

Site fidelity and reproductive timing at a spotted seatrout spawning aggregation site: individual versus population scale behavior

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ABSTRACT: Variability in individual lifetime reproductive success is known to have important consequences for population dynamics, yet it is often poorly understood in marine fishes. We evaluated spotted seatrout *Cynoscion nebulosus* spawning site fidelity and reproductive timing at both the population and individual level at a resident spawning aggregation site. Because males make sounds associated with courtship, we were able to use aggregation sound as an indicator of population spawning activity, monitoring sound at this site with passive acoustics. To assess individuals, we acoustically tagged and released 32 (19 male, 13 female) fish and monitored the spatio-temporal patterns of their movements with a high-density receiver array. Both aggregation sound and detections of tagged fish indicated a truncated spawning season in 2005, apparently due to a persistent red tide event. Individuals exhibited strong intra-seasonal site fidelity, with 23 tagged fish returning to the site to spawn. Most of the fish spawning at this site were drawn from the estuary and returned to the estuary within a 24 h cycle. However, there was individual variability in this spatio-temporal behavior. Aggregation sound indicated daily spawning at this site, but not by the same individuals. Individual estimates of spawning indicated that males spawned more frequently than females (average spawning interval of 2.2 d compared to 9.3 d for females), and that individuals exhibited variability in the time period between spawning events. The probability of an individual spawning at this site was significantly affected by sex and lunar phase (spawning increased on dates near the full moon), but not by current speed or direction.

KEY WORDS: Fish spawning · Site fidelity · Spawning aggregation · Acoustic telemetry

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INTRODUCTION

Reproductive success drives population productivity and allows species to persist. Large differences in individual lifetime reproductive success are common and drive the selection of traits that can have important consequences for population dynamics (Clutton-Brock & Sheldon 2010). While this idea is well integrated into ecology, it is not commonly integrated into our understanding of marine fish population dynamics (Pecquerie et al. 2009). Reproductive success is typically incorporated into stock assessments and fisheries management through the stock–

recruitment relationship, which attempts to evaluate how the future abundance of catchable fish relates to current stock abundance (typically measured as spawning stock biomass). The population's maximum reproductive rate or compensatory reserve is represented by the slope of the spawner–recruit curve near the origin (Myers & Barrowman 1996, Lowerre-Barbieri 2009). However, there is increasing awareness that spawning stock biomass is a poor predictor of reproductive potential (Murawski et al. 2001, Marshall 2009) and increasing evidence of other factors affecting reproductive success, including spawning site selection (Begg & Marteinsdottir 2002), spawn-

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ing site fidelity (Robichaud & Rose 2003, Svedang et al. 2007, Adams et al. 2011), reproductive timing (Wright & Trippel 2009, Lowerre-Barbieri et al. 2011a) and demographic trends in these behaviors (Scott et al. 2006, Anderson et al. 2008, Cooper et al. 2013).

Reproductive success can be defined as the probability that offspring will survive to reproductive age, and has 2 components: (1) reproductive output or rate, and (2) survival rate of that output (Lowerre-Barbieri 2009). For the most part, applied fisheries reproductive biology (Kjesbu 2009) has focused on estimating reproductive output or fecundity. For fish with determinate fecundity these estimates can be made at the individual level. However, most marine epipelagic spawners are batch spawners with indeterminate fecundity (Murua & Saborido-Rey 2003) and, for these species, only batch fecundity is typically estimated at the individual level. Annual fecundity is estimated as the product of batch fecundity and the number of spawns within a season, or spawning frequency (Hunter & Macewicz 1985). However, without the ability to follow individuals over time, spawning frequency is difficult to estimate. Thus, it is typically estimated at the population level by dividing the number of days in the spawning season by the reciprocal of the spawning fraction, which is considered to represent the spawning interval (reviewed in Lowerre-Barbieri et al. 2011a). Estimates of individual spawning intervals and spawning periods are rare. However, spawning intervals can vary over a spawning period and by sex (Asoh 2003, Curtis 2007, Patzner 2008) and population estimates without the resolution to assess this variability may lead to overestimation of spawning frequency and annual fecundity (Curtis 2007). Offspring survival, the second component of reproductive success, is traditionally studied in terms of larval dynamics; however, there is increased interest in understanding how elements of reproductive performance and a parent's reproductive history affect offspring survival (Jørgensen et al. 2008, Jakobsen et al. 2009, Lowerre-Barbieri et al. 2011b).

Recent technological advances as well as efforts to apply spatial management to protect spawning aggregations have resulted in research on behaviors that impact reproductive success at both the population and individual level. In addition, remote sampling techniques, such as passive acoustics to record courtship sound production (Gannon 2008, Luczkovich et al. 2008), acoustic surveys with echosounders (Lawson & Rose 2000, Macchi et al. 2005), and telemetry (Robichaud & Rose 2002, 2003, Metcalfe et al. 2012), provide the ability to monitor reproductive behavior over

time and space in ways that were not previously possible. Passive acoustics can be used to identify the spatial distribution of spawning sites (Lowerre-Barbieri et al. 2008a, Walters et al. 2009) and to monitor reproductive timing based on courtship sounds at known spawning sites (Walters et al. 2007, Fudge & Rose 2009, Locascio et al. 2012). Similarly, passive telemetry (i.e. fixed receivers) can be used to assess spawning migration routes and individual variability in reproductive timing (Rhodes & Sadvoy 2002, Loher & Seitz 2008, Douglas et al. 2009), as well as movements associated with spawning (Loher & Seitz 2008, Adams et al. 2009, Danylchuk et al. 2011). Telemetry can also be used to show differential use of spawning habitat by sex or size, and time spent on spawning grounds (Robichaud & Rose 2002, 2003, Afonso et al. 2009, Bansemmer & Bennett 2009, Semmens et al. 2010).

In this study, we use passive acoustics and acoustic telemetry to assess reproductive timing and intra-seasonal spawning site fidelity of spotted seatrout *Cynoscion nebulosus* at a previously identified spawning aggregation site. Spotted seatrout are pelagic spawners with indeterminate fecundity that spawn large numbers of small, buoyant eggs in multiple batches throughout an extended season. Spotted seatrout make an ideal case study given that their periodic life-history strategy is similar to most recreationally and commercially targeted species (Wine-miller 2005), with moderate to low longevity, relatively short generation times, and a batch spawning or bet-hedging reproductive strategy. Like other batch spawners, spotted seatrout batch fecundity increases with size and age (Lowerre-Barbieri et al. 2009), and spawning activity appears to as well (Cooper et al. 2013). The population structure is believed to consist of a series of overlapping subpopulations, each centered in a natal estuary, with estuarine spawning (Brown-Peterson 2003) and relatively little mixing between populations (Jones 2006). However, in previous studies we found the most consistently used and densely populated spotted seatrout spawning site occurred at an inlet (Lowerre-Barbieri et al. 2009, Walters et al. 2009). Fish moved from their foraging habitat to this inlet to spawn, exhibiting a 97% spawning fraction (Lowerre-Barbieri et al. 2009). Thus, we were interested in using concurrent passive acoustic and telemetric monitoring at this site to test the following hypotheses: (1) individuals exhibit intra-seasonal site fidelity, returning to this spawning site multiple times within the spawning season; (2) fish spawning at this site come from and return to the estuary, supporting the dogma of little mixing between estuarine populations; (3) estimates

of individual spawning will differ from measures of spawning activity at the population level; and (4) the probability of spawning at this site will be affected by sex, size, lunar phase, and current speed and direction. We compared our individual-based results with conventional estimates of reproductive timing and discuss these results within the context of reproductive success in marine fishes.

MATERIALS AND METHODS

Study site

This study was conducted from April 2005 to September 2005 at Bunces Pass, an inlet at the mouth of Tampa Bay, Florida, USA (Fig 1). This location had been previously identified as the most consistently used and densely populated spotted seatrout spawning site in Tampa Bay (Walters et al. 2009, Lowerre-Barbieri et al. 2009). The inlet is approximately 300 m wide, with a relatively deep channel (max depth 8.5 m). It is bordered by sandbars that extend out into the Gulf approximately 1000 m to the north and south, which are partially exposed at the most extreme low tides. The bottom is predominantly shell hash, with no submerged aquatic vegetation or oyster reefs. Currents at this site are tidally-driven and reach velocities of 1 m s^{-1} (1.9 knots) during the strongest spring tides.

