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Site fidelity and movement patterns of wild subadult red drum, *Sciaenops ocellatus* (Linnaeus), within a salt marsh-dominated estuarine landscape

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Abstract During summer and autumn 2002, 12 subadult red drum, *Sciaenops ocellatus* (Linnaeus) (261–385 mm total length) were surgically implanted with ultrasonic transmitters and released within the upper reach of the Duplin River Estuary, Sapelo Island, GA, USA. A fixed array of submerged receivers automatically recorded the time that individual tagged fish were detected at 10 sites within the study area. Ten red drum implanted with transmitters were located within the receiver array for 6–96 days post-release. All fish exhibited a high degree of site fidelity at low tide, and movements appeared to be influenced by both tidal and diel cycles. Dispersal on flood tides was observed, but destinations (upriver or downriver) and paths taken (main channel, intertidal channels or flooded marsh surface) varied among individuals. Flood-tide movements were generally restricted to daylight hours. If the start of flood tide occurred after sunset, fish remained stationary. Variation in details of movement patterns among individuals notwithstanding, predictable behaviour and strong site fidelity make subadult red drum vulnerable to recreational fishing in the restricted tidal channels of the tidal marsh–estuary complex. However, the same predictability provides fisheries managers a means of targeting specific areas for protection of over-fished populations of this species.

KEYWORDS: fish behaviour, red drum, Sapelo Island, *Sciaenops ocellatus*, tidal marsh, ultrasonic telemetry.

Introduction

The red drum, *Sciaenops ocellatus* (Linnaeus), is a common sciaenid fish in the extensive salt marsh–estuarine ecosystems of the southeastern USA from Chesapeake Bay and throughout the Gulf of Mexico. In the south-eastern US Atlantic and Gulf coasts, red drum is among the top sport fishes targeted by recreational anglers. Spawning occurs in late summer and early autumn in nearshore coastal waters, particularly near inlets. The larvae settle in estuarine habitats and are passively distributed throughout networks of subtidal salt marsh creeks. The young red drum occupy these nursery habitats through the subadult stages (Setzler 1977) until they reach reproductive maturity at age 3–5 years. Subadult red drum are known to move onto the intertidal marsh plain during flood tides (Collins, Smith, Jenkins & Denson 2002), where they feed on decapod crustaceans and small fishes (Overstreet & Heard 1978), but there is little additional information available on the movements of individual red drum within the estuary. Furthermore, previous work that focused on habitat use of red drum using conventional (Adams & Tremain 1999) and ultrasonic (Nicholson & Jordan 1994) tagging methods considered large-scale movements along the coastline but did not explore movements and habitat use across finer temporal (tide cycles, hours, minutes) and spatial (subtidal and intertidal salt marsh–creek systems) scales. This paper reports the movement patterns of individual wild-caught red drum in relation to tidal and diel cycles within a tidal salt marsh–estuarine landscape as determined by ultrasonic telemetry.

Materials and methods

This study was conducted in the upper reaches of the Duplin River (Fig. 1) within the Sapelo Island National Estuarine Research Reserve (SINERR), GA, USA. The Duplin River is a tidal tributary of Doboy Sound and experiences semidiurnal tides with a mean range of 2.1 m (Wadsworth 1980). Approximately 10 km^2 of

