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Atlantic sturgeon *Acipenser oxyrinchus* surfacing behaviour

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Atlantic sturgeon *Acipenser oxyrinchus* surfacing behaviour was investigated in Minas Basin (45° 20′ N; 64° 00′ W) and the Bay of Fundy with pop-up satellite archival tags (MiniPAT) measuring physical variables (pressure, temperature, light). Of six tags deployed during June and July, five provided pop-up locations and two were recovered after *c.* 4 months. Analysis of recovered archival data revealed that the frequency of surfacing events was highest (78·9%) when *A. oxyrinchus* were in Minas Basin at depths <10 m. Surfacing frequency decreased substantially when fish migrated into greater depths of the Bay of Fundy (>40 m). The tidal cycle in Minas Basin had a significant relationship to surfacing frequency, with the most surfacing events (49·5%) occurring on the flood tide, from mid- to high-tide. Surfacing events ranged from 0–12 a day and the maximum number occurred between 2300 and 0300 hours. Maximum surfacing ascent speeds ranged from 0·50 to 4·17 m s^{-1} and maximum descent speeds ranged from 0·17 to 3·17 m s^{-1}. Buoyancy control, by gulping air to inflate the gas bladder, is proposed as the main reason for surfacing behaviour in *A. oxyrinchus*.

Key words: buoyancy control; depth effects; pop-up archival tags; surfacing frequency; swim speeds; tidal effects.

INTRODUCTION

Surfacing is a relatively common behaviour among many groups of fishes. Some fishes breach to feed such as African butterfly fish (Pantodontidae), various trout and salmon (Salmonidae), mullets (Mugilidae) and needlefish (Belonidae). Flying fish (Exocoetidae) breach and glide above the water surface to avoid aquatic predators. Many fishes such as lungfishes (Protopteridae) and bowfin (Amiidae) surface to gulp air in low-oxygen environments. Some sharks (Carcharhinidae) may breach to rid themselves of attached remoras (Ritter & Brunnschweiler, 2003; Curtis & Macesic, 2011). For other fishes, however, such as eagle rays (Myliobatidae), silver carp (Cyprinidae) and sturgeons (Acipenseridae), there is no generally accepted agreement on why extensive surfacing or breaching occurs (Chick & Pegg, 2001; Sulak *et al.,* 2002).

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Surfacing behaviour, including porpoising and breaching, has been observed in Atlantic sturgeon *Acipenser oxyrinchus* Mitchill 1815 in Minas Basin (this study), the Bay of Fundy (Taylor *et al.,* 2016) and in Canadian and U.S.A. rivers and estuaries as far south as Florida (Cobb, 1900; Scott & Scott, 1988; Sulak *et al.,* 2002). At certain times in Minas Basin up to 100+ breaches an hour have been observed and individuals often clear the water by up to 2+ m (M. Dadswell, pers. obs.). Surfacing behaviour has been widely observed in several other sturgeon species including Chinese sturgeon *Acipenser sinensis* Gray 1835 (Watanabe *et al.,* 2008, 2013), white sturgeon *Acipenser transmontanus* Richardson 1837 (Parsley *et al.,* 1993; Paragamian & Duehr, 2005), green sturgeon *Acipenser medirostris* Ayres 1854 (Erickson & Hightower, 2007; Van Eenennaam *et al.,* 2012), lake sturgeon *Acipenser fulvescens* Rafinesque 1817 (Bruch & Binkowski, 2002), stellate sturgeon *Acipenser stellatus* Pallas 1771, sterlet sturgeon *Acipenser ruthenus* L. 1758, beluga sturgeon *Huso huso* (L. 1758) and Gulf sturgeon *Acipenser oxyrinchus desotoi* (Sulak *et al.,* 2002). Many explanations for surfacing behaviour among sturgeons have been proposed including: to rid themselves of external parasites (Vladykov & Greeley, 1963), to help shed eggs during spawning (Smith, 1985), to escape predators, to exercise or to communicate (Sulak *et al.,* 2002), as a form of courtship behaviour (Bruch & Binkowski, 2002), or to regulate air in the gas bladder (Watanabe *et al.,* 2008, 2013).

One of the primary functions of the gas bladder in fishes is to maintain buoyancy (Alexander, 1966). Physostomous fishes have their gas bladder connected to their oesophagus *via* the pneumatic duct (Fänge, 1966), but air in the gas bladder is gradually lost over time through diffusion, particularly with increased pressure at greater depths (Watanabe *et al.,* 2013). Sturgeons, like many physostomous fishes, are unable to secrete air into their gas bladder *via* a physiological mechanism (Berenbrink *et al.,* 2005) and therefore must occasionally gulp air at the surface to fill their gas bladder and achieve neutral buoyancy at a desired depth (Alexander, 1966).