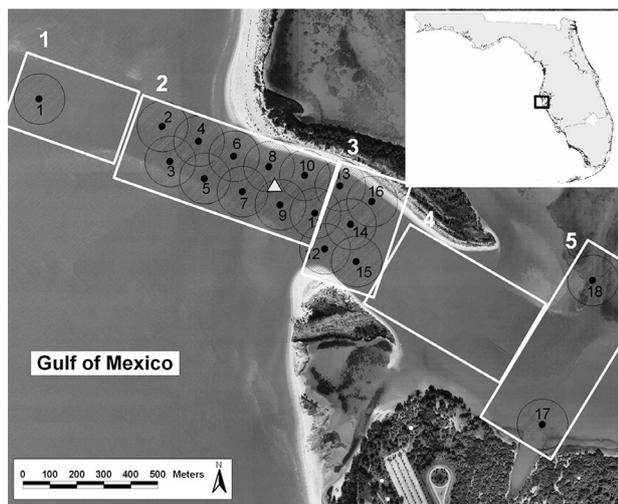


Fig. 1. Receiver array located at Bunces Pass in Tampa Bay, Florida. Receivers 2–16 monitored the spawning site and are considered the core array. Receiver locations are denoted with a black dot surrounded by an 85 m radius range bubble (shaded circle). The white triangle represents the control tag between Receivers 8 and 9. Long-term acoustic recorders (LARS) were located at Receivers 6 and 7. Detection zones are indicated by white rectangles

Receiver array

We deployed a high-density fixed array of acoustic receivers (VR2s, Vemco) to monitor the spawning site. Although we were not interested in fine scale movements within the spawning site, we needed to identify dates when fish moved to the spawning grounds and, for those dates, arrival and departure locations and times. In contrast to most telemetry studies, we also needed an array designed so that a lack of detection corresponded to a fish not moving to the spawning site that day. We defined the expected boundaries of the spawning site (Fig. 1, Zones 2 and 3) based on the area with both aggregation level courtship sound (Walters et al. 2007) and actively spawning females (Lowerre-Barbieri et al. 2009). Long-term range testing was undertaken to evaluate the number and placement of receivers needed to monitor this domain with an expected 100% probability of detection (J. Bickford unpubl.). This was achieved by estimating the fastest time that the largest tagged fish could pass through the spawning site (2 min 44 s), the minimum pings that would be emitted in this time (3), and a constant detection rate of 50% or greater, expected to result in consistent reception even under the worst conditions. The detection range at this site was highly variable and affected by tidal current; the maximum range estimated to result in consistent reception was 85 m (Lowerre-Barbieri et al. 2008, data not shown). Based on this range, we calculated that 15 receivers were needed to effectively monitor the spawning site (Fig. 1). To help assess where fish that spawned at this site were drawn from (i.e. the Gulf of Mexico [GOM] or the estuary), 3 additional receivers were deployed. One of these receivers was moored in the GOM ~200 m west of the spawning site, and the other 2 were used as an 'estuarine gate' and deployed ~400 m east of the spawning site (Fig. 1).

Receivers were deployed at the predetermined locations prior to implantation, with the exception of #18 at the estuarine gate (deployed 18 May). Each VR2 receiver was moored using sand augers and auxiliary anchors made from buckets of cement. A subsurface float (150 mm diameter) was used to keep receivers upright in the water column, 1 m above the bottom. Water depth at receiver locations varied from 2.1 to 6.7 m. The date, time, and tag number of any implanted fish that swam within range was recorded by each receiver. Because the lack of controls can lead to incorrect interpretations of data (Payne et al. 2010), we deployed a control tag (69 kHz Vemco V9sc-2L 139 dB with a 60 to 180 s random delay) cen-

trally within the core array (Fig. 1). Detection data from this control tag was analyzed from 11 May 2005 to 7 July 2005 for a total of 59 d. Receivers were deployed until December 2005; approximately once each month receivers were downloaded and cleaned of biofouling.

Fish tagging

Because seatrout are extremely sensitive to handling stress (Thomas & Boyd 1989), we practiced initial surgical and handling techniques on 30 fish (1:1 sex ratio) held in captivity. Gonadal development of these fish (sacrificed at 2 and 4 months) was compared to that of 30 fish held in an undisturbed tank. All 60 fish had been recently captured by hook and line in Tampa Bay (total length [TL]: range: 250 to 350 mm), transported in 185 l holding tanks to the Fish and Wildlife Conservation Commission Stock Enhancement Research Facility, and placed into 2 indoor circular (15 912 l, 2 m deep, 9.14 m diameter) recirculating tanks. Fish were anesthetized with Aquis-S prior to surgery (1.7 ml per 15 gallons water). Fish in both tanks spawned when subjected to a modified photo-thermal schedule (Arnold et al. 1976), confirming that the stress of implantation did not inhibit gonadogenesis or spawning. Gonad phases and terminology follow that of Brown-Peterson et al. (2011). Regardless of sacrifice time, 92% of tagged females and 100% of the tagged males were spawning-capable. In comparison, 71% of the females and 94% of the males were spawning-capable in the undisturbed tank. However, fish were easily agitated and stressed during the capture and handling process, necessitating field protocols to diminish this stress (described below).

Fish were captured early in the 2005 spawning season at dusk (the expected time of spawning; Walters et al. 2007) using a 122 × 2.4 m knotless haul seine (0.6 cm delta mesh), with a center bag measuring 2.4 × 2.4 × 2.4 m, which was immediately retrieved after deployment. To decrease stress, the bag containing the captured seatrout was kept submerged while by-catch items were removed; individuals remained immersed during transport from the net to boat by swimming from the bag into a plastic sling; and fish were kept in the live well of our boat until it was time for surgery. The live well (795 l capacity) was set up as a flow-through system to ensure fish remained in ambient, oxygenated water. Surface seawater was pumped into the live well with two 4164 l h⁻¹ pumps, and overflow drains were set to maintain the water

level at 0.27 m. Individuals selected for surgery were removed from the live well using the sling, sedated with Aquis-S, and transferred to a measuring board for surgery.

A total of 32 spotted seatrout (19 female, 13 male) were intra-peritoneally implanted with coded tags (Vemco V8sc-2L; 139 dB output, 190 d battery life, 15–45 s random inter-pulse delay) which were individually identifiable based on tag-specific signals emitted at 69 kHz. Fish were implanted over 5 dates in May 2005 and ranged in size from 335 to 583 mm TL (Table 1), similar to the size range previously sampled at this site (Lowerre-Barbieri et al. 2009). Average surgery time was 4 min 49 s and recovery time (regained equilibrium) was 1 min 3 s. The surgical procedure used for captive fish (Lowerre-Barbieri et al. 2008b) was improved in the following ways: (1) incisions were made on the midventral line to prevent cutting into males' sonic muscles or the females' developed ovaries; (2) a metal spatula was inserted into the incision and under the body wall to limit needle depth, ensuring body organs were not sewn into the stitches; and (3) use of the retractor was discontinued as it occasionally tore the flesh. Fish were sexed by strip-spawning prior to surgery, which was also necessary to increase space within the peritoneal cavity for the tag in hydrated females. All 13 males expressed milt on pressure before implantation and were considered as active spawning. Of the 19 females, 14 had hydrated oocytes and were considered active spawning at the time of capture. Five could not be strip spawned, but ovaries were observed during surgery. These fish were assumed to have completed spawning prior to capture. After surgery, fish were again placed in the live well and kept for a minimum of 15 min post-surgery before being released at the site of capture.

