their tags were stationary ($n=6$) and the fish presumed dead, or (ii) no detections were made after the tag date ($n=29$). Individual arrival and departure dates to the TB FSA site varied. Most fish arrived later than the start of the population spawning season (26 August) and left earlier than the end of the population spawning season (18 November). Mean arrival date of fish in 2013 was 13 September, with first-time spawners (i.e. fish tagged as sub-adults in 2012) having a later mean arrival date (29 September, $n=7$) than repeat spawners (8 September, $n=23$). In 2014, mean arrival date was 10 September ($n=49$) and there was no time lag associated with fish spawning for their second year (mean arrival: 9 September 2014, $n=9$). Mean departure dates were similar for all fish and years: 17 October in 2013 and 22 October in 2014. Based on these dates we assigned a core spawning period of 8 September to 22 October for both 2013 and 2014.

Genetic tracking

Of the 9087 fin-clips genotyped for the 3-year sampling period, 199 sets of matching DNA profiles were observed, each attaining *MAPID* classification status within the analysis. Given their high posterior probabilities, all matching sets of DNA profiles were considered to represent discrete individuals. Empirical detectability, conditioned on the observed δ for red drum in this study, was estimated to be greater than 99.99%. Therefore, the potential for bias in abundance estimates due to mistyping error was deemed negligible (see Supplementary File S1).

Large-scale space use

Fish concentrated at the TB FSA site during the reproductive period, dispersing over a much larger area in the non-reproductive period (Figure 3). High detection densities occurred during the reproductive period within the TB FSA site. In the non-reproductive period, detection densities were much lower but occurred over a large area. At least one red drum was detected on every acoustic receiver deployed in the region, an area of ~ 150 km along the coast and 90 km offshore. Detections at the furthest offshore site came from a small array ($n=5$ receivers) deployed in 2014, with multiple fish detected both before and after the core 2014 spawning period. A total of 12 fish were detected at this site (Figure 1b, furthest west site).

Most tracked fish were detected over 3 years (55%, $n=48$) and all but one were detected in the TB FSA site in at least 1 year. There were also fish detected only in the TB FSA site in 2012 and 2013 ($n=16$). However, no fish showed this pattern in 2014. Only 2 of the 87 fish tracked (1%) exhibited discontinuous annual detection patterns (Figure 4). Both were tagged as sub-adults, recruited to adult habitat in 2012, were not detected in

