

EVALUATION OF RADIO TELEMETRY TO STUDY THE SPATIAL ECOLOGY OF CHECKERED PUFFERS (*SPHOEROIDES TESTUDINEUS*) IN SHALLOW TROPICAL MARINE SYSTEMS

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ABSTRACT

Knowledge of the spatial ecology of fishes aids in conservation management and informs the sustainable use of natural resources, although the techniques used to monitor movements are often restricted by the habitats occupied by fishes and our inability to observe them. Due to the rapid attenuation of acoustic signals in shallow (<0.3 m) estuarine environments, we examined the applicability for a novel use of radio telemetry to examine the spatial ecology of checkered puffers, *Sphoeroides testudineus* Linnaeus, 1758, in shallow, tropical tidal creeks. External attachment of radio tags on the dorsal surface of the caudal peduncle resulted in reliable retention (100% after 5 d) for short-term applications, and no differences were observed in swimming ability or standard metabolic rate between tagged individuals and untagged controls. However, external tagging resulted in significant postural differences during routine activity in comparison to untagged controls, although we demonstrate that this can be eliminated by reducing tag burden in future studies. A small sample of puffers ($n = 5$) was subsequently radio tagged and released into a shallow tidal creek whereby attempts were made to relocate individuals both visually and using radio telemetry over a short period (1 hr). Checkered puffers exhibited an ability to move the entire length of a small tidal creek (maximum mobility 389 m), although using radio telemetry to monitor the movements of puffers had limited application with the techniques applied in the present study when individuals occupied water depths >0.2 m and were actively swimming. With minor modifications to tags and by reducing tag burden, radio telemetry could serve as a feasible means of monitoring the movements of site-associated species in shallow tidal creeks.

Telemetry offers unique insights into animal behavior, as it enables the collection of large quantities of near continuous information from animals in their natural environment (Lucas and Baras 2000, Cooke et al. 2004, Porter et al. 2005, Cooke 2008). Limitations are sometimes imposed by the challenging habitats occupied by some species (e.g., complexity of habitats, depth, vastness of a system; Akesson 2002), or an individual species characteristics including small size (see 2% rule: Winter 1996), unique morphology (e.g., flatfishes: Loher and Rensmeyer 2011), or behavior (Broadhurst et al. 2009), requiring modification of previously used techniques to address these challenges. An underlying assumption of all telemetry studies is that tagged individuals behave the same as untagged conspecifics and therefore there exists a need to conduct tag attachment studies to validate this assumption (Cooke et al. 2011).

Several types of telemetry currently are used to track fishes in a variety of habitats and decisions on the type of telemetry used typically are governed by the habitat occupied by the study species. Radio telemetry typically is used to track fish in

freshwater systems such as rivers and shallow lakes, and acoustic telemetry traditionally is used in marine systems due to the rapid attenuation of radio signals in water with high conductivity (Lucas and Baras 2000). Acoustic telemetry can perform poorly at times, particularly in high noise environments (e.g., Thorstad et al. 2000) as well as shallow water (i.e., <1 m; Cooke et al. in press). In some instances the use of combined acoustic/radio tags enables the monitoring of the migrations of anadromous fishes (Niezgoda et al. 1998) or movements of animals between aquatic and terrestrial environments (Brousseau et al. 2004); however, those tags tend to be large due to the incorporation of components for both transmission types.

Checkered pufferfish, *Sphoeroides testudineus* Linnaeus, 1758, is a small [≤ 300 mm total length (TL)] member of the Tetraodontidae family commonly found in tidal creeks and other shallow protected coastal waters throughout the western Atlantic (Robins and Ray 1986). Checkered puffers are able to inflate their body by gulping water or air for predator avoidance, a strategy also used by some other Tetraodontiformes. The inflation stretches the ventral and dorsal skin extending from immediately posterior of the head to the anterior of the dorsal fin, resulting in a substantial increase in surface area (Brainerd 1994) and making it more probable that sutures will rip if tags were surgically implanted into the coelomic cavity. This unique behavior, as well as the habitats occupied, creates a challenge for using telemetry to study the spatial ecology of this species. The objective of this study was to examine the potential applicability of telemetry for studying the spatial ecology of checkered puffers in shallow, tropical tidal creeks. Specifically, we were interested in whether telemetry tags could be attached and retained externally on checkered puffers without any adverse behavioral effects or metabolic costs, and whether the application of radio telemetry could provide information on the movements of checkered puffers in a shallow estuarine environment. Checkered puffers are the only abundant tetraodontid in the tidal creeks of The Bahamas, where this work was conducted. Although the ecological role of puffers is poorly understood, it was our hope that this tagging validation study would expand the tools available for studying the spatial ecology of this and other exceedingly shallow water dwelling marine organisms, thus improving our ecological knowledge of these animals.