Passive acoustic monitoring

Spawning activity at the population scale was monitored based on male courtship sound production, as male seatrout produce species-specific sounds associated with spawning activity (Mok & Gilmore 1983, Walters et al. 2009). Courtship sounds were recorded with 2 long-term acoustic recording systems (LARS) deployed at Receivers 6 and 7 (Fig. 1) from March through September. Ambient sound was detected through external hydrophones (HTI-96 min. sensitivity: -164 dBV re 1 μPa; High-Tech), with a sampling frequency of 22 000 Hz, and recorded for 10 continuous seconds every 10 min. Each LARS was anchored

Table 1. *Cynoscion nebulosus*. Summary of monitoring data for 32 tagged fish in 2005. Dates detected are the number of dates when the fish was detected within the receiver array; Zone 5 dates are when the fish were detected only in the estuary; spawn dates are when fish were detected within the spawning site for ≥ 20 min and departed after 16:30 h. TL: total length

Tag	TL (mm)	Sex	Implant date	Last date detected	Duration (d)	Dates detected	Zone 5 dates	Spawn dates
180	412	M	9 May	10 Jul	63	7	1	5
181	340	M	9 May	29 Jun	52	13		13
182	372	M	9 May	1 Jul	54	28	4	23
183	437	M	9 May	28 Jun	51	13		13
184	491	F	9 May	9 Jul	62	6	5	
185	496	F	10 May	12 Jul	64	13	8	4
186	457	F	10 May	11 Jun	33	2		2
187	467	F	10 May	18 Jun	40	5	1	3
188	485	F	10 May	23 Jun	45	7	4	3
189	442	M	10 May	11 Jul	63	45	26	14
190	338	F	12 May	10 Jul	60	1	1	
191	434	F	12 May	25 Jun	45	4	1	3
192	404	F	12 May	11 Jul	61	8	4	4
193	490	F	12 May	11 Jul	61	7	2	3
194	462	F	12 May	24 Jun	44	5	2	3
195	462	F	12 May	27 May	16	1	1	
196	414	F	12 May	29 Jun	49	4	1	3
197	434	M	18 May	21 Jun	35	4	4	
198	431	F	12 May	17 May	6	2	2	
199	583	F	18 May	21 Jun	35	1	1	
200	473	F	18 May	7 Jul	51	6	3	3
201	435	F	18 May	25 Jun	39	8	3	5
202	361	M	18 May	30 Jun	44	26	4	22
203	335	M	18 May	13 Jul	57	19	6	13
204	403	M	18 May	7 Jul	51	42	14	27
205	361	M	19 May	9 Jul	52	19	2	16
206	446	F	19 May	25 Jun	38	4	3	1
207	355	M	19 May	6 Dec	202			
208	385	M	19 May	8 Jun	21	12	1	11
209	370	M	19 May	9 Jul	52	49	1	48
210	481	F	19 May	31 May	13	1		
211	412	F	19 May	19 May	1	0		

0.5 m off the bottom and floated vertically in the water column. Data were downloaded to a PC, and all sounds were analyzed both by ear and spectrographically in Cool-Edit (Syntrillium). We categorized the number of fish calling as: 1–2, 3–5, small, medium, or large aggregation sound (Walters et al. 2007, 2009).

Data analysis

A database was developed in Access to integrate implantation, detection and courtship sound data (times were recorded in Eastern Standard Time). Current speed was predicted for this site based on Nobeltec Tides and Currents and validated through comparison with actual currents measured nearby at

the Sunshine Skyway bridge ADCP (NOAA station ID t01010). To correct for time drift among receivers (Humston et al. 2005, Heupel et al. 2006), all receivers were time stamped with a reference transmitter. There were a total of 169 928 detections. Detections were filtered to remove potentially spurious detections, defined as those dates when a tag was detected only within the core of the array (i.e. vr2s 2–16), and only once ($n = 7$). Positions were estimated using the weighted means method (Simpfendorfer et al. 2002, Hedger et al. 2008) with detections grouped into 10 min time bins. All averages are presented as mean \pm SE. The average number of detections per time bin was 17.2 ± 0.24 . Because the research objectives focused on movement to and from the spawning site, along the east/west axis, our analysis also focused on this axis. The mean easting position error of our control tag was 35.1 ± 0.69 m, with errors >200 m occurring only 0.1% of the time ($n = 2$ out of 1920); this tag had a detection rate of 99%.

To simplify spatial interpretation, fish positions based on the weighted means method were assigned to one of 5 zones, similar to the approach of Danylchuk et al. (2011). Zones were assigned a number according to their proximity to the GOM (Zone 1 being in the GOM and Zone 5 being at the estuarine gate, Fig. 1). The spawning site was broken

into 2 zones, as detections in the eastern portion of the array (Zone 3) could come from fish within the spawning site or just east of it (i.e. edge effects). Zone 2 corresponded to positions occurring between Receivers 2 and 10, and was considered the core of the spawning site. Zone 3 corresponded to positions east of Receiver 10 but no further east than Receiver 15. Zone 5 referred to the estuarine gate. If fish were detected in both Zones 3 and 5 within a 10 min time bin they were assigned to Zone 4. Although there were no receivers in Zone 4, this zone was significant as it indicated when fish were moving from estuarine habitat to the spawning site.

Analyses were conducted over several temporal scales and based on either estimated position or presence/absence within that time period. To detect any abnormalities in behavior due to the stress of

implantation (Alós et al. 2012), data from the first 48 h (post-release period) were analyzed separately. The study period was considered to start after this time period. To determine the best 24 h cycle in which to group detections (Douglas et al. 2009), we evaluated hourly fish presence (Semmens et al. 2010) in either Zones 2 or 3 (i.e. the spawning site). The hourly fish presences were then compared to hourly patterns of aggregation sound and control tag detections to verify that detection patterns represented behavioral patterns rather than abiotic effects on detection (Payne et al. 2010). Because the fewest fish occurred in the spawning site from 06:00 h to 06:59 h, we adopted a 24 h cycle of 07:00 h to 06:59 h. Date was assigned based on the date a fish was first detected.

Site fidelity was assessed by calculating the number of dates on which a fish was detected and categorizing these dates as either non-spawn dates or spawn dates based on general movement patterns. Spawn dates were defined as those dates when fish were detected in the spawning site for 20 min or more, and did not leave the spawning site before 16:30 h EST (the earliest time spawning was expected to occur; Lowerre-Barbieri et al. 2009). Individual detection durations (e.g. the number of dates from the first to the last detection) were calculated as the number of days from implantation to the last date the fish was detected (March et al. 2010, Alós et al. 2011).

To evaluate whether fish spawning at this site came from the estuary or the GOM, we assessed all spawn dates for their arrival and departure zones and how far west they moved into the spawning site. Movement patterns were assessed by plotting easting positions over all possible 10 min time bins on all dates a fish was detected. Daily arrival and departure zones were assigned as GOM (Zones 1 and 2) or estuarine (Zones 3, 4, and 5) and the difference between arrival and departure zones calculated to assess if movement was in one direction through the inlet or if fish came from and returned to the same area. Lastly, daily arrival and departure zones were assessed for discontinuities (e.g. departure on one date from a GOM zone and on the consequent date an estuarine arrival, or vice versa) to evaluate if 'one-way' movement was indicative of behavior or simply a lack of detections during part of the spawning run.

Reproductive timing was assessed over 3 scales: diel, seasonal, and intra-seasonal (Lowerre-Barbieri et al. 2011a). Diel periodicity of spawning was based on the mean and range of hours with aggregation sound. The window of peak spawning was assumed to correlate with the time period most consistently associated with aggregation sound. To assess the

relationship between aggregation sound and movement to and from the spawning site, hourly fish presence in the spawning site (Zones 2 and 3) were similarly assessed. To better understand the role individual timing played in hourly presence at the spawning site, we plotted individual easting positions by time bins for 2 dates: (1) 22 May with slack low occurring at 19:24 h within the expected time of peak spawning, and (2) 26 May with slack low occurring at 23:59 h and higher current speeds during the expected spawning window. Detection durations of all fish (whether they were detected on spawn dates or not) were calculated and compared to the range of dates with aggregation sound to assess possible truncation of the 2005 spawning season. Spawning intervals were calculated as the difference between spawn dates.

To model the probability of spawning we used a generalized additive mixed model (GAMM). Spawn date was the dependent variable with a binomial response (i.e. if it was a spawn date then spawn date = 1, otherwise spawn date = 0, regardless if the fish was detected on that date or not) for dates between the first and last detected spawn of each fish. Independent variables were TL, sex, average current speed and direction at 19:00 h (time of peak spawning), and lunar phase. Sex was included as a categorical predictor, and TL and current speed were modeled with cubic regression splines. Lunar phase was modeled with a cyclic cubic regression spline, where the predictor was a continuous variable from 0 to 2 across all days (full moon = 1, new moon = 0 and 2; adapted from Duffett-Smith 1988). Alternative spline bases (thin plate regression splines, cyclic P-splines) had a minimal effect on the model. Because data was composed by repeated measures within individuals, we considered its variability by including tag number as a random factor (Alós et al. 2012). The GAMM was fit using the `gamm4` package in R 2.14 (R Development Core Team).