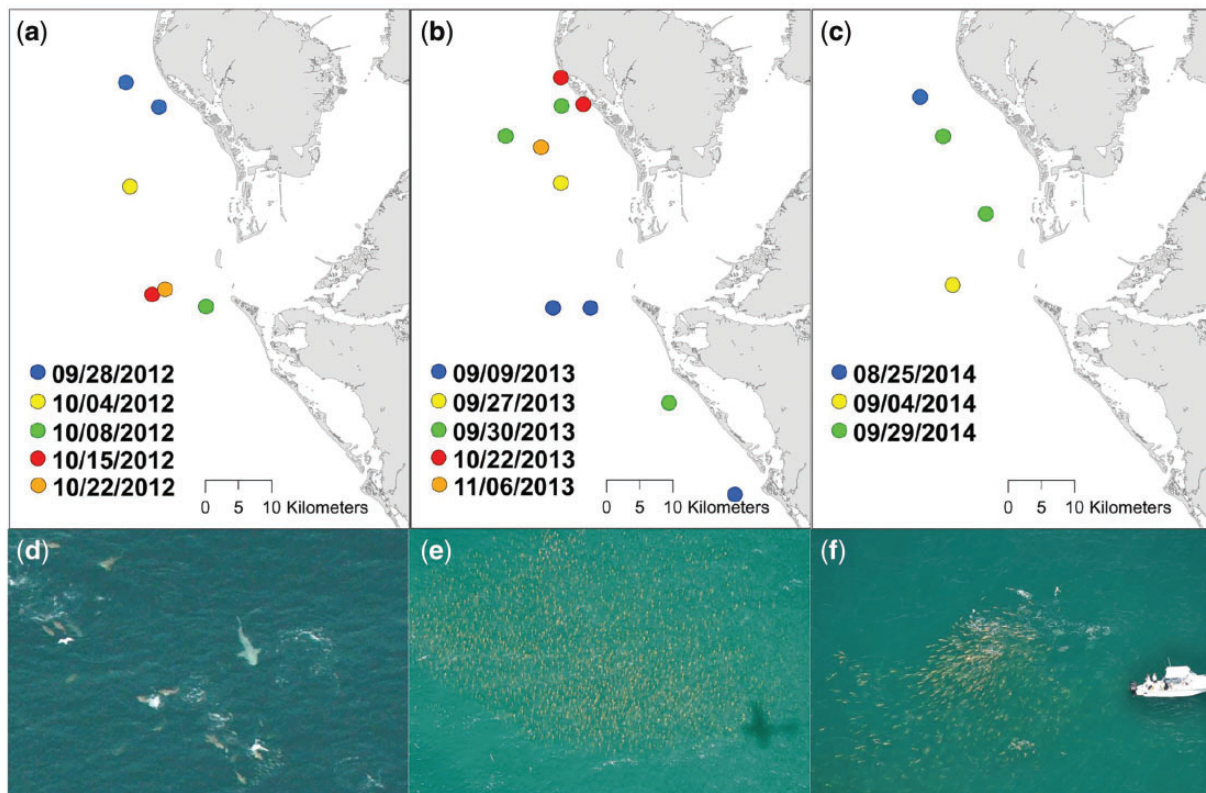


Figure 2. The number and location of red drum aggregations sighted in aerial surveys in the Tampa Bay fish aggregation site by year. In 2012 (a) six aggregations were observed; in 2013 (b) ten aggregations were observed; and in 2014 (c) four aggregations were observed. Aggregations were of various sizes and fish exhibited a range of behaviours, including: (d) small groups feeding on baitfish, with sharks potentially feeding on them; (e) large, subsurface aggregations, often travelling fast; and (f) large aggregations, with a portion coming to the surface to feed.

2013, and then detected again in 2014. Observed annual spawning site fidelity to the TB FSA site was high: 91% in 2013 ($n=64$) and 85% in 2014 ($n=48$). Although adjusted spawning site fidelity was 48% in both years. Straying, although infrequent, did occur, with 6% of tracked fish detected only in the CH FSA site during the core spawning periods in 2013 and 2014 (Figure 5), with one fish showing this pattern in both years (Tag 23). An additional 7% of fishes exhibited potential straying, as they were detected in both the TB FSA site and CH FSA site in the core spawning period.

Annual abundance

Recaptured fish were representative of the sampled population in terms of sex ratio and length. In all 3 years, the proportion of males sampled to females was similar (1.3 males to 1 females). The null hypothesis that the sex ratio of recaptured fish equaled that of all profiled fish could not be rejected ($Z=-0.665$; $p=0.5029$) and there was no evidence of gender-based heterogeneity in recapture rates or differences in size (t -test, $p=0.626$). However, males were significantly smaller (900 mm TL) than females (912 mm TL; t -test, $p<0.0001$).

Annual abundance estimates at the TB FSA differed, with a fourfold decrease in abundance in 2014 compared with 2013. Only one fish was recaptured in 2012. Although sampling effort was similar in October 2013 and 2014, within-year recaptures in October (Figure 6) were much higher in 2014 ($n=94$) than in 2013 ($n=17$). In both years, the best-approximating Huggins

capture–recapture model included time-varying capture and recapture probabilities and a time-varying effect of total length (TL) on capture and recapture probabilities (Supplementary Tables S1 and S2). Parameter estimates from the best-approximating models indicated that capture and recapture probabilities were low and varied through time, with greater variability in 2013 (Supplementary Tables S3 and S4). In 2013, the model-averaged estimate of abundance was $\sim 199\,013$ fish with an unconditional standard error of $\sim 74\,994$. In 2014 it was $\sim 51\,786$ fish with an unconditional standard error of ~ 9845 in 2014 (Tables 2 and 3). The number of aggregations sighted within the TB FSA site also varied from four in 2014 to ten in 2013, with 2012 being intermediate ($n=6$; Table 1, Figure 2).

Fine-scale space use

Horizontal and vertical movement varied at the TB FSA site annually and within fishing periods. Acoustically tagged fish in 2013 were tightly concentrated in an area just north of Tampa Bay's mouth but were a little more spread out in 2014 (Figure 3c and d). Aerial surveys detected aggregations throughout a larger range of sites. Whereas, successful purse seine sets were overlapped more with high concentration acoustic detections, with the exception of one site in 2013. Surface behaviour of acoustically tagged fish was significantly less ($p=0.0002$; $n=92$) in the 2014 fishing period (mean minimum daily depth = 5.4 m) than in the fishing periods in prior years (2012: mean = 3.6 m; 2013: mean = 3.3 m). At the daily scale, the number and location of tagged