METHODS

TAGGING EFFECTS STUDY.—Checkered puffers were captured on 22 February, 2012, from Page Creek, Eleuthera, The Bahamas (24°49'9.75"N, 76°18'29.98"W), on an outgoing tide using a seine net (0.6 cm mesh, 46 m long) positioned across the creek mouth. Upon capture, puffers were immediately transported by boat in aerated coolers to nearby holding facilities at the Cape Eleuthera Institute, where they were held in a recirculating aquaculture tank (1.6 m diam, 0.85 m height; 1400 L) that was aerated and continuously supplied with fresh sea water (1800 L hr⁻¹) at ambient temperatures. Puffers were fed a diet of ground sardines during holding and were released at the point of capture (where applicable) following cessation of the study.

We assessed tag burden for checkered puffers and compared this to untagged controls based on observations of swimming behavior, swimming ability using a chase to exhaustion protocol, and calculations of standard metabolic rate (SMR). Radio tags were attached to 15 individuals on 25 February, 2012 [191 (SE 5) mm TL, 161 (SE 14) g], without the use of anesthetics. Radio tags (Model BD2, Holohil Systems, Ltd.; Carp, Ontario, Canada;

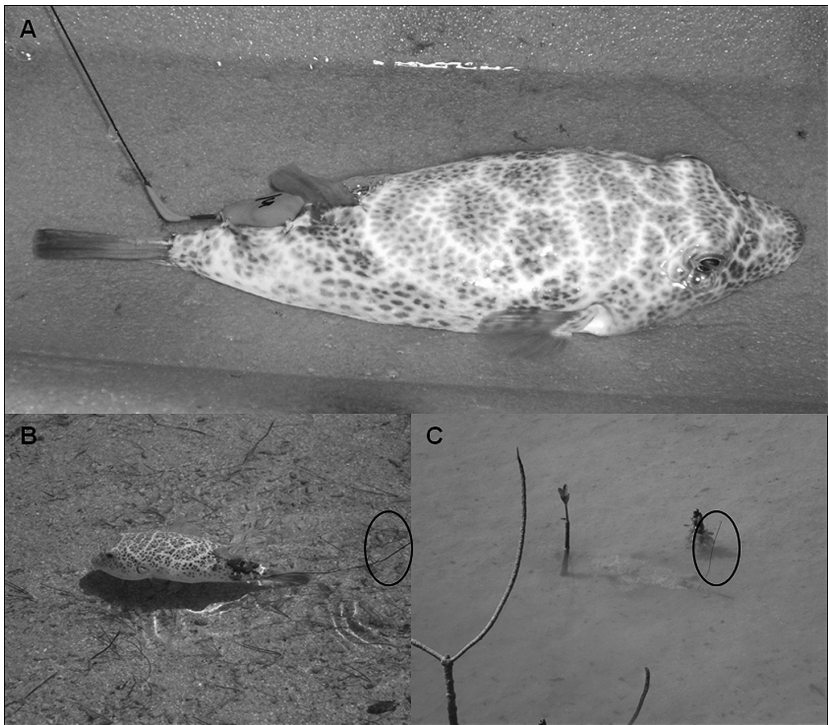


Figure 1. Checkered puffer (A) with a radio tag attached, 5 d post attachment, (B) active swimming following radio tag attachment and release into a shallow tidal creek, and (C) stationary following release (center of picture). Note the radio tag antenna above the water surface in (B) and (C) as indicated by circles.