RESULTS

All fish ($n = 32$) survived the initial implantation process; however, one fish exhibited spatio-temporal behavior in the post-release period that was significantly different than the other fish. Average time of release for implanted fish was 20:33 h \pm 13 min and all fish were released within the spawning site where they had been captured. Time elapsed between the release of a fish and its departure from the spawning site was highly variable, ranging from 10 min to 3 h

40 min, with all fish eventually moving towards the estuary (i.e. departure zones were Zone 3 (n = 18) and Zone 5 (n = 13)). Only one fish (Fish 207) was detected again within the release period. This fish exhibited a movement pattern different from any seen in the consequent study period. The morning after release, it was detected swimming towards the GOM, and then detected in the GOM at Zone 1 from 06:20 h to 13:20 h. After a 5 h gap, it swam back through the array and was detected in the estuary at Zone 5 at 21:00 h, approximately 24 h after being released (Fig. 2). By midnight, 1 d after implantation, the tag was located near Receiver 11 and remained there throughout the 48 h post-release period and the remainder of the study period. This fish was considered dead and removed from consequent analysis.

Hourly fish presence showed a pattern similar to aggregation sound but opposite to that of the control tag (Fig. 3) confirming that our detections were due to movement behavior rather than abiotic factors. The decrease in control tag detections was correlated with current velocity ($r = 0.38$, $df = 1389$, $p < 0.001$), with the strongest currents occurring in the afternoon and on ebb flows.

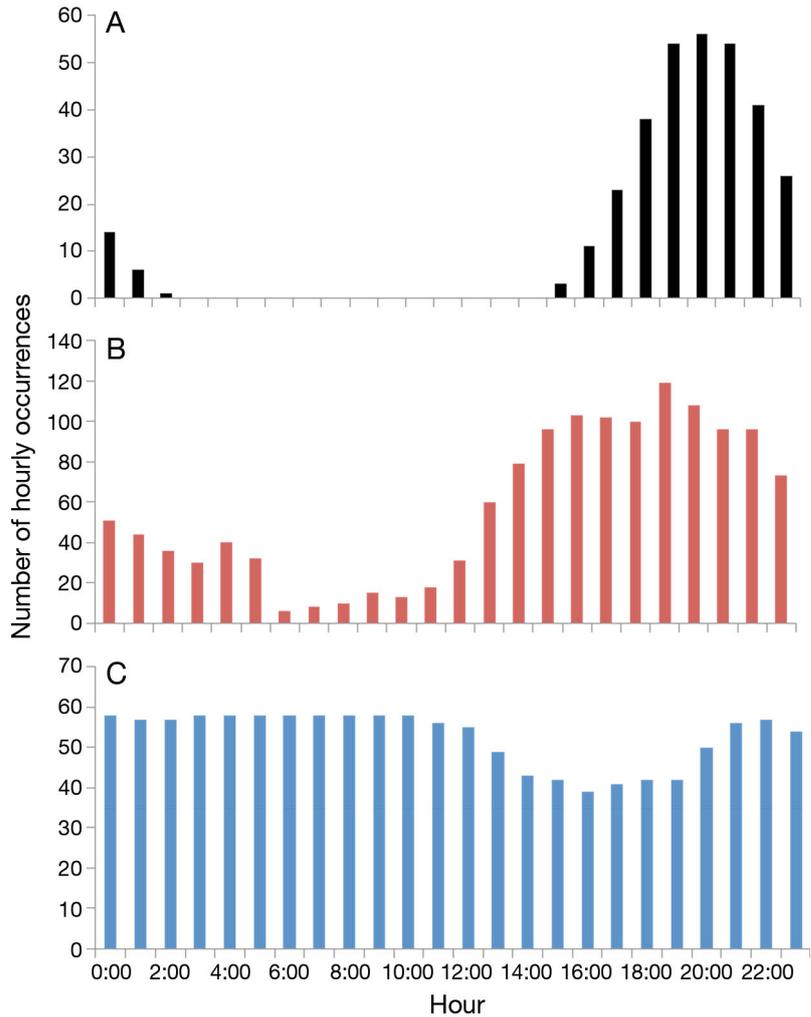


Fig. 3. *Cynoscion nebulosus*. Hourly occurrences of (A) aggregation sound through 13 July (62 dates), (B) fish presence within the spawning site during the study period (56 dates), and (C) control tag detections (58 dates)

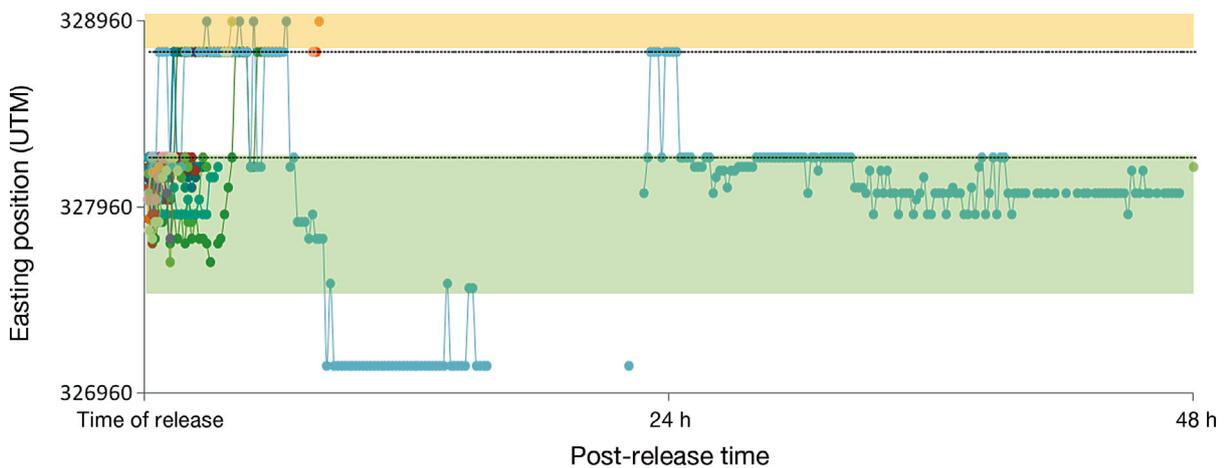


Fig. 2. *Cynoscion nebulosus*. Average easting position by 10-min time bin for all fish during the first 48 h post-release. The yellow rectangle represents Zone 5, east of the spawning site, and the green rectangle represents Zones 2 and 3, which make up the spawning site. Different colored markers represent individual fish. All fish, with the exception of 207 (light blue dots), left the spawning site and did not return within 48 h post-release

Site fidelity

Most fish detected on 2 or more dates (88%; $n = 26$) returned to spawn at the inlet, indicating strong intra-seasonal spawning site fidelity. There were a total of 362 unique combinations of fish number and date detected (Table 1), and approximately two-thirds of these detection dates were spawn dates ($n = 242$), with one third ($n = 105$) corresponding to dates fish were detected only in Zone 5 (the estuarine gate). However, on 15 dates fish were detected in the spawning site but not considered spawning as they either left the site earlier than spawning began or were detected in the site for less than 20 min.

The general movement pattern on spawn dates was for fish to move to the spawning site from the estuary, be detected as far west as Zone 2, and return to the estuary in <24 h (Fig. 4A & B). However, there

was individual variability in this spatio-temporal pattern. Occasionally fish were detected no further west than Zone 3 on spawn dates ($n = 18$; see Fish 202 in Fig. 5B) and sometimes they were detected as far west as Zone 1 ($n = 37$; see Fish 204 and 209 in Fig 5B). In addition, although movement to and from the spawning site was typically completed in less than 24 h, on 7 spawn dates fish spawned on 2 consecutive dates without returning to the estuary in between. These fish had GOM departure zones, and on the next date arrived in a GOM zone during spawning hours and then returned to the estuary, as seen for Fish 180 on 27 and 28 June (Fig. 4C). Fish 181 was the only fish to exhibit behavior suggesting it spent time foraging in the GOM as well as in the estuary. On 3 occasions it was detected leaving the spawning site towards the GOM, then there was a period of multiple days with no detections, after