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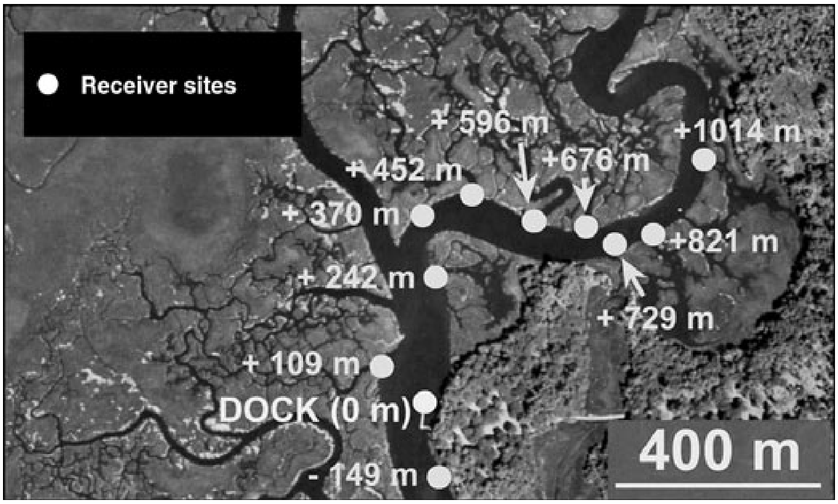

Figure 1. Location of 10 fixed receivers in the upper reaches of the Duplin River. Positive values are distances upriver and the negative value is downriver of the release site at the dock.

the 11 km^2 Duplin River drainage consists of tidal salt marsh, dominated by a vegetation cover of *Spartina alterniflora* Loisel and dissected by abundant sinuous intertidal and subtidal creeks.

Subadult red drum (261–385 mm total length) were captured by hook-and-line between 29 June and 14 September 2002 and implanted in the field with individually coded ultrasonic transmitters (Vemco Ltd, model V8B-2L-R256 measuring 3.8×0.8 cm, 5.4 g in air, 3.5 g in water). The size of individuals selected for this study was partly determined by an attempt to meet the conservative recommendation of 2% tag to fish weight in air (Winter 1996), although some studies have successfully used transmitters sized up to 12% of the fish body weight in air (Bridger & Booth 2003). Transmitters operated at a frequency of 69 kHz, had an expected battery life of 90–110 days and were activated (soldering two wires together and sealing with epoxy) and tested in the laboratory within 48 h of implantation. Transmitters were surgically implanted into the body cavity as described by Winter 1996. Prior to implantation, fish were quickly landed and placed directly into an anaesthetic bath of 70 mg L^{-1} tricaine methanesulfonate (MS-222, Argent Chemical Laboratories) in ambient Duplin River water. When stage-4 anaesthesia was achieved (Summerfelt & Smith 1990), each fish was measured, weighed and placed onto a rigid, foam-cushioned surgical platform equipped with a recirculating anaesthesia pump, modified from a design by Courtois (1981). Transmitters were inserted into the body cavity through a 1-cm-long incision made with a scalpel along the ventral midline midway between the pelvic fins and anus.

All fish were captured and released adjacent to the 'Hunt Camp Dock' (permanent floating dock structure parallel to the east bank of the river with adjacent oyster reef habitat), referred to herein as the dock site (Fig. 1). No subadult red drum were collected from any of the other sites shown in Fig. 1 despite an equal amount of fishing effort. Appropriate measures were taken to minimise surgery time, handling time and overall stress on the fish during transmitter implantation. As described in Thoreau & Baras (1997) and Baras & Jeandrain (1998), incisions were not closed with sutures, staples or adhesives. The successful outcome of laboratory and field trials described in Dresser (2003) also demonstrated that there was no need to close the small incision. Surgical instruments and transmitters were soaked in Betadine® solution, but no prophylaxis or topical disinfectants were applied to the incision site. After implantation, fish were transferred to a 50-L cooler containing aerated Duplin River water and observed through recovery (self-righting and normal swimming behaviour), which occurred within 1–3 min. After an additional 10-min holding period to ensure full post-surgery recovery, fish were released back into the Duplin River. The length, weight, release date and days at large of implanted red drum are given in Table 1.