Acipenser oxyrinchus is a large, long-lived, anadromous fish that occurs in the northwest Atlantic Ocean, from Labrador to northern South America (Vladykov & Greeley, 1963; Scott & Scott, 1988) and migrates extensively north and south along the Atlantic coast (Erickson *et al.,* 2011; Dadswell *et al.,* 2016; Taylor *et al.,* 2016). Historically, there were 35 known spawning populations of *A. oxyrinchus* along the east coast of Canada and the U.S.A., but that number may now be closer to 20 (ASSRT, 2007). In Canada, spawning occurs in the St. Lawrence and the Saint John Rivers during June and July (Scott & Scott, 1988). Juveniles spend up to 10 years feeding and growing in their natal estuary before migrating to sea at a size of approximately 80–100 cm fork length (L_F; Bain, 1997; Dadswell, 2006). Juveniles and maturing adults from northern rivers spend 10–15 years or longer at sea, before they return to their natal river to spawn (Wirgin *et al.,* 2015**;** Dadswell *et al.,* 2017). Both juveniles and adults are obligate, benthos feeders (Scott & Scott, 1988; Dadswell, 2006). Mature adult males are 140+ cm L_F, females, 180+ cm L_F (Stewart *et al.,* 2015).

Minas Basin is an important summer aggregation site for *A. oxyrinchus* because of the rich foraging opportunities on the large, intertidal mudflats (McLean *et al.,* 2014; Dadswell *et al.,* 2016). While in Minas Basin, the juveniles and adults feed primarily at high tide over intertidal, sand–silt substrata on tube-dwelling polychaetes (*Clymanella* sp. and *Spiophanes* sp.) and amphipods (*Corophium* sp.; McLean *et al.,* 2013). They enter Minas Basin from the Bay of Fundy during May to June and depart from August to October (Dadswell *et al.,* 2016; Stokesbury *et al.,* 2016). From November to April, they occupy deeper depths in the outer Bay of Fundy or migrate to their natal rivers for spawning (Beardsall *et al.,* 2016; Taylor *et al.,* 2016). The annual Minas Basin feeding aggregation is composed of *c.* 9000 individuals (Dadswell *et al.,* 2016) from the Saint John River, New Brunswick (NB; 61%) and Kennebec River, Maine (ME; 34–36%), with smaller contributions from more southern U.S.A. rivers (Wirgin *et al.,* 2012).

Based on earlier work by Watanabe *et al.* (2008) we hypothesized that buoyancy regulation, by gulping air at the surface into their physostomous gas bladder, was the main reason for the extensive surfacing behaviour exhibited by *A. oxyrinchus* while in Minas Basin. We tested our hypothesis using archived pressure data from externally attached, mini pop-up archival satellite tags (MiniPAT) to determine the characteristics of surfacing events in Minas Basin and the Bay of Fundy. Minas Basin, because of tides that rise and fall at *c.* 2 m h^{-1}, has a unique environment that results in rapidly changing hydrostatic pressure on a fish's gas bladder and we predicted that if surfacing behaviour was related to buoyancy control by gas bladder regulation then surfacing events would be most common during flooding or ebbing tide when water depth is increasing or decreasing at its fastest rate.

MATERIALS AND METHODS

STUDY SITE

Minas Basin (45° 20′ N; 64° 00′ W) is the south-eastern branch of the inner Bay of Fundy (Fig. 1). Minas Passage is a narrow channel, *c.* 5 km wide, 15 km long and up to 150 m deep, that connects Minas Basin to the Bay of Fundy. On each rise and fall of the tide, approximately 14 billion tonnes of seawater flow through Minas Passage attaining current speeds >5 m s^{-1} (Karsten *et al.,* 2013).

Minas Basin is a megatidal embayment, approximately 30 km wide and 75 km long, experiencing semi-diurnal tides with the greatest tidal range in the world. The average tidal range is 13 m but it can surpass 16 m during spring tides (Bousfield & Leim, 1960; Percy, 2001). At low tide, the depth across most of Minas Basin is less than 25 m and an extensive, low-gradient, intertidal zone is exposed, extending from shore an average of 1–2 km (Yeo & Risk, 1981; Percy, 2001). Temperatures during summer reach a maximum of 17–20° C and during winter, a minimum of −1·5° C. Salinity varies from 25 to 28 in the inner reaches of Minas Basin to 30 in Minas Passage (Bousfield & Leim, 1960).

CAPTURE

During 2014, *A. oxyrinchus* taken as by-catch in a commercial, intertidal fishing weir near Bramber, Nova Scotia were sampled and tagged (Fig. 1). Following tagging, fish were released into a recovery pool, approximately 25–50 cm deep, until the tide returned. Fishing was performed under the Department of Fisheries and Oceans Scientific License to Fish #322595. Handling procedures were performed under Acadia University Animal Care Committee protocol #07–11.