weight 3.2 g in air, 20 cm trailing whip antenna, 148 MHz, pulse rate 40 pulses per min, 22 ms pulse width) were attached externally to the dorsal surface of the fish, immediately posterior to the dorsal fin (Fig. 1) on the caudal peduncle and represented 2.30% (SE 0.16; range 1.21%–3.33%) of body weight in air. Following disinfection in an iodine solution, two hypodermic stainless steel needles (16 ga) were pushed through the dermis and 20-lb monofilament line (previously inserted through the tag via pre-made holes) was passed through the lumen of the needles and secured using two surgeon's knots consisting of a triple and then a double wrap. The entire tag attachment process took <2 min. Prior to tag attachment, radio tag antennas were modified to permanently remain at 90° to the tag to promote clearance of the antenna in shallow water and aid in radio signal detection range (Fig. 1); this was done by bending the antenna wire and applying a small amount of glue to the bend. Following tag attachment, puffers were returned to the holding tank and held for 5 d along with 10 control fish [184 (SE 8) mm TL, 173 (SE 22) g]. There were no significant differences in TL (independent samples *t*-test: $t = -0.774$, $P = 0.450$) or weight ($t = 0.466$, $P = 0.648$) between tagged and untagged puffers.

Two days following tagging, a chase experiment was conducted on the same tagged fish ($n = 15$) and untagged controls ($n = 10$) mentioned above. Individually, fish were dip netted from their holding tank and immediately placed into a shallow circular tank (1.22 m diameter with filled with 15 cm of water). The circular tank was divided into four equal quadrants by black lines on the floor of the tank. A circular plastic container (0.46 m diam) was placed in the center of the tank to create an annular swim flume. A chase test was performed where two experimenters chased individual puffers by hand, and the number of annular lines crossed prior to exhaustion was recorded. Distances swum by puffers were

converted to swim speed estimates based on the outside diameter of each quadrant of the annular flume, as fish typically swam around the outside perimeter. Distance values were multiplied by the number of lines crossed until exhaustion, and data were scaled to the number of body lengths swum per second (bl s^{-1}). The time until exhaustion was the time at which three deliberate, consecutive tail grabs could be performed without an active reflex response (Kieffer 2000). This protocol provided a comparative swimming performance measure between tagged and untagged individuals and has been effectively used in previous studies (Heath et al. 1993, Portz 2007). Following cessation of the chase trial, individuals were returned to the holding tank.

Following tagging, observations of the same tagged and untagged individuals (as above) were made after 3 and 4 d, respectively, to determine if the added burden from tagging resulted in changes in body posture. Observations were made during diurnal periods at approximately the same time of day at 1 min intervals over a focal period of 5 min for each individual. The predominant body and head angle, in 15° increments, was visually determined by the same observer and recorded during routine behavior (predominantly swimming) in a circular tank with 0.5 m water depth and a glass viewing window.

Standard metabolic rate (SMR) was measured to determine the effect of tag burden on checkered puffer (Claireaux and Lefrancois 1998). SMR was determined using intermittent-flow respirometry on an additional group of checkered puffers, with SMR of tagged individuals [$n = 8$, 179 (SE 5) mm TL, 136 (SE 14) g] compared with untagged control fish [$n = 8$, 179 (SE 8) mm TL, 142 (SE 20) g]. There were no significant differences in TL ($t = -0.014$, $P = 0.989$) or weight ($t = 0.215$, $P = 0.833$) between tagged and untagged puffers used in the SMR calculations. Fish were not fed 48 hrs prior to all experiments, tagging occurred 24–48 hrs prior to SMR measurement, and tagging procedures were identical to those described above. The respirometry system, operating procedures, and calculations were identical to those previously described by Shultz et al. (2011), with the exception of the duration of individual cycles that consisted of a 5 min flush, 1 min wait, and 18.3–25 min measurement cycle due to the lower levels of oxygen consumed by checkered puffers. Oxygen consumption rate (MO_2 , $\text{mg O}_2 \text{ kg}^{-1} \text{ hr}^{-1}$) for each fish was calculated using the average of the six lowest values collected overnight (between 20:00 and 06:00), and when the coefficient of determination (r^2) for slope measurements was >0.95 during each measurement cycle, which is indicative of constant oxygen consumption (Schurmann and Steffensen 1997). All calculated dissolved oxygen values were corrected for background oxygen consumptions generated for each specific fish and chamber prior to commencing experiments.