Tagged fish were located using an array of 10 stationary hydrophone receivers (Vemco Ltd, model VR-1) that recorded the date and time each transmitter was within detection range (200–400 m). An initial 24-h time delay was incorporated into the post-processing of data to reduce the likelihood that observed movements were influenced by the surgical

Table 1. Characteristics of 10 subadult red drum implanted with ultrasonic transmitters and released within the upper Duplin River study area during 2002

Fish ID number	Total length (mm)	Weight (g)	Date tagged	Days at large	Tide cycle replicates
21	271	210	29 June 2002	86	164
23	268	180	30 June 2002	6	9
*24	274	185	30 June 2002	97	185
25	261	180	30 June 2002	97	185
26	314	315	14 August 2002	54	101
27	342	380	14 August 2002	65	119
*28	344	410	14 August 2002	99	119
30	332	355	15 August 2002	64	118
31	385	615	14 September 2002	21	38
33	375	545	14 September 2002	9	15
Mean	317.6	334.6	–	55.9	105.3

Two fish (nos. 22 and 29) not listed were at large < 1 day. Three other transmitters not listed (nos. 32, 34 and 35) failed to transmit a signal upon activation and were not implanted into any fish. A tide cycle replicate is a 12-h period between one low tide and the next low tide.
*Confirmed angler recoveries during November 2002.

procedure. Two post-processing software macros were used in Microsoft Excel® to filter: (1) simultaneous detection of an individual transmitter at multiple sites within the detection array to ensure that all transmitter detections were unique to a particular receiver site at a discrete location in the study area; and (2) simultaneous detections that occurred at intervals of < 45 s (the minimum detection interval of a unique transmitter signal at the receiver). Receivers were anchored approximately 1 m above the bottom of the channel and distributed throughout a 1.1-km section of the main river. Each receiver was positioned adjacent to a discrete habitat feature such as the mouth of an intertidal creek, an oyster reef, the marsh–river interface or a floating dock structure.

Tide data for the study area were estimated using Tide® tidal prediction software (Micronautics, Inc.). Tides were divided into three stages of approximately 4 h each: 'low' was defined as the 4-h interval with low tide at the midpoint, 'high' was the 4-h interval centred on the time of predicted high tide, and 'mid'-tide stage was represented by the combined 2-h intervals between alternate low and high stages (i.e. 4 h low stage + 2 h mid-stage + 4 h high stage + 2 h mid-stage). When combined, the 12-h period between one low tide and the next low tide (represented by low-, mid- and high-tide stages) was defined as a tide cycle replicate for purposes of grouping the number of tagged fish detected by the hydrophone array.

The Kolmogorov–Smirnov test (D_{MAX}) was used to test for significant ($\alpha = 0.05$) differences in the frequency of occurrence of implanted fish at the location of their initial capture and release with tidal stage. Linear regression was used to test for a relationship between number of detections (log-transformed) and distance from the initial site of capture and release.

Results

A total of 65 334 individual detections for 12 subadult red drum implanted with ultrasonic tags and released in the vicinity of the dock site were recorded between June and September 2002. All but one (fish no. 29) of the 12 implanted fish were initially detected by at least one hydrophone receiver within minutes or hours after release. Fish no. 22 was not detected after the initial 24-h period following release. Eight of the remaining 10 implanted fish exhibited a persistent affinity for the dock site, particularly at low tide. Three receivers located within the vicinity of the dock site accounted for 91% of all fish detections, confirming that red drum were attracted to the habitat or structure at this site. There also was a significant negative linear relationship ($r^2 = 0.470$, $P = 0.029$) between the total log-transformed detections and distance from the original point of capture and release (i.e. number of detections declined with upriver distance from point of release).