MINIPAT DEPLOYMENTS

Six adult *A. oxyrinchus* (165+ cm L_F) were selected for tagging (Table I). Each was measured to the nearest cm, tagged for individual identification with an external Floy FT–1–94 dart tag (www.floytag.com) at the base of the dorsal fin as well as a 12·5 mm passive integrated transponder (PIT) tag (www.biomark.com) on the opposite side. A pelvic-fin clip was taken for genetic analyses. A rough measure of the ectoparasite load was recorded (low, medium, or high), along with the location of any observable wounds. Each was then externally tagged with

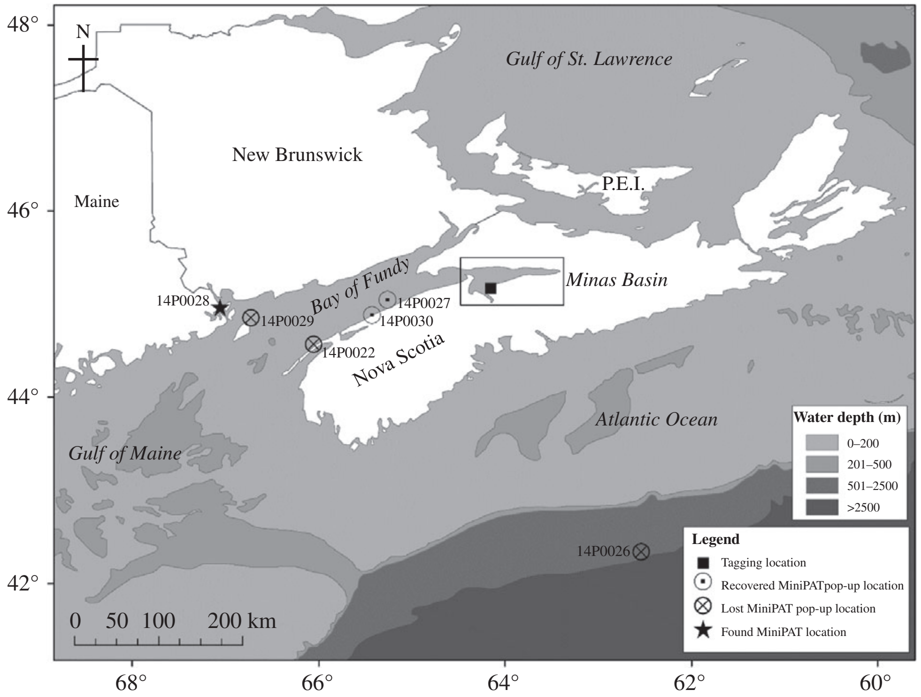

FIG. 1. Location of the *Acipenser oxyrinchus* tagging site in Minas Basin during summer, 2014 and MiniPAT pop-up and recovery locations in the Bay of Fundy and Atlantic Ocean during autumn, 2014. ■, ⊙, ⊗, ★.

a MiniPAT (40 × 115 mm, 53 g; www.wildlifecomputers.com; Table I). Beardsall *et al.* (2013) and McLean *et al.* (2014) have documented the associated high post-release survival rate of acoustically tagged *A. oxyrinchus* in Minas Basin.

MiniPATs gather detailed data on depth (range 0–1700 m, resolution 0·5 m, accuracy ±1% of depth reading), temperature (range −5 to 45° C, resolution 0·05° C, accuracy ±0·1° C) and ambient light level (sensitivity 5×10^{-12} W cm^{-2}) and archive it in the tag's internal memory. MiniPATs were attached externally by drilling a hole, approximately 3–4 mm in diameter, through the ridge of the fourth or fifth dorsal scute anterior to the dorsal fin. One end of a 12 cm

TABLE I. Fork length (L_F), population river of origin, MiniPAT identification number (ID), deployment date, programmed release date, ARGOS transmission start date, days at large and tag recovery status for six *Acipenser oxyrinchus* tagged in Minas Basin during 2014

Fish #	L_F (cm)	River	ID	Deployment date	Programmed release date	Transmission start date	Duration (days)	Status
1	165	Kennebec	14P0022	17 June	2 October	3 October	108	Lost
2	180	Kennebec	14P0026	24 June	8 October	14 November	143	Lost
3	206	Saint John	14P0028	24 June	22 October	na	na	Found
4	168	Saint John	14P0027	1 July	15 October	20 October	111	Recovered
5	172	Saint John	14P0029	1 July	29 October	30 October	121	Lost
6	176	Saint John	14P0030	6 July	5 November	6 November	122	Recovered

na, not available.

piece of 300 lb. test nylon monofilament leader was looped around the release mechanism of the MiniPAT and secured by crimping two silver lock sleeves. The other end was passed through the dorsal scute hole and secured similarly. MiniPATs activate upon immersion in salt water and this was confirmed by blinking lights on the tag.