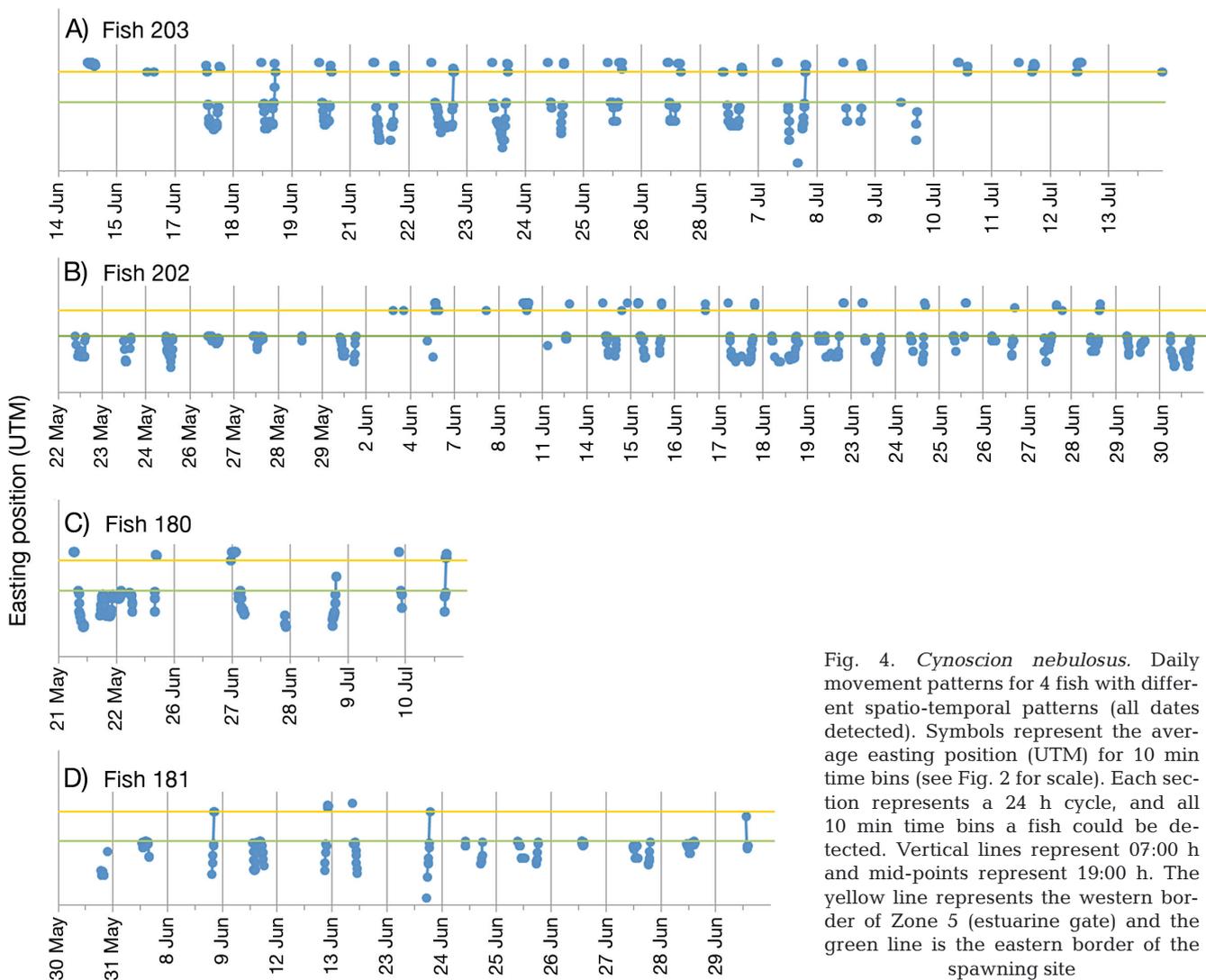


Fig. 4. *Cynoscion nebulosus*. Daily movement patterns for 4 fish with different spatio-temporal patterns (all dates detected). Symbols represent the average easting position (UTM) for 10 min time bins (see Fig. 2 for scale). Each section represents a 24 h cycle, and all 10 min time bins a fish could be detected. Vertical lines represent 07:00 h and mid-points represent 19:00 h. The yellow line represents the western border of Zone 5 (estuarine gate) and the green line is the eastern border of the spawning site

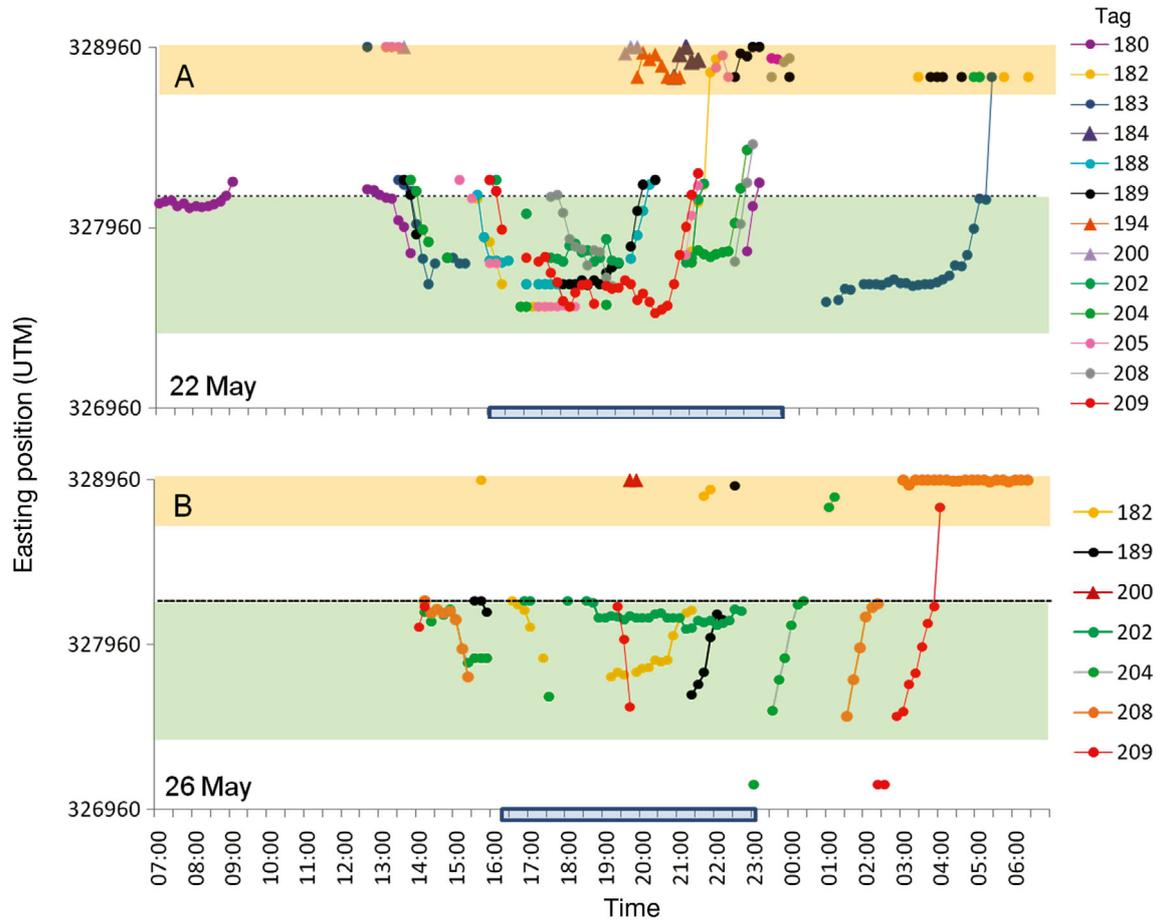


Fig. 5. *Cynoscion nebulosus*. Individual movement patterns based on the average easting position for 10 min time bins over 2 dates: (A) 22 May and (B) 26 May. The yellow rectangle represents Zone 5 (estuarine gate) and the green rectangle Zones 2 and 3 (the spawning site). Fish detected only in Zone 5 on that date have triangular markers. The blue rectangles on the x-axis represent the time period over which aggregation sound was recorded on that date. Individual fish are represented by different colored markers

which it was detected returning to the spawning site from the GOM (Fig. 4D). For example, on 31 May this fish was last detected in Zone 2 moving towards the GOM. It was not detected again until 8 June when it was first detected in Zone 2. It then moved through the array and was detected at the estuarine gate. A similar pattern occurred when the fish was detected moving towards the GOM on 9 June and returning from the GOM on 12 June, and then again on 13 June and 23 June. However, after 23 June, this fish exhibited the more common movement pattern of coming from and returning to the estuary in <24 h.