Aggregations of tagged subadult red drum appeared restricted to specific areas and times, especially during low and mid-tides. In particular, the vicinity of the dock site was the only monitored location where two or more implanted fish were detected simultaneously. The number of implanted fish recorded near the dock site was greater during low and mid-stages of the tide than during the high-tide stage. Comparisons of the number of fish located at the dock site during 58 tidal cycles from mid-August to mid-September indicated

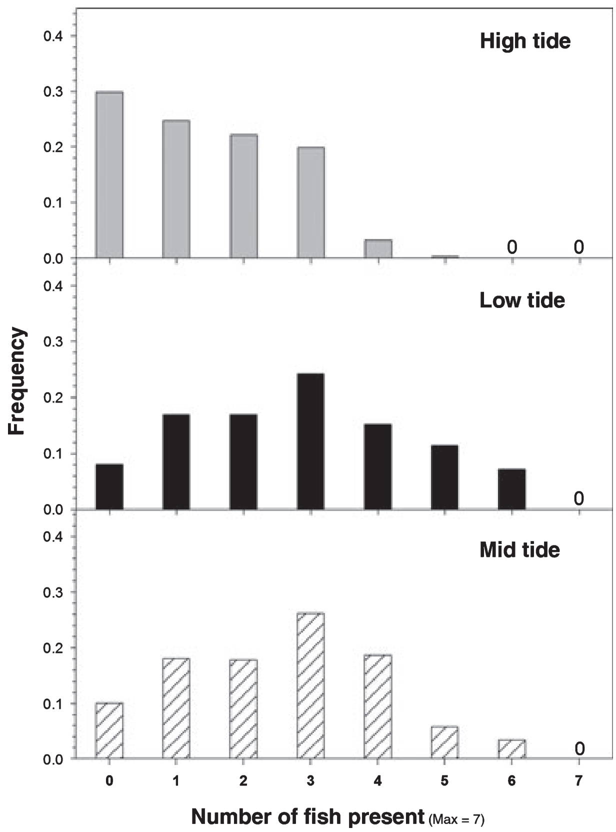

Figure 2. Frequency distributions of the observed number of fish present for three different tide-groups at the dock site, autumn 2002. Data shown are from a continuous period (20 August to 19 September 2002) when seven fish were at large within the Upper Duplin study area. Distribution of fish at high tide was significantly different than at low tide (Kolmogorov–Smirnov, $D_{MAX} = 0.347$, $P < 0.001$) and mid-tide (Kolmogorov–Smirnov, $D_{MAX} = 0.305$, $P < 0.001$). Distributions of fish at mid- and low tide did not differ significantly (Kolmogorov–Smirnov, $D_{MAX} = 0.095$, $P = 0.087$).