The six MiniPATs were programmed to release on specified dates, one week apart, from early October to early November, 2014 (Table I). Once on the surface, the tags' GPS coordinates were accessed through the online Advanced Research and Global Observation Satellites (ARGOS) network. When a MiniPAT's most recent location indicated that it may have washed up in the intertidal zone, an attempt to recover it *via* a ground-based search was conducted. For this procedure, a hand-held ARGOS AL−1 platform transmitter terminal (PTT) locator and an AA−1 Yagi antenna (http://www.com-spec.com) were used.

GENETIC ANALYSES

Microsatellite DNA analysis at 11 loci and mitochondrial (mt)DNA) control-region sequence analyses were used to determine the population of origin of each MiniPAT-tagged *A. oxyrinchus*. DNA samples were obtained from fin clips that were preserved in 95% ethanol prior to shipping to New York University School of Medicine, NY. DNA isolations, microsatellite DNA-fragment analyses and mtDNA sequencing were conducted as described in Wirgin *et al.* (2015). The assignment of each sample to a population of origin was conducted using the reference baseline data set described in Stewart *et al.* (2017) and individual based assignment testing implemented in software for genetic stock identification (ONCOR; Kalinowski *et al.,* 2008).

DATA ANALYSES

MiniPAT archival data downloaded from recovered tags were filtered for surfacing events by examining the depth data in Microsoft Excel (www.microsoft.com). Depth changes of 2 m or greater, over a period of 3 s, were examined further to determine if a surfacing event took place. The timestamp for each surfacing event was recorded as the one taken before the fish presumably broke the water surface. All figures and statistical analyses were completed in R 3.2.2 (www.r-project.org).

Some data collected at the beginning of a data set were removed in order to account for the period of time each fish was probably recovering from the tagging event. Recorded depths were relatively constant during the recovery period but became more variable after a period of time indicating active swimming behaviour. For fish 14P0027, the first 10 h of data were removed. For fish 14P0030, recovery was apparently much faster and only the first 4 h of data were removed. Data were also removed at the end of each set, before corrosion of the tag's metal pin began at the time of tag detachment set for 2000:00 UTC on the pop-up date.

To determine tide stage, each surfacing event time stamp was assigned an elevation value (from −8·0 to 8·0) and a speed (from −1·0 to 1·0) based on a tidal model (Karsten *et al.,* 2008). A time stamp assigned a positive elevation value above mid-tide, whereas a negative elevation value occurred below mid-tide. A time stamp assigned a positive speed value occurred during flood tide, whereas a negative speed value occurred during ebb tide. The model was focused on an area off Bramber, Nova Scotia, in the southern bight of Minas Basin, where *A. oxyrinchus* had been captured in the intertidal weir (Fig. 1). Only surfacing events that occurred in Minas Basin, defined as maximum start depth of 40 m, were included**.** Surfacing events occurring from depths >40 m were presumed to be in Minas Passage or the Bay of Fundy.

A surfacing event start depth was defined as the depth at which the fish swam for a constant period, even briefly and after which the fish travelled continuously to the surface. Shallow surfacing events were classified as having a start depth of <10 m, mid-depth surfacing events had a start depth between 10 and 40 m and deep surfacing events had a start depth > 40 m. For each surfacing event, a maximum ascent and descent speed were calculated based on the greatest change in depth (m) exhibited over a period of 3 s. From these, mean ± 1 S.*D.* maximum ascent and descent speeds were calculated for each fish. All maximum ascent and descent speeds occurred when fish were near the surface. These speeds, however, represent minimum maximum speeds because the fish were assumed to be moving in a straight line.

RESULTS

MINIPAT DEPLOYMENTS

The six MiniPATs deployed on adult *A. oxyrinchus* (165–206 cm L_F) in June and July 2014 were at large for a duration of 108 to 143 days (Table I). Five tags reported to ARGOS and provided pop-up locations (Fig. 1). Four MiniPATs popped up in the Bay of Fundy while one tag reported approximately 250 km southeast of Nova Scotia. Two MiniPATs washed up in the Bay of Fundy on the western shore of Nova Scotia and were recovered (Fig. 1). Three MiniPATs were not recovered. The final tag (that did not report to ARGOS satellites) was discovered by a local citizen on a beach in Gleason Cove, near Perry, ME, U.S.A. (44° 58′ 15″ N; 67° 03′ 30″ W) in early September 2015. Regardless of considerable effort made to recover the tag from this individual it has not been returned to us.