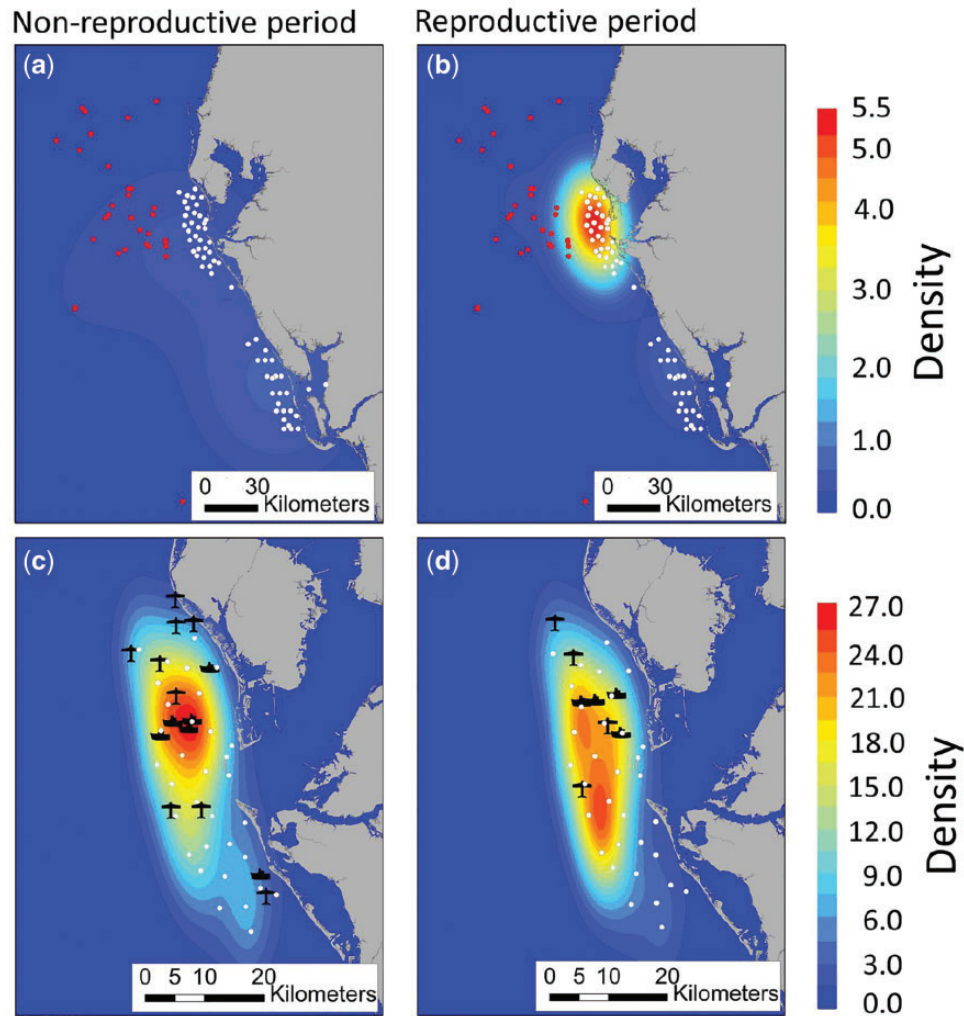


Figure 3. Kernel density estimates of acoustic tag detections of red drum during the non-reproductive (a) and reproductive periods (b) from data pooled over 2013 and 2014. White dots are receivers in study arrays and dark dots are receivers from other studies providing opportunistic detections. Kernel density estimates of tag detections at the Tampa Bay fish aggregation site during the spawning season in 2013 (c) and 2014 (d), as well as purse seine sampling locations (boat marker) and aggregation locations (plane markers). Relative densities of tagged fish are indicated by the colour bar to the right.

fish detected in the diel window of sampling varied with sampling date. More fish were detected on purse seine dates in 2013 (mean = 10 fish/date, range: 4–16) than in 2014 (mean = 3 fish/date, range: 2–5). In both years, mean location of acoustically tagged fish differed between sampling dates by ~7 km. Disparate detection locations and realistic swim speeds indicate multiple aggregations in the TB FSA site on purse seine sampling dates. Acoustically tagged fish, however, were detected near all purse seine sets with the exception of the southernmost set, when detected fish were within the core detection area but the purse seine set was not.

The proportion of red drum at the TB FSA site varied weekly due to temporary migration. Although the fishing period was longer in 2013 (33 days) than in 2014 (22 days), the proportion of tagged fish detected at the TB FSA site during the annual fishing periods was similar: 45% in 2013 and 55% in 2014 and non-

significant ($\chi^2 = 0.7538$, $p = 0.3853$, $n = 65$). However, the proportion of fish available for capture on any given week varied (Figure 7), with a higher mean proportion of fish on the TB FSA site during fishing weeks in 2013 (mean = 0.51 ± 0.04 , $n = 5$) than in 2014 (mean = 0.39 ± 0.01 , $n = 4$) and these differences were significant (t -test, $p < 0.001$, $n = 9$). In addition, opportunistic offshore detections occurred in each week of the fishing period in 2014, whereas none occurred during the 2013 fishing period.