RANGE TESTING.—We quantified the effect of water depth on radio and acoustic transmitter detection range, given the known poor detection range of acoustic transmitters in shallow environments and the possible alternative of using radio transmitters, particularly when radio tag antennas were protruding from the water surface. Tags were moored on the bottom of the water column (to emulate the benthic nature of puffers) in locations of different depth and the maximum linear distance at which audible signals could be detected (to simulate manual tracking) was recorded. Depth of acoustic tags was recorded as the distance from the tag to the water surface. Depth of radio tags was recorded as the distance from the tag to the water surface and the distance from the tip of the antenna to the water surface (Table 1). An additional range test was conducted using a radio tag with an antenna lying flat along the surface of the water. Range tests were conducted in the upper reaches of Page Creek and the nearby Kemps Creek, and occurred in habitats characterized as algal plains with sparse mangrove prop roots. For radio telemetry, a radio tag (Model BD2, Holohil Systems, Ltd.) with a modified antenna (see above) was monitored using a receiver (Biotracker, Lotek Engineering, Inc., Newmarket, Ontario, Canada) and a three-element yagi antenna (AF Antronics, Urbana, Illinois), which were connected via 1 m of RG58 coaxial cable. Distances between tag location and maximum detection distance were measured either via tape measure for short distances, or by noting global

Table 1. Detection ranges of radio and acoustic tags in the upper reaches of a tropical, shallow tidal creek.

Radio tag			Acoustic tag	
Tag depth (cm)	Radio antenna location	Detection range (m)	Tag depth (cm)	Detection range (m)
0.5	19.5 cm above surface	1,281.0	2.0	1.8
15.0	5.0 cm above surface	428.2	5.5	4.7
20.5	0.5 cm below surface	56.1	11.0	12.3
25.0	5.0 cm below surface	3.5	25.0	24.0

positioning system coordinates (GPS, Garmin E-Trex, Garmin International, Inc., Olathe, Kansas, United States of America) and later calculating distances using Google Earth. For acoustic telemetry, an acoustic tag (model V9 continuous tag, 76 kHz, 2000 ms pulse interval, power output 146 dB re 1 μ Pa @1m Vemco, Inc., Shad Bay, Nova Scotia, Canada) was moored and maximum detection range in several water depths was determined using a wide band manual tracking receiver (USR-5W, Sonotronics, Inc., Tucson, Arizona) and a directional hydrophone (DH-4, Sonotronics, Inc.) mounted on a piece of PVC pipe (1.25 m long, 2.4 cm diam). Water temperature, conductivity, salinity, and dissolved oxygen at the site were 28.6 (SE 0.1) °C, 44.0 (SE 0.2) mS cm⁻¹, 28.3 (SE 0.2), and 10.6 (SE 0.5) mg L⁻¹, respectively. In all cases unobstructed line of sight was maintained to simulate optimum conditions.

FIELD TRACKING.—A small sample of checkered puffers [$n = 5$, 207 (SE 12) mm TL, 206 (SE 32) g] captured from Page Creek were fitted with radio tags using the method described above, released into the upper reaches of Page Creek over a period of 3 d (27, 28, and 29 February, 2012), and their movements monitored for 1 hr post-release to validate field deployment of the technique. Following release, attempts were made to manually relocate checkered puffers every 5 mins for 1 hr using a radio receiver and a three element yagi antenna. Where possible, visual contact was maintained from a distance and spatial locations were recorded using a handheld GPS unit. Habitat occupied and water depth estimates were noted, and a creek-wide scan for individuals released on preceding days conducted, both visually and using the radio receiver. Movements were reconstructed over time and distances between GPS locations measured using Google Earth. Total range was calculated as the maximum linear distance between the most upstream and downstream locations in the 1-hr period, and mobility was calculated as the cumulative movements between consecutive 5 min locations, summed over 1 hr. Ground speed was normalized for fish size by calculating speed as the body lengths moved per second and was used instead of swimming speed as tidal flow was not quantified.