PARASITES AND WOUNDS

Five of the tagged *A. oxyrinchus* had low ectoparasite loads, meaning that few parasites were observed. One, fish 14P0027, had a medium infestation and parasites were observed around the head and on the fins. Based on photographs taken of this fish, these parasites were a pisicolid leech. None of our tagged *A. oxyrinchus* had wounds from ectoparasites that have been found in other studies (Munroe *et al.,* 2011). Parasite samples were not taken and therefore species were not formally identified or counted.

GENETIC ANALYSES

The mean accuracy of assignments of baseline specimens to the 11 reference rivers in which they were collected using individual based assignment (IBA) testing was 85·8% (Stewart *et al.,* 2017). For the present study, IBA testing indicated that two of the MiniPAT-tagged *A. oxyrinchus* were genetically identified to be of Kennebec River ME origin and the remaining four fish were of Saint John River NB origin (Table I). Assignment probability for all Saint John River and one of the Kennebec River specimens was 100%. Assignment probability for the remaining Kennebec River specimen was 59% with a 41% probability of secondary assignment to the Saint John River. The two recovered MiniPATs were both deployed on fish of Saint John River origin.

ARCHIVAL DEPTH AND SURFACING

Archival depth data and surfacing events for *A. oxyrinchus* were examined from the two recovered MiniPATs (14P0027 and 14P0030; Table I). Fish 14P0027 spent most of its time (70·9%), from July to October, in depths <10 m and never surpassed a maximum depth of 63·5 m. Fish 14P0030 spread its time across a wider range of depths but still spent 59% of its time at depths <10 m while in Minas Basin. This fish descended deeper, down to a maximum depth of 106 m. Both fish spent little time in mid-range depths, from 20 to 40 m (14P0027) and 30 to 50 m (14P0030). Over the course of the deployment, the mean ± S.D. depth for 14P0027 was 13·63 ± 17·35 m (range = 0·5–63·5 m), while the mean ± S.D. depth for 14P0030 was 51·74 ± 29·89 m (range = 0·5–106 m), which were significantly different (two sample *t*-test, $t = -2018{\cdot}3$, $P < 0{\cdot}001$, d.f. = 5 782 700).

TABLE II. MiniPAT identification number (ID), deployment period, total and monthly counts of surfacing events in Minas Basin, Minas Passage and the Bay of Fundy during July to October 2014 from archival data for two recovered MiniPAT tags deployed on *Acipenser oxyrinchus* in Minas Basin

			Surfacing events by month			
ID	Deployment (days)	Total events	July	August	September	October
14P0027	111	410	131	174	99	6
14P0030	122	248	131	97	9	11

Overall, fish 14P0027 surfaced more often than fish 14P0030 (Table II). Fish 14P0027 surfaced most often from July to September and least during October. Fish 14P0030 surfaced most often in July and August and least during September and October. The mean ± S.D. number of surfacing events a day for 14P0027 was $3{\cdot}87 \pm 2{\cdot}38$ (range = 0–10) and for 14P0030, $2{\cdot}03 \pm 2{\cdot}82$ (range = 0–12), which were significantly different (two sample *t*-test, $t = 5{\cdot}33$, $P < 0{\cdot}001$, d.f. = 225·82).

The surfacing frequency declined substantially for fish 14P0027 on 28 September 2014 and for fish 14P0030 on 15 August 2014 (Table II). The sudden drop in the frequency of surfacing events for each fish was related to departure from Minas Basin, as confirmed with swim depth data.

Surfacing frequency of *A. oxyrinchus* was not uniformly distributed over a 24 h day for both fish 14P0027 (Rao's spacing test, $U = 338{\cdot}93$, $P < 0{\cdot}001$) and fish 14P0030 (Rao's spacing test, $U = 325{\cdot}16$, $P < 0{\cdot}001$). For fish 14P0027, the greatest number of surfacing events (Fig. 2) occurred between 2300 and 0000 hours ($n = 37$), while the fewest occurred between 1200 and 1300 hours ($n = 10$). For fish 14P0030, the greatest number of surfacing events (Fig. 2) occurred between 0200 and 0300 hours ($n = 20$), while the fewest occurred between 0900 and 1000 hours and 1200 and 1300 hours ($n = 3$ each).

Inside Minas Basin the phase of the tide had the greatest influence on the frequency of *A. oxyrinchus* surfacing behaviour. For both fish, more surfacing events occurred on the flood tide (70·3%) than on the ebb tide (29·7%) and more surfacing events occurred above mid-tide (61·2%) than below mid-tide (38·8%; Fig. 3). Nearly half of all surfacing events (49·5%) by both fish occurred on the flood tide when it was above mid-tide. The least number of surfacing events (11·8%) occurred on the ebb tide when it was above mid-tide. The number of surfacing events below mid-tide on the flood (20·8%) and ebb (17·9%) were similar. There was a significant positive association (more surfacing events than expected) for the flood tide, above-mid tide and for the ebb tide, below mid-tide (χ^2-test, $\chi^2 = 49{\cdot}92$, $P < 0{\cdot}001$) and there was a significant negative association (fewer surfacing events than expected) for the flood tide, below mid-tide and for the ebb tide, above mid-tide (χ^2-test, $\chi^2 = 49{\cdot}92$, $P < 0{\cdot}001$).