Relatively high mixing rates were observed between spawning aggregations within the spawning season in both years. Recaptured fish on each purse seine sampling date (Figure 6) came from multiple (range: 2–10) original sampling dates, and presumed aggregations. In addition, on 17 October 2013, three acoustically tagged fish were captured by the purse seine (Figure 8). The individual movements of these fish before and after capture indicated aggregation dynamics can be quite fluid. Each of these fish was originally

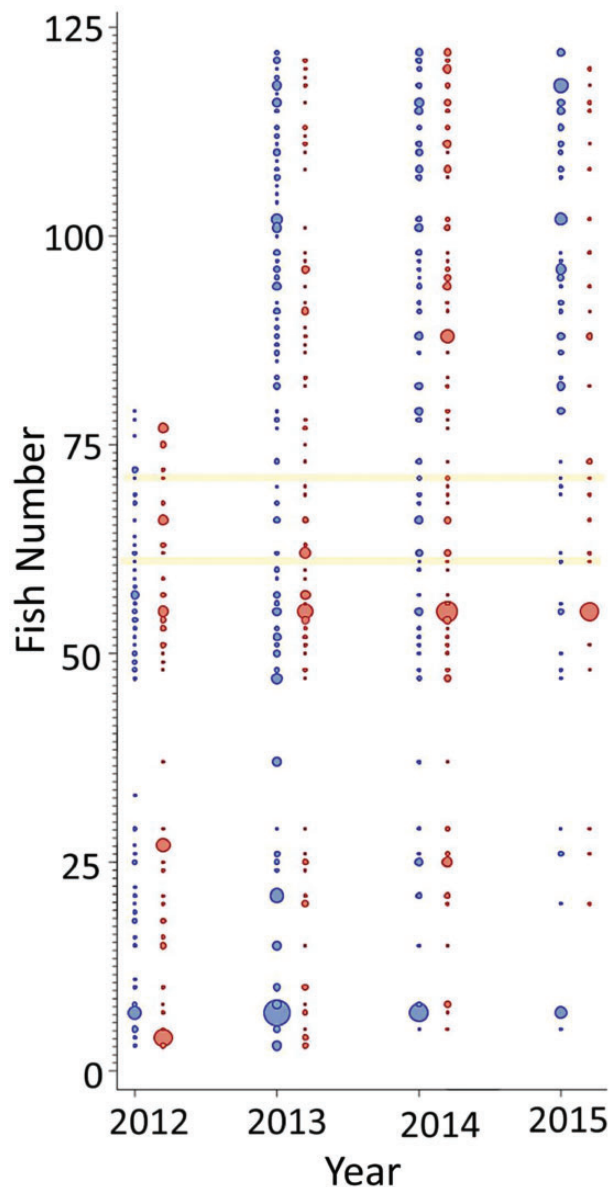


Figure 4. Individual annual detection histories (detection number is represented by bubble size) of red drum at the Tampa Bay spawning aggregation site during the reproductive period (left) vs. detected anywhere else in the region at any time (right). Two fish exhibited discontinuous annual detections at the regional scale (bar).

captured on a different date, and presumably aggregation, in 2012. They were first detected in the TB FSA site on differing dates in 2013, indicating they did not move to the TB FSA as a group. Nor did they show synchronized detections over space (Figure 8a) or the day prior to capture (Figure 8b). After release they also exhibited different movement patterns.

Discussion

Space use affects vulnerability and productivity and has important management implications (Allen and Singh, 2016). Animals rarely distribute themselves randomly or uniformly across space but often aggregate in specific locations to feed or breed (Wagner and Danchin, 2003). Spawning site selection in marine fish is

especially important as birth site constrains where eggs and larvae can disperse and potentially constrains later space use (Ciannelli *et al.*, 2014). This results in complex spawner-recruit systems, which in addition to mature abundance are affected by where and when fish spawn and species-specific adult and offspring behaviours. Populations spawning in high density at relatively few spawning sites are expected to have lower reproductive resilience to disturbance (Lowerre-Barbieri *et al.*, 2017). However, potential effects of spatial aggregation on population dynamics and recruitment remain poorly appreciated and rarely investigated, even in well-studied species such as Atlantic salmon, due to the extensive amount of data needed to do so (Bouchard *et al.*, 2018).

In this study, we used acoustic telemetry to evaluate space use important to population processes. As expected in an aggregating species, red drum space use was highly concentrated within the reproductive period in the TB FSA site and dispersed in the non-reproductive period, with fish detected throughout a much larger area. Previous analysis indicated in the non-reproductive period many fish move south (Lowerre-Barbieri *et al.*, 2016). Detections from the iTAG data exchange indicated that during the non-reproductive period fish are also offshore. However, due to sparse receiver coverage it was not possible to track fish throughout their annual migratory cycle nor measure adult dispersal distances. This is a common limitation of acoustic telemetry, where a fish must swim within range of a receiver to collect location data (Hebblewhite and Haydon, 2010; Crossin *et al.*, 2017).