DATA ANALYSIS.—Independent samples *t*-test was used to compare length and weight between tagged and control puffers in both the tagging trials and when comparing SMR. An independent samples *t*-test was also used to compare the time until exhaustion and swimming speed of tagged and untagged controls in the chase experiments. A linear regression was used to test for differences between posture (modal difference between head and tail angles during routine activity) of tagged individuals and body weight. Where appropriate, data were first tested for the assumptions of normality and homogeneity of variance following the methods outlined by Grafen and Hails (2002). All statistical analyses were deemed significant at $P < 0.05$ and conducted using R (version 2.14.2, R Development Core Team 2012). All data are presented as mean (SE) unless otherwise stated.

RESULTS

We observed no mortality of checkered puffers over the 5-d monitoring period following tagging and had 100% tag retention. Four individuals showed slight tearing of the skin around one ($n = 2$) or both ($n = 2$) puncture wounds, although in all cases the tag remained attached and in position. In addition, two tags were detached at one puncture/suture location, although the tags remained attached by the second suture. One of these individuals had a suture torn during the chase experiment, although the cause of the second detaching is unknown. All remaining individuals exhibited no tearing, loose tag attachment, inflammation, or fungal infection around the tagging site and were largely identical to the individual shown in Figure 1A.

Radio tagged puffers demonstrated noticeable differences in orientation during routine activity in comparison to untagged controls. The modal tail angle of tagged puffers was 15° (range 0° – 90°) and the modal head angle was 0° (range 0° – 30°), with a modal difference between the head and tail of 15° (range 0° – 60°). In comparison, the modal tail angle of untagged puffers was 0° (range -15° to 30°) and the modal head angle was 0° (range -15° to 30°), with in a modal difference between the head and tail never observed to be different than 0° . There was a significant negative linear relationship between weight (g) of puffers and the body posture ($^\circ$) of tagged individuals (difference between head and tail angle; $r^2 = 0.398$, $F = 6.617$, $P = 0.028$) explained by the fitted model: Posture difference = $45.356 - 0.154$ (weight). Solving this equation to result in 0° postural difference between the tail and head (assuming that the linear relationship extends beyond the observed data) would require tagging a puffer with a minimum weight of 294.5 g using the radio tags in this study, or reducing tag weight ($<1.1\%$ of body weight in air) to enable tagging of smaller individuals.

There were no significant differences in the swimming performance between tagged and untagged controls in terms of time until exhaustion ($t = 0.684$, $P = 0.501$; Fig. 2). Likewise no significant differences existed between tagged and untagged controls in terms of swimming speed ($t = -0.331$, $P = 0.744$; Fig. 2) during the chase experiments. The SMR of radio tagged puffers was 99.70 (SE 7.05) $\text{mg O}_2 \text{ kg}^{-1} \text{ hr}^{-1}$ and 121.59 (SE 12.56) $\text{mg O}_2 \text{ kg}^{-1} \text{ hr}^{-1}$ for untagged controls, with differences not significant ($t = -1.520$, $P = 0.151$).

The detection range of radio telemetry exceeded that of acoustic telemetry at all water depths in Page Creek when the antenna of the radio tag extended above or was immediately below the water surface (Table 1). Once the radio tag antenna was submerged, detection range was poor. In comparison, the detection range of the acoustic tag increased with increasing water depth (Table 1) and this trend is expected to continue to greater ranges.

Checkered puffers exhibited an ability to move extensive distances over short periods of time, exhibiting total linear ranges of 38–327 m and exhibiting mobility estimates of 104–389 m over 1 hr (Table 2). Ground speeds varied among individuals and ranged from 0– 3.31 bl s^{-1} (Table 2), although these are not directly indicative of swimming speed due to the unquantified influence of tidal movements. Radio signals were not always discernible during the 1-hr tracking period, with the proportion of radio tag detections averaging 46.6% (SE 18.7%) of tracking observations (range 8%–100%; Table 2) and typically dependent upon depth