Both fish 14P0027 and fish 14P0030 surfaced from shallow, mid-range and deep depths. There were far more surfacing events from shallow (0–10 m) and mid-range depths (10–40 m) for each fish than from deeper depths (>40 m). Most surfacing events for fish 14P0027 (90·5%; Fig. 4(a)) and fish 14P0030 (59·7%; Fig. 4(b)) began at a start depth < 10 m. Fish 14P0030 began surfacing events at a wider range of start depths

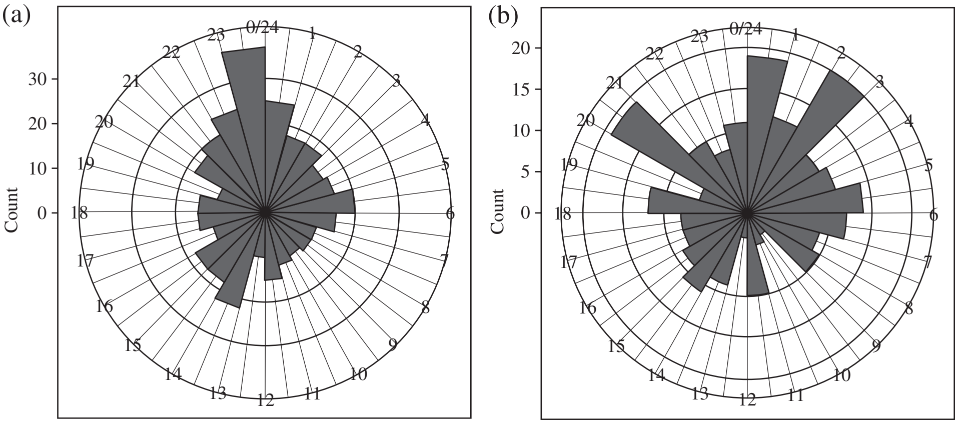

FIG. 2. Frequency of all surfacing events in Minas Basin and the Bay of Fundy hour^{-1} of the day from July to October 2014 for *Acipenser oxyrinchus* (a) 14P0027 and (b) 14P0030.

than fish 14P0027 and its maximum start depth (89·5 m; Fig. 4(b)) was nearly double that of 14P0027 (46·5 m; Fig. 4(a)). The mean ± S.D. start depth for fish 14P0027 was 6·15 ± 5·79 m (range = 1·0–46·5 m), whereas the mean ± S.D. start depth for fish 14P0030 was 15·77 ± 18·93 m (range = 2·0–89·5 m), which were significantly different (two sample *t*-test, $t = -7.78$, $P < 0.001$, d.f. = 275·2).

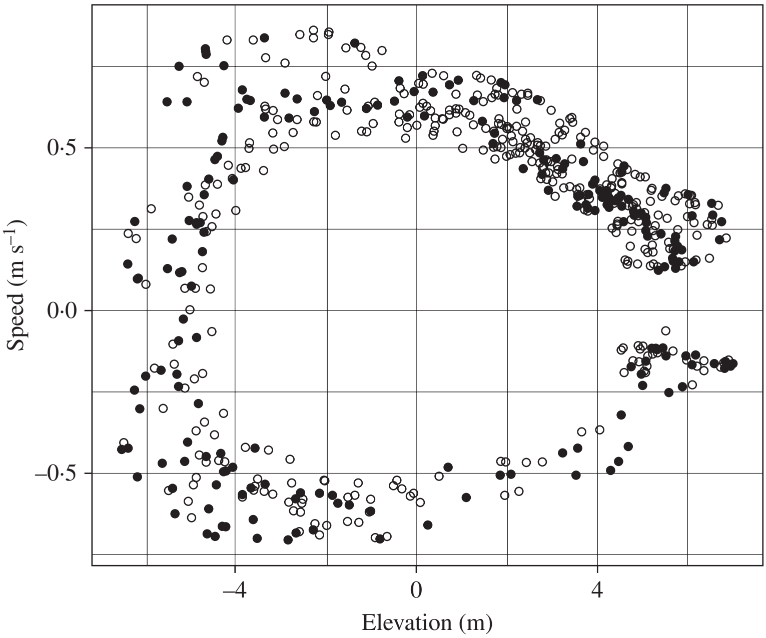

FIG. 3. Surfacing events in depths <40 m (Minas Basin; $n = 596$) by tidal elevation and current speed for *Acipenser oxyrinchus* tagged with MiniPATs 14P0027 (○) and 14P0030 (●).