We hypothesized that if space use was relatively constant over multiple years, fish would not exhibit discontinuous annual detection patterns and only two fish (both acoustically tagged as sub-adults) went undetected the year after recruiting and presumably skip spawned. Given this pattern of detection and previous reports of natal homing to the TB FSA site (Patterson *et al.*, 2004; Lowerre-Barbieri *et al.*, 2016), we assumed fish acoustically tagged and undetected within a year of release died outside our detection area. Based on this assumption, observed spawning site fidelity was quite high (91% in 2013 and 85% in 2014) and straying to the CH FSA was relatively low, ranging from 6% to 13%. However, long-term shifts in spatial use cannot be ruled out given limited receiver coverage outside the FSA sites and the temporal scale of tracking (4 years) vs. the expected reproductive life span of at least 30 years (Winner *et al.*, 2014). Patterson *et al.* (2004) reported 75% site fidelity at the TB FSA site and our adjusted spawning site fidelity rates were 48% in both 2013 and 2014. Thus, acoustically tagged fish which went undetected may be due to a mixture of mortality and long-term changes in space use.

To estimate abundance at the TB FSA site we sampled more than 9000 fish non-lethally and genetically profiled them for the mark-recapture data base. Genetic profiling for CMR studies is still uncommon in fisheries studies but expected to become increasingly used (Miller *et al.*, 2015) as it provides a number of benefits, including: 100% tag retention and the ability to estimate effective breeding population size, an important parameter as mature census abundance may not be a good indicator of reproductive success (Lowerre-Barbieri *et al.*, 2017). It can also help inform mixed population stock assessments (Whitlock *et al.*, 2018). Lastly, when juveniles are also collected and profiled connectivity between reproductive processes and offspring location and survival can be assessed (Whitlock *et al.*, 2017; Bode *et al.*, 2018).

However, genetic methods can also produce bias through false discoveries and false rejections. When using genetic recapture

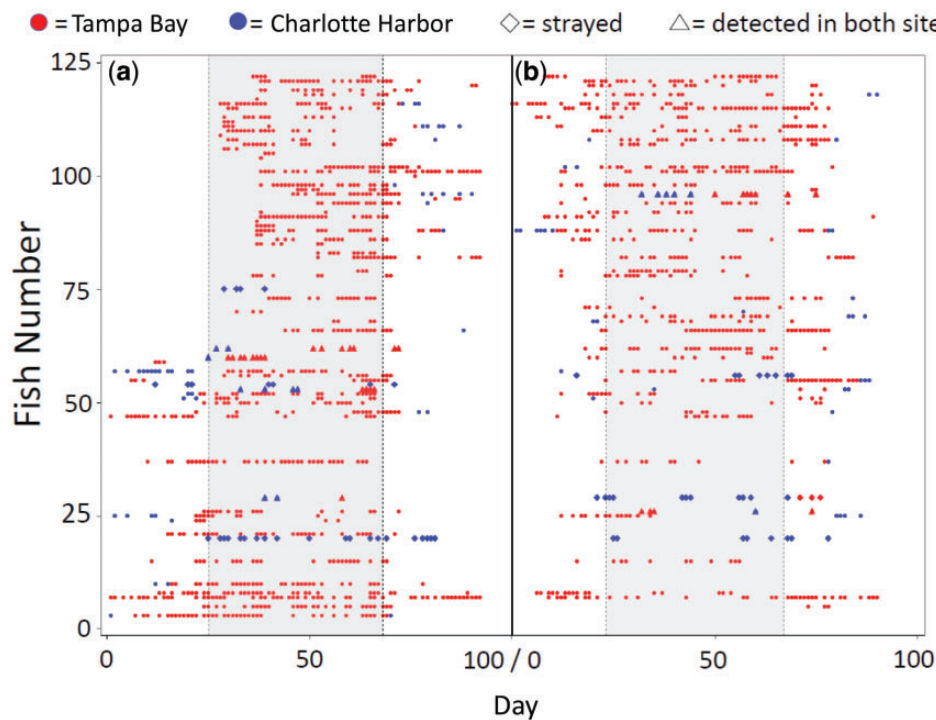


Figure 5. Individual red drum daily detection histories over the population spawning season (26 August–18 November) and core spawning periods (between dashed lines, 8 September–22 October) for 2013 (a) and 2014 (b). Day one and day 101 indicate the first day of the population spawning season. In the core spawning period, most fish were detected in the Tampa Bay (TB) FSA site, even if they were detected in the Charlotte Harbor (CH) FSA site before and after the core spawning period. However, some fish strayed (diamonds), being detected only in the CH FSA site during the core spawning period and others were detected at both FSA sites during the core spawning period (triangles).