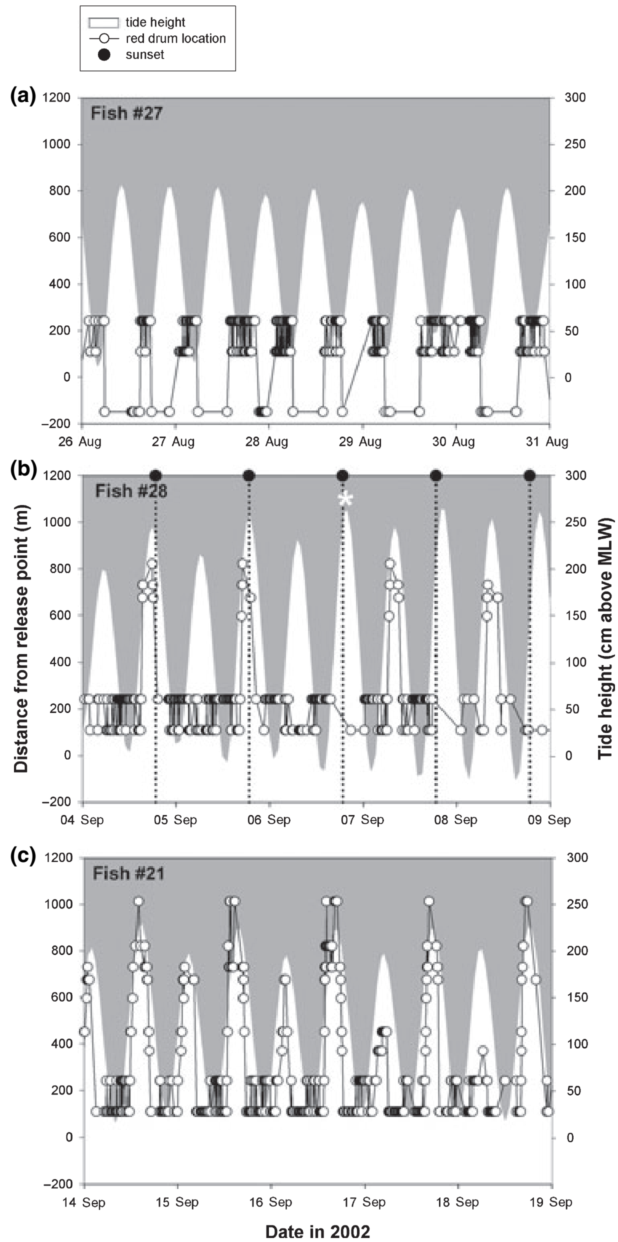

Figure 3. Examples of red drum movements during the tidal cycle: six fish moved to unmonitored locations and/or downriver on flood tides (a), four fish moved upriver on alternate (b), or consecutive (c), flood tides.. Note that the timing of high tide on panel (b) occurred prior to sunset until the evening of 5 September. As a result, no upriver movements were detected on 6 September when both high tides occurred during darkness. The asterisk (*) indicates the high tide when upriver movement was expected. However, fish no. 28 did not move upriver until the next diurnal tide. Panel (b) also shows where 'site skipping' (no detections at the receivers located at 370 or 452 m) occurred for fish no. 28.

that the high-tide distribution was significantly skewed toward the presence of fewer fish than during low ($D_{MAX} = 0.347$, $P < 0.01$) and mid-tides ($D_{MAX} = 0.305$, $P < 0.01$). During this period, two or more individuals were present in the vicinity of the dock site during 75% of low tides, but two or fewer individuals were present at this same site during 77% of high tides. The mid-tide distribution was similar to that at low-tide and reflects a transitional stage where movement into the dock area on the ebb tide was similar to movement out of the dock area on the flood tide (Figure 2).

Of the 10 implanted fish at large beyond the initial 24-h post-surgery, six moved to unmonitored locations (*viz.* intertidal marsh) or downriver on flood tides (Fig. 3a) and four fish moved upriver on flood tides (Fig. 3b, c). The timing of sunset appeared to influence the tidal movements of all implanted red drum. When high tides occurred during daylight hours, the fish moved from the dock to various high-tide locations, but when the beginning of high tide coincided with sunset or occurred anytime during the night, the fish remained in the vicinity of the dock site. This crepuscular/nocturnal effect accounted for the pattern of movement on alternate flood tides (Fig. 3b). As the timing of high tide shifted such that both flood tides began during crepuscular or night-time conditions, two of the implanted fish did not move for two consecutive tide cycles (Fig. 3b, 6–7 September). With the next daylight high tide, the fish resumed the pattern of moving on alternate flood tides (i.e. day–night cycle).

In many instances (approximately 82% of combined upriver tide cycle movements), fish were not detected by every hydrophone receiver along their apparent path in the river channel. All four of the upriver-moving fish exhibited such 'site-skipping' behaviour as illustrated by fish no. 28 (Fig. 3b), which consistently bypassed receiver sites at +370 or +452 m upriver of the dock when moving between the dock and receiver sites more than 500 m upriver (Fig. 1). The dense marsh vegetation reduced the detection range of the transmitter signal, such that implanted fish travelling through the flooded intertidal marsh adjacent to the river channel would pass undetected by the receiver array. 'Site-skipping' suggested that some fish may have found a more direct path upriver through the flooded intertidal marsh, rather than following the broad bend in the main river channel between the receivers at +242 and +596 m upriver of the dock.

