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The effects of pop-up satellite archival tags (PSATs) on the metabolic rate and swimming kinematics of juvenile sandbar shark *Carcharhinus plumbeus*

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ABSTRACT

Pop-up satellite archival tags (PSATs) have been used since the 1990s to document the movements and post-release survival of numerous fish species. The effects of PSAT attachment on metabolic rate, cost of transport, and swimming kinematics have, however, not been broadly investigated. We therefore quantified the acute effects of PSAT attachment on these parameters in juvenile (47–87 cm fork length) sandbar shark *Carcharhinus plumbeus*. Using a water tunnel, we also measured the lift and drag forces of PSATs from three manufacturers which allowed us to calculate the theoretical power costs of towing these devices. We found no evidence that PSAT attachment results in increases in metabolic rate or cost of transport, or influences swimming kinematics of juvenile sandbar shark at volitional swimming speeds. Applying drag force measurements obtained for PSATs to our data showed that the predicted fractional increase in metabolic rate engendered by towing one of these devices at a specified velocity, normalized by the metabolic rate when swimming at that velocity minus the standard metabolic rate, would be below 5%. Our results are therefore congruent and suggest that PSAT attachment does not negatively impact juvenile sandbar shark (and by extension other elasmobranch species of equivalent or larger body sizes and employing a similar swimming mode).

1. Introduction

Since the 1990s, pop-up satellite archival tags (PSATs) have been used to document the horizontal, vertical, and seasonal movements of a variety of marine fishes (reviewed by Arnold and Dewar 2001; Block et al., 2001; Musyl et al., 2011b). These devices have also been used to quantify rates of post-release mortality in both teleost and elasmobranch species (e.g., Graves et al., 2002; Horodysky and Graves, 2005; Horodysky et al., 2007; Kerstetter et al., 2003; Kerstetter and Graves, 2006; Musyl et al., 2011a; Filmalter et al., 2013; Marcek and Graves, 2014; Marshall et al., 2015; Eddy et al., 2016). However, the potential consequences of PSAT attachment on movements, energetics, and post-release survival remain poorly documented.

The original PSAT models manufactured by Microwave Telemetry, Inc. and Wildlife Computers measured 175 mm and 180 mm (excluding the antennae) and weighed 68 g and 75 g in air (Grusha

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Abbreviations: ρ, density (kg m^{-3}) of the fluid; %TAX, (Tag Altered eXertion, dimensionless); CD, drag coefficient (dimensionless); FL, fork length (cm); F_D, drag force of a PSAT (N); F_L, lift force of a PSAT (N); F_T, total force of a PSAT (N); *M*, fish mass (kg); MR, metabolic rate, expressed as the rate of oxygen consumption (mg O$_2$ kg^{-1} h^{-1}); N, Newton (measure of force: kg m s^{-2}); *P*, power required to overcome the drag force on a PSAT at a given velocity (W); PSAT, pop-up satellite archival tag; S, projected wetted surface area of a PSAT (m^2); SMR, standard metabolic rate, the metabolic rate of a post-absorptive animal (i.e., not digesting a meal) and at zero overt activity (mg O$_2$ kg^{-1} h^{-1}); SP, swimming power (W); U, velocity (m s^{-1}); W, watts.

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and Patterson, 2005), respectively. These tags were often deployed on large pelagic fishes such as tunas (Lutcavage et al., 1999; Block et al., 2005, 2011; Stokesbury et al., 2004), billfishes (Graves et al., 2002; Domeier et al., 2003; Horodysky and Graves, 2005; Kerstetter and Graves 2006; Graves and Horodysky, 2008), and sharks (Moyes et al., 2006; Musyl et al., 2011a). For teleosts, PSATs are often attached to the fish just posterior and ventral to the anterior insertion of the first dorsal fin with a tether of monofilament and an intramuscular anchor (Lutcavage et al., 1999; Graves et al., 2002; Domeier et al., 2003; Horodysky and Graves, 2005); whereas a wire harness fastened through the dorsal fin is commonly used for attaching PSATs to sharks (Moyes et al., 2006; Musyl et al., 2011a). Early PSAT models had limited data archiving and transmission abilities and therefore could only be used for short (10–30 days) deployments (Graves et al., 2002) after which the tags activate a release mechanism, detach from the animal, and float to the surface where they transmit archived data to the ARGOS system.

Manufacturers have markedly improved PSAT designs during the last several years, which have resulted in smaller devices (Musyl et al., 2011b) and improved rates of data transmission. Manufacturers have also considered the consequences of their PSAT designs with the aim of minimizing effects on fish (Hoffman, 2013). Specifically, PSAT models are now available that are approximately two-thirds the size of the original models tested for drag characteristics by Grusha and Patterson (2005). These more compact devices have subsequently been deployed on species such as striped bass *Morone saxatilis* (Graves et al., 2009), Greenland halibut *Reinhardtius hippoglossoides* (Peklova et al., 2012), and juvenile Atlantic bluefin tuna *Thunnus thynnus* (Galuardi and Lutcavage, 2012). Although PSATs remain one of the best tools to quantify rates of post-release mortality and to monitor the horizontal and vertical movements of free-swimming fishes (e.g., Block et al., 1998; Weng and Block, 2004; Wilson et al., 2005), there are no data on the drag forces associated with these smaller PSATs.