| | | | | | | | | | | | | |
|------------|-----|-----|-----|-----|-----|-----|-----|-----|-----|------|-----|------|
| | 526 | 668 | 635 | 140 | 689 | 689 | 109 | 975 | 816 | 1018 | 333 | 1137 |
| 28-10-2014 | 2 | 0 | 2 | 2 | 2 | 8 | 0 | 3 | 1 | 22 | 6 | 24 |
| 22-10-2014 | 4 | 2 | 0 | 0 | 5 | 3 | 1 | 4 | 2 | 9 | 32 | |
| 20-10-2014 | 2 | 0 | 0 | 1 | 2 | 1 | 0 | 1 | 0 | 1 | | |
| 09-10-2014 | 0 | 2 | 0 | 0 | 2 | 3 | 0 | 1 | 0 | | | |
| 17-10-2013 | 1 | 3 | 3 | 0 | 1 | 4 | 0 | 0 | | | | |
| 15-10-2013 | 1 | 3 | 2 | 0 | 5 | 10 | 0 | | | | | |
| 03-10-2013 | 1 | 0 | 0 | 1 | 0 | 0 | | | | | | |
| 01-10-2013 | 0 | 2 | 6 | 0 | 1 | | | | | | | |
| 19-09-2013 | 1 | 0 | 1 | 1 | | | | | | | | |
| 17-09-2013 | 0 | 0 | 1 | | | | | | | | | |
| 17-10-2012 | 1 | 0 | | | | | | | | | | |
| 05-10-2012 | | | | | | | | | | | | |
| 03-10-2012 | | | | | | | | | | | | |
| 17-10-2012 | | | | | | | | | | | | |
| 17-09-2013 | | | | | | | | | | | | |
| 19-09-2013 | | | | | | | | | | | | |
| 01-10-2013 | | | | | | | | | | | | |
| 03-10-2013 | | | | | | | | | | | | |
| 15-10-2013 | | | | | | | | | | | | |
| 17-10-2013 | | | | | | | | | | | | |
| 09-10-2014 | | | | | | | | | | | | |
| 20-10-2014 | | | | | | | | | | | | |
| 22-10-2014 | | | | | | | | | | | | |

Figure 6. Tag, recapture matrix indicating on any given recapture date the number of red drum recaptured from the range of previous dates/aggregations sampled. The total number of unique fish sampled on any given date is at the top of the table. Higher numbers of recaptures are indicated with darker grey shading. Sampling dates in October 2013 and 2014 are highlighted by rectangles, as sampling effort was similar, but the number of recaptures was not.

histories to estimate abundance, false discoveries will cause an underestimate whereas false rejections have the opposite effect. False discoveries arise almost solely during the analytical process, when different individuals share matching DNA profiles by chance. However, the high MAP-classified posterior probabilities for matching DNA profiles in this study indicated that false discoveries could be safely neglected during population-abundance

modelling. False rejections occur due to mistypings and other lab errors. We minimized mistyping occurrences by assay optimization, laboratory quality control, analytical detection, planned repetition, and (at least in theory) by limiting the analysis to the smallest set of reliable and sufficiently informative markers. DNA quality and quantity also affect the potential for genotyping error (Lampa *et al.*, 2013) but in this study, there was no difficulty in

Table 2. Model-specific weights (w), abundance estimates, and standard errors (SE) used to calculate the 2013 model-averaged abundance estimate (N -hat), unconditional standard error (SEU) and lower (LCL) and upper (UCL) 95% confidence limits.

| Model | w | Estimate | SE | SEU | LCI | UCI |
|--|--------|----------|--------|--------|--------|---------|
| $p(t) = c(t) + TL(t)$ | 0.465 | 198 666 | 74 529 | | | |
| $p(t) = c(t) + TL(t) + \text{Male}(t)$ | 0.362 | 199 184 | 75 334 | | | |
| $p(t) = c(t) + TL(t) + \text{Male}(\cdot)$ | 0.174 | 199 600 | 75 566 | | | |
| $p(t) = c(t) + M(t)$ | 0.001 | 199 275 | 74 994 | | | |
| $p(t) = c(t)$ | 0.001 | 198 701 | 74 095 | | | |
| $p(t) = c(t) + TL(\cdot) + M(t)$ | <0.001 | 200 098 | 75 939 | | | |
| $p(t) = c(t) + M(\cdot)$ | <0.001 | 199 738 | 75 249 | | | |
| $p(t) = c(t) + TL(\cdot)$ | <0.001 | 199 625 | 75 158 | | | |
| $p(t) = c(t) + TL(\cdot) + M(\cdot)$ | <0.001 | 200 566 | 76 198 | | | |
| N -hat, weighted average | | 199 014 | 74 994 | 74 996 | 52 021 | 346 007 |

Parameter definitions: p , initial capture probability; c , recapture probability; TL, total length, and M, male. Model intercepts and coefficients for individual covariates (TL and M) were modelled as either constant (\cdot) or time-varying (t).