Attempts to actively track tagged fish using a directional hydrophone (Vemco Model VR28T System) from a moving boat during flood tides were largely unsuccessful. While each of the 10 at-large tagged fish was located at least once within the vicinity of the dock site during low tide using this method, the 45- to 75-s interval between transmitter signal pulses precluded tracking fast-moving fish, especially in the presence of vegetation or other large structural features of the habitat (e.g. long sand bars and narrow intertidal channels). Only on one occasion was an individual fish tracked for more than a few minutes. Fish no. 31 was located and tracked for 45 min on 20 September as it moved approximately 200 m upriver from the dock site on a flooding tide. This fish was followed from an oyster reef near the dock site to the mouth of the intertidal creek near the stationary receiver site at +242 m (Fig. 1). It remained <5 m from the marsh edge the entire time. The signal was lost once the fish entered the intertidal creek where it may have gained access to the flooded vegetated marsh surface. This location was also where fish that exhibited the suggested 'site-skipping' behaviour were suspected to deviate in course from the main subtidal river channel.

The current findings also provided evidence of fishing mortality on subadult red drum in the study area. Local anglers who were aware of the study voluntarily returned transmitters from fish no. 24 and fish no. 28 along with general information on when and where the implanted fish were harvested. In the previous year (2001), 19 implanted red drum were released into the study area, and one of those transmitters was returned voluntarily by a local angler several months after the fish had been harvested.

Transmitter detection patterns from two other fish (nos. 21 and 33) that had been at large for 86 and 9 days suggested they too were harvested by anglers in the vicinity of the dock (Fig. 4). Both fish had previously exhibited regular tidal migration patterns that abruptly changed at precisely the same time on the same day. From then on, the transmitters remained stationary at the receiver site immediately downriver of the dock for the duration of the study. Both fish were presumed to have been caught and cleaned on-site – a common practice for overnight campers at this

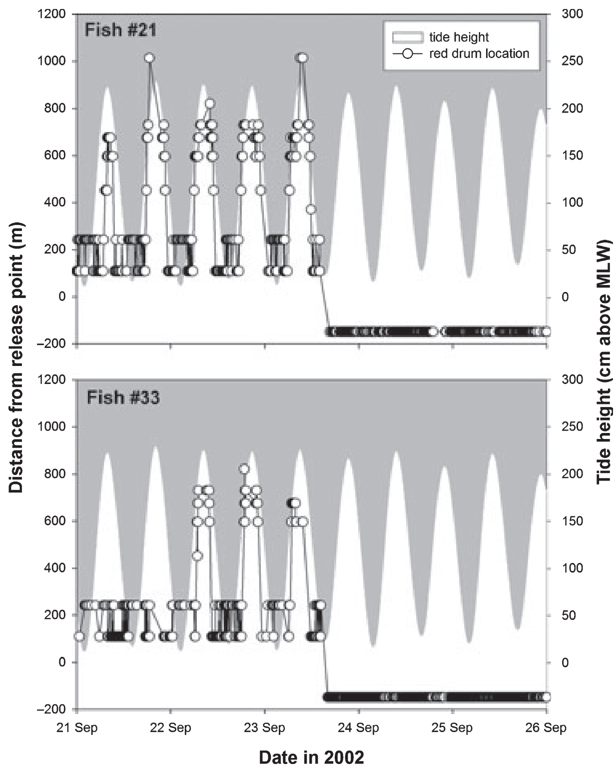

Figure 4. Evidence of angler capture of fish no. 21 and fish no. 33 at the dock site. Both fish were presumed caught and transmitters discarded with viscera into the river at approximately the same time on 23 September 2002.

location. The transmitters were likely discarded with the viscera into the river and continued to transmit a signal where they came to rest on the bottom. The two confirmed angler removals (tags returned) and two suspected angler removals (tags stationary near the dock structure) suggest that, at a minimum, four of the 12 (33%) implanted red drum in 2002 were harvested in the recreational fishery. The remaining eight implanted red drum either: (1) stayed within the study area for the duration of the transmitter battery life; (2) were harvested by recreational anglers; (3) were taken by other predators (e.g. dolphins or sharks); or (4) emigrated from the study area.