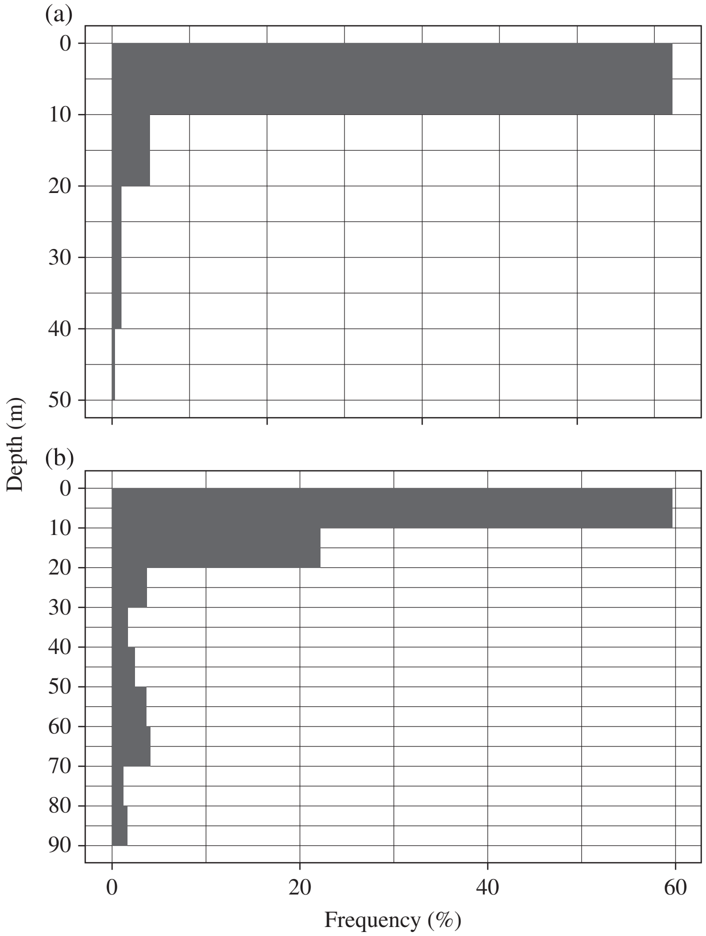

FIG. 4. Frequency of surfacing event start depths in Minas Basin, Minas Passage and the Bay of Fundy for *Acipenser oxyrinchus* tagged with (a) MiniPAT 14P0027 and (b) MiniPAT 14P0030.

Both fish 14P0027 and fish 14P0030 exhibited swimming speeds between 0·0 and $0{\cdot}5\,\mathrm{m\,s^{-1}} > 99\%$ of the time but both exhibited a faster maximum speed on the ascent into a surfacing event than on the descent after surfacing. Fish 14P0030 exhibited faster maximum ascent and descent speeds than fish 14P0027. The mean ± S.D. maximum ascent speed for fish 14P0027 was $1{\cdot}11 \pm 0{\cdot}39\,\mathrm{m\,s^{-1}}$ (range = $0{\cdot}50$–$3{\cdot}17\,\mathrm{m\,s^{-1}}$), while the mean ± S.D. maximum descent speed was $0{\cdot}87 \pm 0{\cdot}30\,\mathrm{m\,s^{-1}}$ (range = $0{\cdot}17$–$2{\cdot}50\,\mathrm{m\,s^{-1}}$). The mean S.D. maximum ascent speed for fish 14P0030 was $1{\cdot}33 \pm 0{\cdot}61\,\mathrm{m\,s^{-1}}$ (range = $0{\cdot}50$–$4{\cdot}17\,\mathrm{m\,s^{-1}}$), while the mean ± S.D. maximum descent speed was $1{\cdot}08 \pm 0{\cdot}67\,\mathrm{m\,s^{-1}}$ (range = $0{\cdot}33$–$3{\cdot}17\,\mathrm{m\,s^{-1}}$). The maximum ascent speeds for both fish most often fell between 1·0 and $1{\cdot}5\,\mathrm{m\,s^{-1}}$, while the maximum descent speeds most often fell between 0·5 and $1{\cdot}0\,\mathrm{m\,s^{-1}}$.The ascent and descend speeds for the two fish were, however, significantly different (ascent, two sample *t*-test, $t = -5{\cdot}18$, $P < 0{\cdot}001$, d.f. = 366·44; descent, two sample *t*-test, $t = -4{\cdot}64$, $P < 0{\cdot}001$, d.f. = 309·35).

DISCUSSION

Every year during the annual summer feeding aggregation of *A. oxyrinchus* in Minas Basin, inner Bay of Fundy (Dadswell *et al.,* 2016) large numbers of these fish are observed breaching daily. The occurrence and intensity of the behaviour is so pronounced that people concentrate at good sites to watch. Such predictable, repetitive behaviour appeared to us to be linked to a necessary, daily function of their biology such as feeding over the intertidal flats at high tide (McLean *et al.,* 2013, 2014) and under physiological control. Maintaining buoyancy over soft substrata to enhance feeding success seemed a logical postulation for our study.