More importantly, recent studies have shown that attachment of a PSAT may have significant detrimental effects that appear to be both species- and size-specific (Burgerhout et al., 2011; Grusha and Patterson, 2005; Methling et al., 2011; Steinhausen et al., 2006). There is growing concern that electronic devices attached to aquatic animals can negatively affect energetics (i.e., increase metabolic rate and cost of transport), behaviors, rates of immediate post-release mortality, and long term survival (Wilson and McMahon, 2006; Jones et al., 2013; van der Hoop et al., 2014; Jepsen et al., 2015). We contend, therefore, that it is necessary to take into account the potential influences of towing a PSAT; especially if the devices are deployed on relatively small individuals. We hypothesized that: (1) PSAT attachment would induce an increase in metabolic rate at volitional swimming speeds, (2) towing a PSAT would alter the swimming kinematics of juvenile sandbar shark by increasing tailbeat frequency and decreasing stride length, and (3) the exertion required to maintain swimming speed would increase following PSAT attachment.

To investigate these issues, we measured metabolic rates and swimming kinematics, at volitional swimming speeds, in juvenile sandbar shark before and following attachment of one of the newer, smaller PSAT models. In addition, using a water tunnel we quantified the drag and lift forces associated with the newer, smaller PSATs at different velocities to estimate the potential for these devices to change the metabolic rate, cost of transport, and swimming kinematics of juvenile sandbar shark.

2. Material and methods

All animal capture, handling, and experimental procedures followed approved Institutional Animal Care and Use Committee protocols (VIMS # 2013-04-26-8704 and U. Mass. Dartmouth # 10-01) and all applicable U.S. laws and regulations. Juvenile sandbar shark (47–87 cm fork length [FL], 1.0–6.5 kg body mass) were captured using standard recreational hook-and-line fishing gear in the tidal lagoon system near the Virginia Institute of Marine Science's Eastern Shore Laboratory in Wachapreague, VA. The hook was removed immediately after landing, and fish placed in a ~600 l circular plastic tub (1.5 m diameter × 0.7 m depth filled with aerated seawater) for transport back to shore. Fork length was measured during transfer to a 500,000 l circular holding tank (~7 m diameter × ~2 m depth). The holding tank was supplied with filtered seawater pumped from the adjacent tidal lagoon. Temperature and salinity ranged from 22 to 29 °C and 30–33‰, respectively and reflected normal seasonal fluctuations. Individuals were acclimated to captivity for 7–15 days, offered pieces of Atlantic menhaden *Brevoortia tyrannus* every two days, but were fasted for 48 h prior to use in an experiment. At the completion of experiments, individuals were released back into the estuary from which they were caught.

2.1. Respirometry

Two circular plastic tanks (3560 l vol, 2.3 m diameter × 0.9 m depth) served as a respirometer and a seawater reservoir. The tanks were connected via a plastic pipe that allowed the former to be flushed with seawater from the latter. The reservoir tank was continuously bubbled with both atmospheric air (to remove CO_2) and pure oxygen (to elevate oxygen content). Oxygen levels in the reservoir ranged from ~9 to 12 mg $O_2\ l^{-1}$ and temperature ranged from ~24 to 26 °C. The respirometer was covered with a tight fitting lid constructed from 6.3 mm thick Plexiglas, supported with a wood frame, to impede gas transfer between the water and the atmosphere. Oxygen levels and water temperatures were monitored continuously in the respirometer and reservoir tanks using a WTW (Weilheim Oxi 340im Weilheim, Germany) and YSI (YSI 5739 Yellow Springs, OH) oxygen meters, respectively. Temperature and dissolved oxygen concentration data from the former were collected using a personal computer and custom designed software developed in DASYLab (Measurement Computing Norton, MA).

For each trial, a shark was transferred from the holding tank to the respirometer tank, the lid secured, and the fish allowed to acclimate for 12–18 h under natural day/night light cycles. During this time, the water was continuously exchanged between the respirometer and reservoir to ensure oxygen levels in the former remained above 80% air saturation.

Metabolic rate (MR, mg O_2 $kg^{-1}\ h^{-1}$) was subsequently determined using the intermittent-flow respirometry technique (Steffensen, 1989; Steffensen et al., 1984; Sepulveda et al., 2007; Svendsen et al., 2016). In brief, flushing of the respirometer was stopped, and oxygen levels recorded every 5 s for 120–150 min. Metabolic rate was determined by multiplying the rate of decrease of oxygen content (determined by linear regression of oxygen level against elapsed time) by tank volume (which was corrected for shark volume estimated from animal mass) minus background oxygen consumption (i.e., the rate of oxygen content decrease when a shark was not present). Water exchange between the respirometer and reservoir was resumed for 30–60 min to return the oxygen level in the former to at least 80% air saturation. Four to ten metabolic rate measurements were thus obtained for each shark during the 24-h following the recovery period.

Following this, the fish was removed from the respirometer, fitted with a PSAT (model: "miniPAT", Wildlife Computers, Redmond, WA, Fig. 1), and then immediately returned to the respirometer. A tether (11 cm long × 0.16 cm diameter plastic-coated braided wire) connected to the PSAT was affixed to the dorsal fin using a small J-hook (barb removed). Metabolic rate measurement data were then