Discussion

This study characterised individual movement patterns and site fidelity of subadult red drum within an inshore estuarine landscape. It also provided some insights into the potential impact of recreational fishing mortality on the population within a portion of the Sapelo Island National Estuarine Research Reserve.

Movements and site fidelity

Although receivers were positioned near areas expected to attract red drum (mudflats, the mouths of subtidal and intertidal creek channels, oyster reefs), fidelity of red drum for the vicinity of the dock site superceded association with any other habitat type monitored in this study. Use of other monitored habitats outside of the dock vicinity was limited to transient movements between the dock site and more upstream reaches of the Duplin River or the intertidal vegetated marsh surface. Many fish species use structure, particularly overhead structure, to conceal their presence from both potential predators and prey (Helfman 1981). The low-tide aggregation of red drum in the vicinity of the dock site may be explained by such visual advantages gained from the above-water structure of the floating dock at this location. All individuals abandoned the dock area for varying time periods, suggesting that the suitability of this habitat varied temporally among individuals with different propensities for site fidelity or for specific habitat use during the flood tide. Fraser, Gilliam, Daley, Le & Skalski (2001) demonstrated differences in 'boldness' with regard to the exploration of new habitats and the distanced moved by individuals within a population of freshwater killifish from riverine systems in the West Indies. They suggested that there was sufficient variation in the proclivity for movement among individuals that the population could be parsed into 'movers' and 'stayers', with such a behavioural polymorphism having consequences for adaptation in different ecological contexts. For example, if mortality risk or foraging success varies temporally within an area, it may be advantageous to sample multiple sub-habitats ('mover' behaviour), but if certain areas are consistently safer or more productive, the 'stayer' behaviour could lead to higher survivorship.

Modification of red drum tidal movement patterns by diel cycles was an unexpected finding of the present study. Lack of movement at night suggests that visual cues may be important for either foraging or avoidance of predators by subadult red drum. The twilight period prior to sunrise and following sunset is significant in the life histories and behaviour of many aquatic organisms, especially for some counter-shaded fish species (Hobson 1972; Helfman 1993). This may explain why red drum did not typically initiate dispersal away from their sheltered dock habitat beyond sunset. In this scenario, tidal and diel cycles may be functioning as triggers that scale the movements of red drum within the estuarine landscape, or perhaps as part of an internal clock-setting mechanism for initiating foraging activity (e.g. Leiner, Han & MacKenzie 2000).

Mortality, emigration and transmitter malfunction

Fish that were suddenly no longer detected, especially those with a history of regularly remaining in the area monitored by the receiver array, probably were removed by either aquatic predators (e.g. bottlenose dolphins *Tursiops truncates* [Montagu]; Barros & Wells 1998; Young & Phillips 2002) or recreational anglers. A minimum of 33% of these losses were attributable to recreational angling. The dock site, for which fish showed strong site fidelity, is a popular recreational fishing area. Six of the red drum implanted with transmitters were smaller than the minimum legal size (14 inches; 356 mm), but given the rapid growth rates reported for this species (Murphy & Taylor 1990) likely would have recruited into the legal fishery within weeks of their release. Further, the illegal harvest of undersized fish also has been well documented. A creel survey by the Georgia Department of Natural Resources between 2000 and 2003 indicated that 11–17% of the harvest comprised undersized (10–13 inches; 254–330 mm) fish. During that same period, the lower end (14–15 inches; 360–380 mm) of the legally harvestable slot limit (14–23 inches; about 356–584 mm) comprised 40–59% of the total harvest of red drum (http://crd.dnr.state.ga.us/assets/documents/2003_MRFSS_Summary.pdf). These estimates, based on voluntary creel survey data, most likely provide conservative estimates of illegally harvested undersized red drum on the Georgia coast.