Reproductive timing

Diel periodicity of aggregation sound and fish detections were similar. Average time of aggregation sound was 19:20 h \pm 7 min. Most aggregation sound (82% of

aggregation hours, $n = 327$) occurred from 18:00 h to midnight; this was considered the window of peak spawning activity (Fig. 3A). However, aggregation sound was detected from as early as 15:00 h (3 dates) to as late as 02:00 h (1 date). Tagged fish exhibited similar diel periodicity, with the highest number of occurrences in the spawning site during 19:00 h. However, often fish were detected in the spawning site earlier than aggregation sound and remained on the spawning grounds after aggregation sound had ended (Fig. 5). Most occurrences of tagged fish in the spawning site (81%, $n = 1366$) were between 14:00 h and 02:00 h (Fig. 3B), but timing was highly variable and at least some fish were detected in all hours. Although a few individuals exhibited similarly timed movements, there was a high degree of individual variability in when fish moved to and left the spawning site (Fig. 5). For example on 22 May, the arrival times of 10 fish detected in the spawning site ranged

from 12:40 h to 17:40 h; on 26 May, the arrival times ranged from 14:00 h to 16:50 h (6 fish in the spawning site). Departure times were even more varied, ranging from 20:20 h to 05:30 h on 22 May and from 21:20 h to 03:50 h on 26 May.

Both courtship sound and fish detections indicated a truncated spawning season in 2005. Spawning aggregation sound occurred daily between 9 May and 13 July, with the exception of 2 days in May. No aggregation sound occurred after 13 July until 18 August, when on 6 consequent dates small aggregation sound was detected (Fig. 6A). Similarly, no tagged fish were detected on any receivers after 13 July (Fig. 6B). The maximum detection duration was 64 d for females and 63 d for males, which was similar to aggregation sound duration (63 d).

On average, fish spawned at this site 9 times (Table 1). The time between implantation and an individual's first spawn date was highly variable, but on average males returned within 10 ± 2.7 d and females within 24.3 ± 4.2 d (Fig. 7A). For most fish spawning on multiple dates ($n = 22$), the average spawning intervals (males: 2.2 ± 0.3 d; females: 9.3 ± 1.6 d) were shorter than the period between implantation and first

spawn date. However, individual spawning intervals varied widely. Male spawn intervals, averaged over the time period from the first to last spawn, ranged from 1.0 to 12.5 d; females ranged from 4.0 to 17.5 d. There was no clear relationship with size for either sex (Fig. 7B). In addition, intervals between spawns were not consistent for individuals within the spawning season. Both males and females were capable of spawning 2 days in a row. However, this was a common pattern for males ($n = 153$ times) and uncommon in females ($n = 3$ times). Males often spawned on multiple consecutive dates, interspersed with dates when they were detected only at Zone 5 in the estuary (Fig. 8). Individual females, in contrast, typically exhibited multiple dates between spawns; the number of days varied between spawning events (Fig. 8).

Probability of spawning

Fidelity to this spawning site was very high, with tagged fish detected at the spawning site every day from 18 May to 11 July. However, the number of tagged fish spawning on any given date varied from

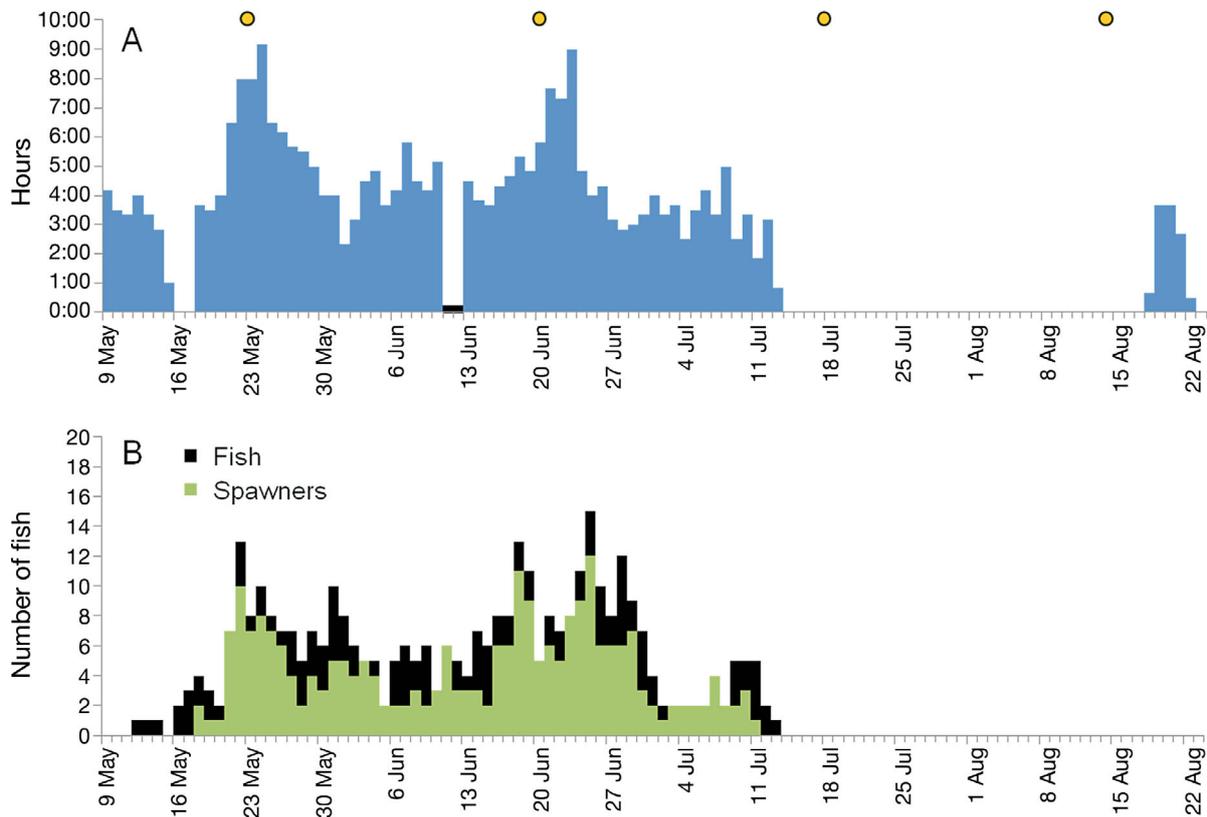


Fig. 6. *Cynoscion nebulosus*. (A) Duration of daily aggregation sound. The black marker on 11 and 12 June indicates equipment failure. Full moons are represented by yellow circles. (B) Number of fish detected by date regardless of location indicated by black bars, and the number of spawning fish are indicated by green bars

1 to 12 (Fig. 6B), with the largest numbers on 22 May (n = 10), 18 June (n = 11) and 25 June (n = 12). The GAMM model provided an estimate of the probability of an individual spawning as a function of multiple predictor variables. Significant predictor variables were sex (p < 0.05) and lunar phase (p < 0.0001).

Males had a higher probability of spawning than females, and fish were most likely to spawn on dates near full moon and least likely to spawn on dates close to new moon (Fig. 9). Current velocity and fish size (TL) did not have a significant effect on the probability of spawning.

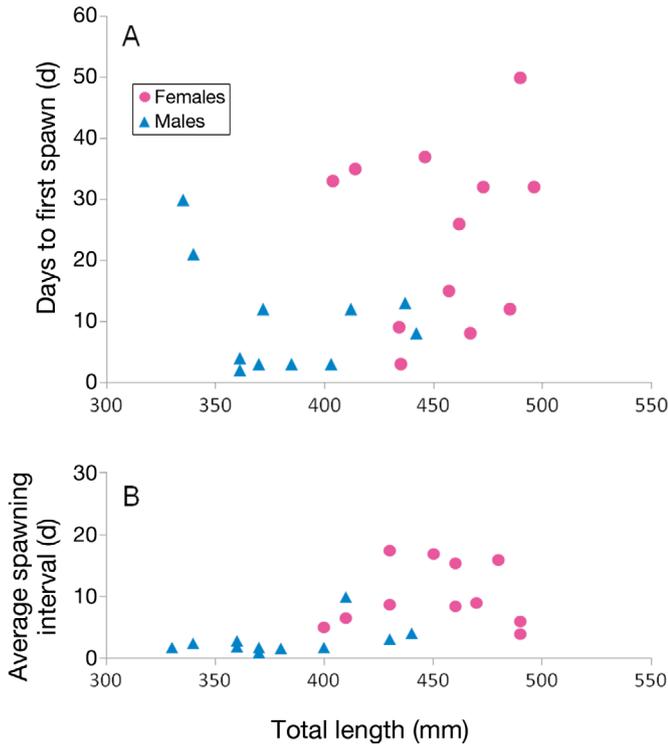


Fig. 7. *Cynoscion nebulosus*. (A) Number of days between implantation and an individual's first spawn date and (B) average individual spawning interval over the study by total length