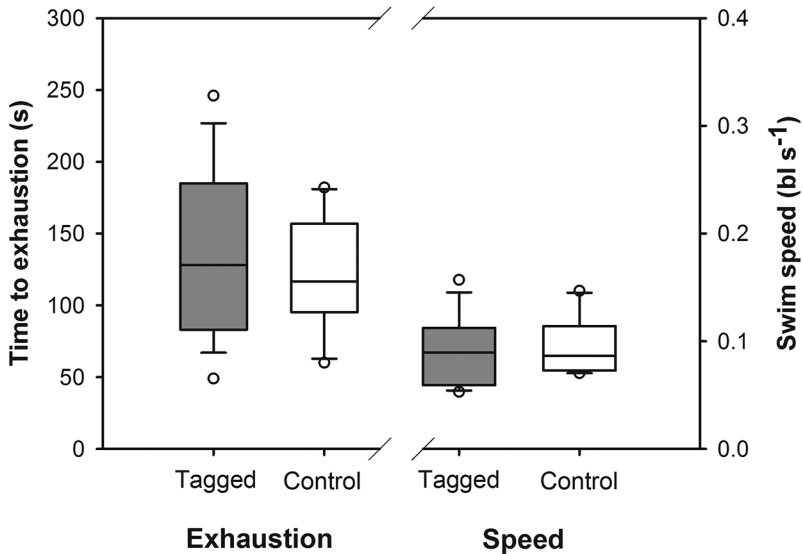


Figure 2. Comparative time until exhaustion and swimming speed (body lengths per second, bl s^{-1}) between tagged and untagged (control) checkered puffers. Boxes represent 25th and 75th percentiles with the median enclosed within, and whiskers represent 10th and 90th percentiles.

occupied. In addition, visual contact of ID 1 was lost on nine occasions predominantly due to use of mangrove habitats, although positive locations based on radio signals were present on all but two occasions. Visual contact was maintained on all other occasions, except for once on ID 3. A radio tagged checkered puffer was observed near the entrance of Page Creek on two separate days following release, although water depth was too great to enable detection of its radio frequency and provide a positive identification. Separately, the radio signal of ID 1 was detected briefly 1 d following release during a scan of the entire length of Page Creek, although the radio signal was intermittent and we were unable to determine the location of this individual. Furthermore, ID 4 was recaptured by one of the authors in a separate study at Page Creek, 93 d after release on 31 May, 2012. Despite some biofouling, the tag was still attached securely and the individual was healthy.

DISCUSSION

The external tagging method applied in this study was successful in terms of tag retention over short time periods, and no negative effects of tagging were observed in the swimming ability or SMR of checkered puffers. We did not measure active metabolic rate because we did not have access to a swim tunnel, but we surmise that there would be added metabolic costs for swimming for those animals that exhibited altered posture. Although measuring SMR was useful in terms of understanding metabolic costs when stationary (i.e., confined to the respirometer; Claireaux and Lefrancois 1998), the postural changes suggest that active swimming may be more impaired. The lack of impacts of tagging on swimming performance in the annular swim flume are suggestive that if there are metabolic costs of tag burden that they are

Table 2. Movements of checkered puffers monitored by radio telemetry and visually over a 1-hr period, with spatial locations and water depth determined every 5 mins. Note that water depth was not recorded for ID 1 due to loss of visual contact as this fish predominantly occupied mangrove habitats.

Fish ID	TL (mm)	Weight (g)	Total mobility (m)	Total range (m)	Ground speed (min-max) bl s ⁻¹	Water depth occupied (cm)		Proportion of radio detections	Proportion of visual observations
						Median	Range		
1	221	244	389	327	0–0.90	n/a	n/a	83%	25%
2	233	280	260	256	0–1.25	25	(15–35)	17%	100%
3	184	139	355	183	0–3.31	18	(10–30)	25%	92%
4	222	244	130	38	0–0.51	5	(5–7)	100%	100%
5	175	122	104	59	0–0.47	15	(10–25)	8%	100%

small. However, differences in body posture between untagged controls and tagged individuals demonstrated the necessity to tag larger individuals or reduce tag burden. Limitations were imposed by the unique morphology of this species precluding intracoelomic implantation or locating external tags close to the centre of mass due to their ability to inflate and potentially rupture sutures. The results presented here reinforce the importance of tagging validation studies as researchers study an increasingly diverse array of marine animals with biotelemetry technology.