Table 3. Model-specific weights (w), abundance estimates, and standard errors (SE) used to calculate the 2014 model-averaged abundance estimate (N -hat), unconditional standard error (SEU), and lower (LCL) and upper (UCL) 95% confidence limits.

| Model | w | Estimate | SE | SEU | LCI | UCI |
|--|-------|----------|------|------|--------|--------|
| $p(t) = c(t) + TL(t)$ | 0.425 | 51 733 | 9806 | | | |
| $p(t) = c(t) + TL(t) + \text{Male}(t)$ | 0.406 | 51 772 | 9857 | | | |
| $p(t) = c(t) + TL(t) + \text{Male}(\cdot)$ | 0.169 | 51 957 | 9915 | | | |
| N -hat, weighted average | | 51 787 | 9845 | 9845 | 32 490 | 71 084 |

Parameter definitions: p , initial capture probability; c , recapture probability, TL, total length, and M, male. Model intercepts and coefficients for individual covariates (TL and M) were modelled as either constant (\cdot) or time-varying (t).

obtaining quality DNA in concentrations exceeding 100 ng/μl and only minimal need for PCR repetition due to unmet peak-amplitude thresholds.

Given the reliability of our genetic profiling and multiple indicators suggesting lower abundance at the TB FSA site in 2014, annual differences in abundance at this site are likely. However, red drum exhibit collective movement within three-dimensional space and this could affect availability or mixing and over short time periods. Both recapture histories and acoustic tracking suggested mixing amongst aggregations is rapid and did not affect our results. However, fine-scale space use results suggest the assumption of population closure may have been violated, i.e. there was emigration/immigration of individuals or recruitment/mortality during the sampling period. In 2014, surface behaviour, which can affect spotter plane efficacy, was less and aggregations were sighted over a shorter time period than in 2013. One factor affecting surface behaviour is availability of baitfish schools within the TB FSA site and this is expected to vary both within the reproductive period (potentially daily) and across years. Similarly, surface behaviour may vary with region depending on food availability and may explain the sighting of fewer aggregations in the CH FSA site, where there is a larger shrimp population.

We assumed there would be recruitment and mortality within the reproductive period but that it would be minimal and similar across years. If the greater abundance in 2013 was due to a large year class recruiting to the adult population, mean TL was expected to be significantly smaller and it was not. Similarly, if there was an episodic mortality event which caused much higher natural mortality in 1 year than another, we expected to see a significant drop in the proportion of acoustically tagged fish detected between years,

and we did not. But again, it is worth mentioning that it is not possible to know if the fish tracked are fully representative of the population. Many populations have contingents exhibiting differential movement ecology or movement syndromes (Abrahms *et al.*, 2017) and there may have been red drum contingents untracked by our study. Lastly, FSA sites are predictable in space and time at the population scale, but not always at the individual scale (Lowerre-Barbieri *et al.*, 2013, 2014) and thus we expected temporary migration to and from the TB FSA site. But we assumed temporary migration rates would be similar throughout the spawning season and between years. This was not the case, as there was a significantly lower weekly proportion of tagged fish detected in the 2014 fishing period (mean = 0.39) than in the 2013 fishing period (mean = 0.51) and more offshore opportunistic detections in 2014. But a caveat with opportunistic detections is that receiver coverage can also change, and there were more receivers deployed in offshore studies in 2014.

Conclusions

Red drum aggregations have been consistently documented at the TB FSA site (Murphy and Crabtree, 2001; Winner *et al.*, 2014) and move to this site in schools. These schools then coalesce into larger aggregations of 5000 (Winner *et al.*, 2014) to 10 000 individuals or more. Both horizontal and vertical movement in red drum aggregations appears linked to following and feeding on bait fish, although the high observed spawning site fidelities would suggest spawning site selection is more complicated than simply following food. Like other aggregating species, red drum are vulnerable to over-fishing, as well as other spatially explicit stressors such as red tide events. In 2012, when no aggregations were detected in the presumed CH FSA site, there was a red tide