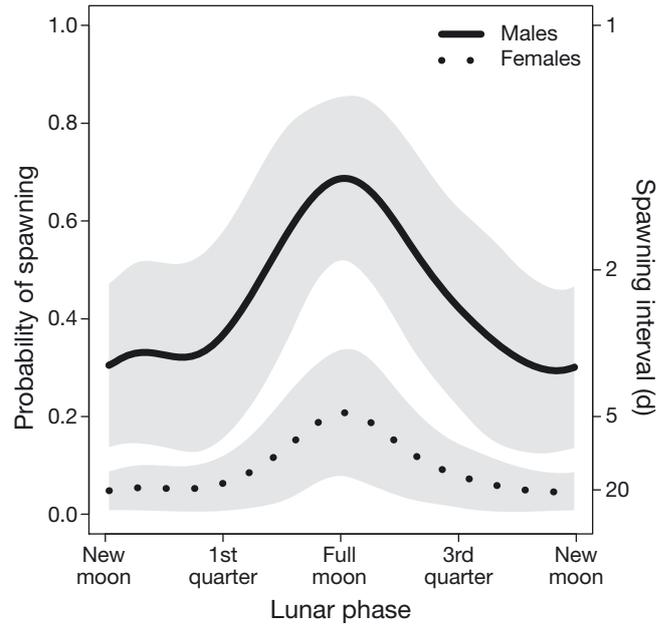


Fig. 9. *Cynoscion nebulosus*. Predicted probability of spawning and instantaneous spawning interval (1/probability) from the GAMM for both males and females across a full lunar cycle. The shaded regions represent the 95% confidence intervals. These predicted probability values were calculated for the average total length of males and females (390 and 455.5 mm, respectively) and the average current velocity at 19:00 h (-0.61m s^{-1})

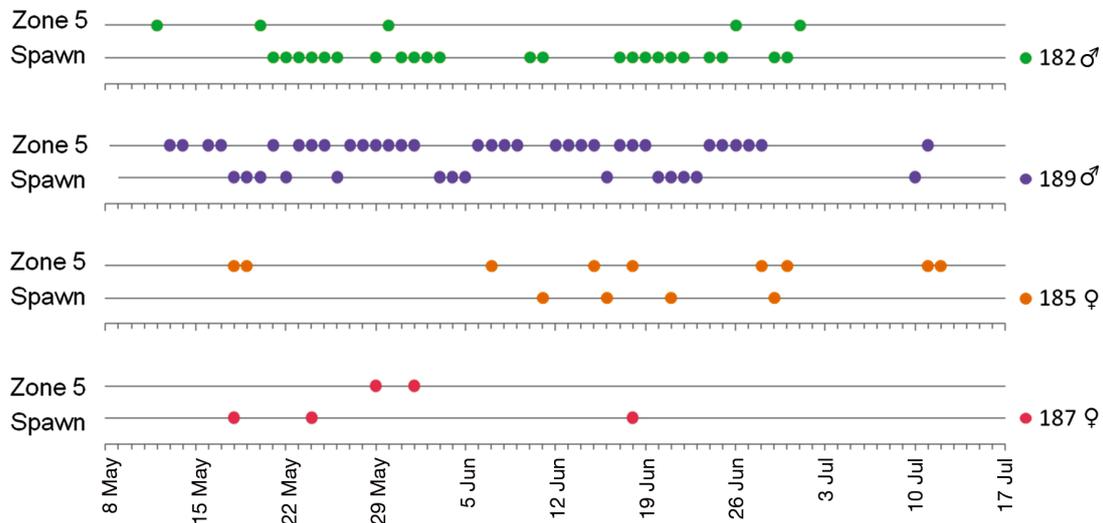


Fig. 8. *Cynoscion nebulosus*. Individual intervals between detection dates categorized as spawn dates compared to dates fish were detected only in Zone 5 (the estuarine gate) for 4 individual fish (see Table 1)

DISCUSSION

Spawning site fidelity

The spawning aggregation at this site exhibited the characteristics of a resident spawning aggregation: drawing from nearby regions, forming daily, and persisting for a relatively long period of time (Domeier & Colin 1997, Claydon 2004). However, this aggregation site differed from other spotted seatrout spawning sites in Tampa Bay, where spotted seatrout spawning occurred predominantly in shallow-water habitats near seagrass (Walters et al. 2009). It also differed from the literature on spotted seatrout reproduction, where spawning fractions are reported to range from 7 to 44% in estuarine habitats (reviewed by Brown-Peterson 2003), well below the 97% demonstrated at this site (Lowerre-Barbieri et al. 2009). The intermixing of spawning and non-spawning fish at estuarine spawning sites, as well as the presence of seatrout at these sites at times not associated with spawning suggests that these spawning sites overlap with feeding areas/home ranges. In contrast, fish moved to this inlet spawning site specifically to spawn, presumably increasing their reproductive success at the expense of greater energetic costs and potentially greater predation risk (Claydon et al. 2012).

There is strong site fidelity to this spawning site at both the population and individual scale. However, what cues fish to return to this site and spawn remains unknown. Aggregation sound confirmed that this spawning site is used throughout the spawning season and over multiple years (Walters et al. 2007). Of the tagged fish, one or more returned to spawn at this site every day from 18 May to 11 July, and on 3 dates roughly a third of the tagged fish were detected spawning at this site. For reef fish, consistently used spawning sites are increasingly reported to be associated with the abiotic conditions resulting in self-recruitment (Karnauskas et al. 2011). Eddies may similarly retain eggs at this site regardless of the general current, which would explain the lack of significance we found between current and spawning, but further research is needed to determine this. Self-recruitment, however, does not explain spawning site fidelity as there is no overlap between this spawning site and nursery habitat. Natal homing has been hypothesized to act as the feedback loop between spatial reproductive performance and fitness (Thorrold et al. 2001, Svedang et al. 2007), but is difficult to assess at the small spatial scale of this study. For fishes with similar spatial dynamics, it has been hypothesized that spawning site selection may be

learned by following the behavior of adults with overlapping home ranges, or forming 'spawning groups' at first maturity (Colin 1996, Adams et al. 2009). Site fidelity may then result from risk avoidance (i.e. less risk associated with returning to a site which has resulted in past spawning success) or simply a lack of awareness of other potential spawning sites (Claydon et al. 2012).

Reproductive timing

Reproductive timing, or the temporal pattern of reproduction over a fish's lifetime, plays an important role in reproductive success as it defines the number of reproductive opportunities and the environment in which eggs or offspring are released (Imms 1990, Yamahira 2004, Wright & Trippel 2009, Lowerre-Barbieri et al. 2011a). In this study we evaluated reproductive timing at seasonal, diel, and intra-seasonal scales. Aggregation sound and tagged fish exhibited similar seasonal trends, indicating a truncated spawning season in 2005. Typically, spawning would continue at this site through mid-September (Walters et al. 2007, Lowerre-Barbieri et al. 2009), whereas in 2005 both aggregation sound and tag detections stopped mid-July, with a short resumption of small aggregation sound over a few days in late August. This truncated spawning season was apparently caused by the ichthyotoxic dinoflagellate *Karenia brevis*, as there was an unusually persistent red tide event with concentrations high enough to cause fish kills in this area during the study period. Red tide entered Tampa Bay in the summer of 2005, occurring at this site in June and July (Walters et al. 2013) and its impact on spotted seatrout reproductive success was indicated by a significant decrease in juvenile spotted seatrout abundance in Tampa Bay in 2005 and 2006 (Flaherty & Landsberg 2011).

At the diel scale, spotted seatrout are reported to spawn at dusk throughout their range (Brown-Peterson 2003) and this was the central tendency in our data. However, individual variability was high. The average time of aggregation sound over the spawning season was 19:20 h, and the hour with the greatest occurrences of tagged fish in the spawning site was also 19:00 h. Similarly, although sample size is small ($n = 10$), the average time that ovulatory females were sampled at this site was 19:02 h (Lowerre-Barbieri unpubl. data). However, the individual range of spawn times is quite wide. Although most females sampled at this site in the evening were within 2 h of spawning (Lowerre-Barbieri et al. 2009),

an additional 11 females were collected with ovaries containing oocytes undergoing early oocyte maturation (Lowerre-Barbieri unpubl. data), indicating they would spawn in 6 to 14 h (Brown-Peterson 2003). This wider range of individual spawn times is supported by both the range of aggregation sound (15:00 h to 02:00 h) and the wide range of individual arrival (12:40 h to 17:40 h) and departure times (20:20 h to 05:30 h). Spawn times and duration on the spawning grounds will impact reproductive success, as this will define the number of breeding opportunities on a given date, energetic cost, and the environment in which eggs or offspring are released (Lowerre-Barbieri et al. 2011a) and thus the probability of fertilization, rate of egg predation, and egg dispersion (Morgan & Christy 1994, Yamahira 2001, Cowen et al. 2007, Gladstone 2007).