Radio-tagged checkered puffers exhibited an ability to move the entire length of a small tidal creek over relatively short periods of time. Further, retention of tags using the external attachment technique described here appeared suitable in both the lab and the field (following a reduction in tag burden), and recapture of an individual 93 d following release appears promising given potential increased snagging and predation risks associated with tagging and antenna modification. Using radio telemetry to monitor the movements of puffers in these types of systems had limited application with the techniques applied in the present study when individuals occupied water depths >0.2 m. Combined radio/acoustic tags could provide an alternative option (Niezgodna et al. 1998), and these tags have previously been used to monitor movements between deep and shallow (or terrestrial) estuarine environments (e.g., Brousseau et al. 2004). However, combined radio/acoustic tags are inherently larger than a single transmission mode, which would be limiting for smaller species. Alternatively, radio tags could be modified with a longer, floating antenna that could remain vertical in deeper water depths (i.e., 0.5 m). The greater length and added buoyancy also would enable the antenna to float along the surface of the water in shallower habitats, providing for continuous and consistent radio signals (although raising obvious concerns regarding altered behavior).

Preliminary tests with the radio transmitter antenna lying on the water surface and using identical tags and tracking equipment to that described here resulted in a detection range of approximately 250 m. As such, rather than dismissing radio telemetry for marine applications, we believe that it has merit for fishes and other animals (e.g., arthropods, gastropods) in shallow marine or estuarine systems. We are unaware of any studies that have used this method given the fact that radio signals are attenuated in marine waters. However, similar to when satellite tags transmit radio signals from the surface of the water once disconnected from the tracked animal, if conventional radio tags can be configured such that the antennas break the water surface then radio telemetry has promise for some unique applications. In fact, given the larger detection distance, radio telemetry has some potential advantages over acoustic telemetry for tracking animals in very shallow marine habitats.