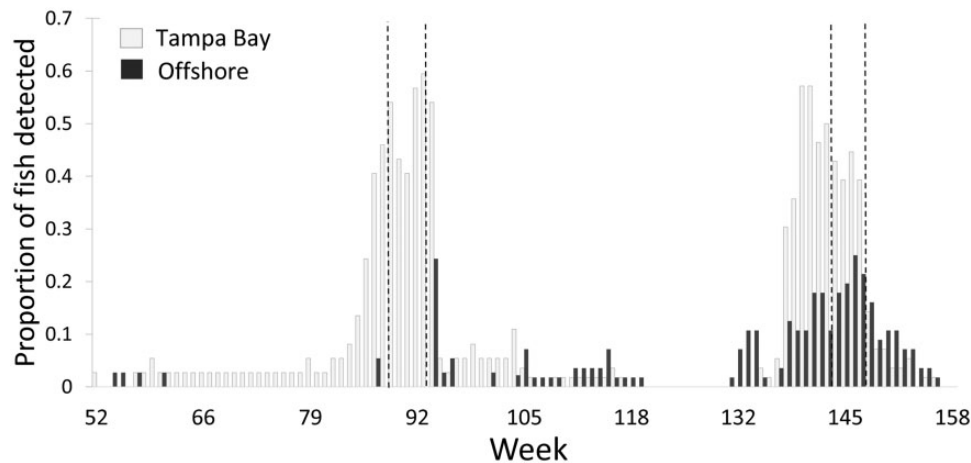


Figure 7. Weekly proportion of annually detected red drum by habitat (grey = Tampa Bay FSA site, black = opportunistic offshore detections). The area between the dashed lines delineates the annual fishing period, i.e. the time period within which purse seine sampling occurred in each year.

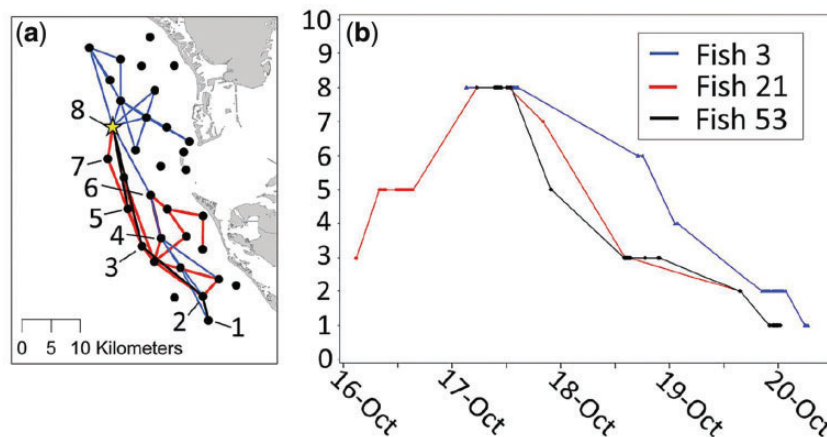


Figure 8. Fine-scale movements of three acoustically tagged red drum recaptured together by the purse seine on 17 October 2013 (star). (a) Tracks of these three fish over the 2013 core spawning period indicate their movements were not synchronized in terms of space usage; (b) zooming into a shorter temporal scale (one day before capture, capture date, and 3 days after release) and looking at detection location (numbers on (a)) by date and time also indicates movement was not synchronized over this shorter time period. Only one fish was detected within the Tampa Bay fishing aggregation site the day before capture and the only time that the three fish were at the same place at the same time is when they were captured by the purse seine.

in the area (Lowerre-Barbieri *et al.*, 2016). Similarly, Winner *et al.* (2014) reported no red drum aggregations were spotted in 31 flights over the TB FSA site in 2005 when a major red tide (*Karenia brevis*) occurred (Flaherty and Landsberg, 2011; Walters *et al.*, 2013). Due to the local source dynamics, these episodic events can affect recruitment and year class strength, as seen for red drum in Tampa Bay after the 2005 red tide (Flaherty and Landsberg, 2011).

Understanding the impacts of anthropogenic change on wildlife populations necessitates research at large spatial and temporal scales (Zipkin and Saunders, 2018) integrated with mechanistic understanding of processes typically studied at much smaller scales. FSA sites and annual abundance at these sites are the result of a complex range of processes including reproductive strategy, movement ecology, and trophic dynamics. These processes affect space use at both large and fine scales and thus the efficacy of

MPAs as conservation measures (Grüss *et al.*, 2015; Boucek *et al.*, 2017) and our ability to estimate abundance, which is especially challenging in large-scale marine systems (Hewitt *et al.*, 2010; Dudgeon *et al.*, 2015). Improved mechanistic understanding of these processes was the focus of this study, but future work will use these results to develop a Hierarchical Bayesian Cormack Jolly Seber model, a superpopulation approach (Kendall *et al.*, 1997; Williams *et al.*, 2011) which is useful for aggregations where individuals exhibit intra-seasonal spawning site fidelity and can help with more accurate estimations of spawning population abundance (Zarada, 2018).

Supplementary data

Supplementary material is available at the ICESJMS online version of the manuscript.

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