Our spawning interval results have important implications for traditional methods to estimate annual fecundity in batch spawners with indeterminate fecundity. Spawning intervals are typically assessed at the population level based on spawning fractions (Hunter & Macewicz 1985, Lowerre-Barbieri et al. 2011a, Uriarte et al. 2012) and the assumption of no immigration or emigration from the sampled areas (Hunter & Macewicz 1985). Spawning frequency is then estimated as the average number of days in the spawning season divided by the spawning interval. We found that both males and females moved in and out of this site, and that although spawning occurred at this site daily, it was not by the same individuals as is assumed with traditional methods to estimate spawning intervals. In contrast, our estimates based on individual behavior over time indicated an average female spawning interval of 9.3 d, highlighting how skewed results can be if the assumption of no movement in or out of the sampling area is violated. Because fecundity in these species is not limited by body cavity size, but rather by energetics and the environment (Pecquerie et al. 2009), we speculate that spotted seatrout spawning intervals would be similar at other spawning sites. However, both the density of spawning at this site and the energetic cost associated with moving to it might affect spawning interval and there is a need for further research to assess the interaction between spawning interval and the habitat/dynamics associated with a given spawning site.

Although we have no way of proving that tagged fish did not also spawn at additional sites, our results of sex-specific differences and variable spawning intervals over an individual spawning period are similar to the few studies that present individual results (Asoh 2003, Curtis 2007, Patzner 2008). In this study,

the average male spawning interval was 2.2 ± 0.3 d and for females it was 9.3 ± 1.6 d. Because testes lack histological indicators of imminent or recent spawning similar to hydrated oocytes and post-ovulatory follicles in females, little is known about male spawning frequency in wild populations. However, males clearly play an important role in reproductive success and population productivity (Trippel 2003), and telemetry studies provide an important tool to better understand the mating behavior of both sexes and how it may interact with natural and fishing mortality. For example, Robichaud & Rose (2003) used telemetry to track cod on the spawning grounds and found that females moved in and out of male-dominated spawning aggregations, concluding that fisheries on spawning grounds could disrupt these movements and/or lead to sex-biased harvest rates.

Probability of spawning

Males spawned more frequently than females. Increased spawning frequency in males has also been reported in several reef fish (Claydon et al. 2012) with the assumption that this is due to the lower cost of sperm production compared to egg production. In spotted seatrout, however, there are a number of male-specific behaviors and life history parameters to consider. For example, spotted seatrout males have the added energetic cost of producing sounds associated with reproduction. They also mature at a smaller size (Lowerre-Barbieri et al. 2009) and exhibit lower growth rates than females (Murphy & Taylor 1994). Because all life history strategies are tradeoffs between how behavior increases the probability of reproductive success versus adult survivorship, within the energy limitations imposed by physiology and habitat (Stearns 1992), life history theory suggests reproductive success in spotted seatrout males is more closely associated with increased numbers of reproductive events than with increased size, as would be expected if males were territorial.

Both sexes had an increased probability of spawning on dates near the full moon. Patterns in moon-related reproductive timing and reproductive success have been previously reported in marine fish (Yamahira 2004, Takemura et al. 2010). The lunar effect in spawning at this site does not appear to be driven by the correlated current or tidal regime, as these are quite similar with the full and new moon phases. In addition, although there was increased spawning on dates near the full moon, spotted seatrout did not exhibit an approximate 30 d spawning interval, as oc-

curs for synchronous spawners with a lunar cycle (Takemura et al. 2010). Such synchronicity is often associated with spawning sites with clear temporal patterns in offspring survival, such as intertidal spawning during spring tides and synchronous development of secondary growth oocytes (Takemura et al. 2010). In contrast, the oogenesis pattern of spotted seatrout is asynchronous, as is the case for many other exploited fishes (Murua & Saborido-Rey 2003). This oogenesis pattern is necessary to support variable spawning intervals, as there must always be a reserve of vitellogenic oocytes which can recruit to oocyte maturation and be spawned. This pattern allows for greater diversity in reproductive timing and potentially confers greater resilience to fishing pressure, given the proposed relationship between resilience and intraspecific diversity (Frank & Brickman 2001). For species with asynchronous oocyte development, increased spawning on dates near the full moon may simply be a means of increasing the number of conspecifics spawning at a given time, which has been hypothesized to also increase reproductive success (Claydon et al. 2012).

Increased spawning activity with increased fish size has been previously reported for this species (Kupschus 2004, Roumillat & Brouwer 2004, Lowerre-Barbieri et al. 2009), as well as other species with indeterminate fecundity (Ganias et al. 2003, Claramunt et al. 2007, Mehault et al. 2010, Fitzhugh et al. 2012) so the lack of significance in our model with size was surprising. However, this could have been due to the relatively large size of implanted females. Females attain 50% maturity at 261.7 mm TL (Lowerre-Barbieri et al. 2009) and the size range of implanted females was 404–496 mm TL. Thus, it is doubtful that we tracked any first-time spawners, which would be expected to show the lowest spawning activity (Lowerre-Barbieri et al. 2009). Another factor which may have impacted our results was the truncated spawning season. Because larger, older females often exhibit more extended spawning seasons (Wright & Trippel 2009), they may also sustain a given spawning interval for a longer time period, whereas smaller fish may have to decrease their frequency of spawning as the spawning season progresses.

Conclusion

Fisheries and conservation science focus on understanding factors driving population dynamics, and predicting future population abundance given a certain level of fishing mortality (Metcalfe et al. 2012).

However, our understanding of how fishing impacts populations is changing and there is a need to recognize that fishing can affect reproductive success and thus population productivity in many ways beyond those traditionally assessed (Lowerre-Barbieri et al. 2011a). Many marine species appear to exhibit 'sweepstakes reproduction', i.e. year classes are produced only by a small fraction of the population (Hedgcock 1994, Christie et al. 2010), with the reproductively successful population associated with temporal, spatial, and demographic factors (Berkeley et al. 2004, Hutchings & Reynolds 2004) that are not currently known or adequately protected.

Demographic variability in reproductive performance and consequently success is the factor most easily integrated into population dynamics models, and age truncation has been hypothesized to decrease a stock's resilience (Caddy & Agnew 2004) and increase its recruitment variability (Anderson et al. 2008). Reproductive traits exhibiting trends with size and age will vary with species, but include fecundity (Berkeley et al. 2004), reproductive timing (Wright & Trippel 2009, Lowerre-Barbieri et al. 2011a), skipped spawning (Rideout et al. 2005), and egg quality (Kamler 2005).

However, the interaction between fishing and reproductive behavior over space and time will also greatly impact reproductive success and thus productivity. Of particular importance is if spatially distinct and relatively small spawning sites disproportionately contribute to either reproductive potential (Taylor et al. 2012) or fished biomass, as seen at some fish spawning aggregation sites (Erisman et al. 2012). Thus, the need to better understand behavior and feedback loops at spawning 'hot spots' is critical to our understanding and ability to predict population production in marine species. As we have shown in this study, biotelemetry linked with traditional capture-based studies can greatly increase our understanding of behavior over spatio-temporal scales, and in the future improve our understanding of how this reproductive behavior may impact other life history traits such as growth and natural mortality. But there is also the need to conduct more research measuring individual reproductive success through DNA parentage analysis (Planes et al. 2009) and assessing the role spawning site selection and fidelity plays in reproductive success.

Acknowledgements. We thank D. Mann and J. Locascio for providing the long-term acoustic recorders and their expertise. We thank D. Westmark and J. Tunnell for assistance in the field. We also thank 3 anonymous reviewers and S.

Cooke, P. Alós and D. Villegas for a number of helpful suggestions to improve the manuscript. This project was supported by Grant F-59 from the US Fish and Wildlife Service Sport Fish Restoration program.

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Editorial responsibility: Janet Ley,
St. Petersburg, Florida, USA

Submitted: September 10, 2012; Accepted: December 12, 2012
Proofs received from author(s): March 27, 2013