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LITERATURE CITED

- Akesson S. 2002. Tracking fish movements in the ocean. *Trends Ecol Evol.* 17:56–57. [http://dx.doi.org/10.1016/S0169-5347\(01\)02418-1](http://dx.doi.org/10.1016/S0169-5347(01)02418-1)
- Brainerd EL. 1994. Pufferfish inflation: functional morphology of postcranial structures in *Diodon holocanthus* (Tetraodontiformes). *J Morphol.* 220:243–261. <http://dx.doi.org/10.1002/jmor.1052200304>
- Broadhurst BT, Ebner BC, Clear RC. 2009. Radio-tagging flexible-bodied fish: temporary confinement enhances radio-tag retention. *Mar Freshwat Res.* 60:356–360. <http://dx.doi.org/10.1071/MF08141>
- Brousseau LJ, Sclafani M, Smith D, Carter D. 2004. Acoustic-tracking and radio-tracking of horseshoe crabs to assess spawning behavior and subtidal habitat use in Delaware Bay. *North Am J Fish Manage.* 24:1376–1384. [http://dx.doi.org/10.1577/1548-8675\(2004\)24<1376:AAROHC>2.0.CO;2](http://dx.doi.org/10.1577/1548-8675(2004)24<1376:AAROHC>2.0.CO;2)
- Claireaux G, Lefrancois C. 1998. A method for the external attachment of acoustic tags on roundfish. *Hydrobiologia.* 371/372:113–116. <http://dx.doi.org/10.1023/A:1017017810099>
- Cooke SJ. 2008. Biotelemetry and biologging in endangered species research and animal conservation: relevance to regional, national, and IUCN Red List threat assessments. *Endang Species Res.* 4:165–185. <http://dx.doi.org/10.3354/esr00063>
- Cooke SJ, Hinch SG, Lucas MC, Lutcavage M. In Press. Biotelemetry and Biologging. In: Zale AV, Parrish DL, Sutton TM, editors. *Fisheries Techniques*. 3rd ed. Bethesda: American Fisheries Society.
- Cooke SJ, Hinch SG, Wikelski M, Andrews RD, Kuchel LJ, Wolcott TG, Butler PJ. 2004. Biotelemetry: a mechanistic approach to ecology. *Trends Ecol Evol.* 19:334–343. PMID:16701280. <http://dx.doi.org/10.1016/j.tree.2004.04.003>
- Cooke SJ, Woodley CM, Eppard MB, Brown RS, Nielsen JL. 2011. Advancing the surgical implantation of electronic tags in fish: a gap analysis and research agenda based on a review of trends in intracoelomic tagging effects studies. *Rev Fish Biol Fish.* 21:127–151. <http://dx.doi.org/10.1007/s11160-010-9193-3>
- Grafen A, Hails R. 2002. *Modern statistics for the life sciences*. Oxford University Press: Oxford. PMID:12183132.
- Heath AG, Cech JJ, Zinkl JG, Finlayson B, Fujimura R. 1993. Sublethal effects of methyl parathion, carbofuran, and molinate on larval striped bass. *Am Fish Soc Symp.* 14:17–28.
- Kieffer JD. 2000. Limits to exhaustive exercise in fish. *Comp Biochem Physiol A.* 126:161–179. [http://dx.doi.org/10.1016/S1095-6433\(00\)00202-6](http://dx.doi.org/10.1016/S1095-6433(00)00202-6)
- Loher T, Rensmeyer R. 2011. Physiological responses of Pacific halibut, *Hippoglossus stenolepis*, to intracoelomic implantation of electronic archival tags, with a review of tag implantation techniques employed in flatfishes. *Rev Fish Biol Fish.* 21:97–115. <http://dx.doi.org/10.1007/s11160-010-9192-4>
- Lucas MC, Baras E. 2000. Methods for studying spatial behaviour of freshwater fishes in the natural environment. *Fish Fish.* 1:283–316. <http://dx.doi.org/10.1046/j.1467-2979.2000.00028.x>
- Niezgoda GH, McKinley RS, White D, Anderson G, Cote D. 1998. A dynamic combined acoustic and radio transmitting tag for diadromous fish. *Hydrobiologia.* 371/372:47–52. <http://dx.doi.org/10.1023/A:1017010802404>
- Porter J, Aazberger P, Braun HW, Bryant P, Gage S, Hansen T, Hanson P, Lin CC, Lin FP, Kratz T, Michener W, Shapiro D, Williams T. 2005. Wireless sensor networks for ecology. *BioScience.* 55:561–571. [http://dx.doi.org/10.1641/0006-3568\(2005\)055\[0561:WSNFE\]2.0.CO;2](http://dx.doi.org/10.1641/0006-3568(2005)055[0561:WSNFE]2.0.CO;2)
- Portz DE. 2007. Fish-holding-associated stress in Sacramento River chinook salmon (*Oncorhynchus tshawytscha*) at South Delta Fish Salvage Operations: effects on plasma constituents, swimming performance, and predator avoidance. PhD dissertation, University of California, Davis.

- R Development Core Team. 2012. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Available from: <http://www.R-project.org/>.
- Robins CR, Ray GC. 1986. A field guide to Atlantic coast fishes of North America. Boston: Houghton Mifflin Company.
- Schurmann H, Steffensen JF. 1997. Effects of temperature, hypoxia and activity on the metabolism of juvenile Atlantic cod. *J Fish Biol.* 50:1166–1180.
- Shultz AD, Murchie KJ, Griffith C, Cooke SJ, Danylchuk AJ, Goldberg TL, Suski CD. 2011. Impacts of dissolved oxygen on the behaviour and physiology of bonefish: implications for live-release angling tournaments. *J Exp Mar Biol Ecol.* 402:19–26. <http://dx.doi.org/10.1016/j.jembe.2011.03.009>
- Thorstad EB, Økland F, Rowsell D, McKinley RS. 2000. A system for automatic recording of fish tagged with coded acoustic transmitters. *Fish Manage Ecol.* 7:281–294.
- Winter J. 1996. Advances in underwater biotelemetry. *In:* Murphy BR, Willis DW, editors. *Fisheries Techniques*. 2nd ed. Bethesda: American Fisheries Society. p. 555–585.

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