Emigration from the study area could explain the loss of fish, but should have been evidenced by a terminal detection at either the extreme upriver or downriver receiver in the array if the path travelled was the main channel of the Duplin River. This occurred in one case (fish no. 26). Emigration from the study area without detection would most likely occur in individuals with a tendency for moving into and across the vegetated intertidal zone. Four of the 10 fish tracked in this study exhibited this behaviour pattern on approximately 82% of combined upriver tide cycle movements. This behaviour suggests that at least five fish (these four, plus known emigrant fish no. 26) may have ultimately emigrated from the area without being detected.

Transmitter malfunction or battery failure also may have accounted for some portion of tag losses during this study. According to the manufacturer, the transmitters have a battery life of 90–110 days from the time of activation. However, three of the 15 transmitters (nos. 32, 34 and 35) purchased for this study failed to transmit a signal upon activation and were not used. These failures were caused by either a faulty connection upon activation or a manufacturing defect. The remaining 12 transmitters were functional upon initial activation, but one fish (no. 29) was never detected by any receivers after its release into the study area. Another study that used the same Vemco V8 transmitters observed a transmitter failure rate of 7.1% in implanted fish (W.E. Pine, personal communication).

Even without precise knowledge of the ultimate fate of each individual in this study, the strong site fidelity and predictable tidal movements demonstrated by most subadult red drum enhanced their vulnerability to angling. The predictable behaviour of red drum also offers fisheries managers a potential opportunity to mediate effects of over-fishing because discrete areas where the fish aggregate can be identified and protected with special regulations (e.g. catch and release). The predictable diel and tidal components of the movement pattern in many subadult red drum also provides an opportunity to manage the timing as well as location of fishing effort for this species. Such management approaches might be particularly effective in extant National Estuarine Research Reserves in the USA, which are presumably already under some degree of federal or state protection.

Given the growing recognition that many fish stocks (including red drum) are seriously over-fished (Pauly & Palomares 2005) and that reducing the abundance of large predatory species is having cascading effects within marine and estuarine food webs (Jackson, Kirby, Berger, Bjorndal, Botsford, Bourque, Bradbury, Cooke, Erlandson, Estes, Hughes, Kidwell, Lange, Lenihan, Pandolfi, Peterson, Steneck, Tegner & Warner 2001), it is perhaps surprising that none of the 26 National Estuarine Research Reserves in the USA currently have any special regulations on recreational fishing within their boundaries. Although the Sapelo Island National Estuarine Research Reserve (SINERR) within which the present study was conducted has a stated policy of restricted access and a mandated primary management objective to maintain the property's 'integrity for research and education purposes and to protect it from both internal and external sources of stress which may alter or affect the nature of the ecosystems' (from the Special Award Conditions establishing the SINERR in 1976), to date there has been no effective mechanism by which this is accomplished. There is little effective restriction on access to research sites or local interest in even considering temporary moratoria on recreational fishing in that portion of the reserve in which research is conducted. In the absence of such protection for research, the estimated minimum cost to this project was $1200 in transmitters lost to recreational harvest plus the incalculable cost of the data they may have provided. If recreational angling could have been eliminated as a possible source of mortality, any losses not attributable to emigration would have provided an estimate of natural mortality for the population of subadult red drum inhabiting this portion of the SINERR.

Finally, in light of the increased use of hatchery-reared individuals to supplement the recreational red drum fishery, the behaviour and habitat requirements of extant wild red drum populations should be considered carefully when implementing stocking programmes. Populations of hatchery-reared fish are likely to have less genetic diversity than wild stocks and, if the differences observed among individuals in this study have a genetic component, stocked and wild fish may exhibit different movement and habitat use behaviour. Given the range of individual variation observed among wild subadult red drum, their displacement or replacement by hatchery-reared individuals may have unintended effects on the population's susceptibility to fishing as well as on the trophic dynamics and functioning of estuarine ecosystems.

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