Four of five MiniPATs sent their first transmission to ARGOS satellites from locations along the coast in the Bay of Fundy during October and November. Similar release locations were also obtained during autumn in a previous study on *A. oxyrinchus* tagged in Minas Basin with pop-up satellite tags (Beardsall *et al.,* 2016). Data from the two studies confirm that *A. oxyrinchus* of both Saint John River and Kennebec River genetic ancestry were utilizing the Bay of Fundy during autumn when they moved into their overwintering phase at deeper depths.

All ARGOS locations received from MiniPAT 14P0026 were off the continental shelf. There are currently no records of *A. oxyrinchus* occupying habitats beyond the continental shelf, but they are known to occur in offshore waters (Vladykov & Greeley, 1963; Scott & Scott, 1988). Beardsall *et al.* (2016) also had a pop-up satellite tag from an *A. oxyrinchus* report in the Atlantic Ocean, off the continental shelf. As the first transmission from MiniPAT 14P0026 occurred over one month after its scheduled pop-up date, it may have released or broke free in the Bay of Fundy but drifted offshore with ocean currents before it transmitted a signal to ARGOS.

MiniPAT 14P0028 did not transmit any information to ARGOS but was found on a beach in Maine in early September 2015. Without the archival MiniPAT data, we are unsure whether the host fish survived initial tagging in Minas Basin.

Acipenser oxyrinchus from which MiniPATs were recovered spent most of their time at depths <20 m and we attribute this to time spent in Minas Basin, foraging over the intertidal flats. This pattern was also observed in *A. oxyrinchus* archival depth data collected by Beardsall *et al.* (2016). There was, however, clear variability in individual depth preference, since fish 14P0030 spent more time at greater depths than fish 14P0027. A similar difference in depth preference between two *A. oxyrinchus* tagged by Beardsall *et al.* (2016) was also observed but during December and January.

Acipenser oxyrinchus surfaced up to 10 or 12 times a day while in Minas Basin. Time of day and therefore light levels appeared to have little influence on surfacing frequency since the number of surfacing events were nearly equal during night and day and during dawn and dusk. Both fish, however, exhibited a maximum number of surfacing events during 1 h at night and a minimum number of surfacing events between 1200 and 1300. Sulak *et al.* (2002) observed a similar high surfacing rate at night and a lower rate during midday for *A. oxyrinchus desotoi*. It is unclear whether this is simply a coincidence or whether there may be another explanation for this behaviour. Sulak *et al.* (2002) also observed a peak in surfacing events at dawn and to a lesser degree at dusk, but similar behaviour was not observed during our study.

Significantly more surfacing events occurred on the flood tide than on the ebb tide for both tagged fish. We propose that this observation relates to *A. oxyrinchus* buoyancy regulation. In Minas Basin, during the flood and ebb tide, water depth increases or declines rapidly (*c.* 2 m h^{-1}) and there would be a corresponding rapid increase or decrease in pressure on the gas bladder of a fish remaining near the bottom to feed. The proportional increase in pressure at depth is the greatest in the upper 10 m of the water column (50%; Boyle's Law), which means a fish would need to surface relatively often to gulp air and re-inflate its gas bladder in order to maintain neutral buoyancy just above the substratum. Maintaining neutral buoyancy would be particularly crucial for *A. oxyrinchus* moving over the intertidal zone to feed (McLean *et al.,* 2013, 2014), since they would not want to disturb potential prey by resting on the bottom. Pearson *et al.* (2007) observed *A. oxyrinchus* feeding excavations, formed by the mouth and occasionally fin traces on the mudflats at Mary's Point, NB, but never an outline of the fish body. It is probable that *A. oxyrinchus* maintain neutral buoyancy just above the surface of the substratum when feeding. Conversely, on the ebb tide, as the water level falls, the pressure on the gas bladder would decrease and *A. oxyrinchus* could release air from its gas bladder *via* the pneumatic duct to regain neutral buoyancy without surfacing as often. *Acipenser fluvescens* have been observed releasing air bubbles following porpoising behaviour (Bruch & Binkowski, 2002), suggesting they were also using this mechanism to regulate buoyancy.

In addition to maintaining neutral buoyancy, *A. oxyrinchus* may surface more often on the flood rather than the ebb tide to reduce their risk of being stranded in the intertidal zone. In the inner Bay of Fundy, where shallow bathymetric gradients and fast moving tides occur, fish stranding events are common, particularly during spring tides (Bleakney, 1972). In 2014, eleven *A. oxyrinchus* were stranded on the intertidal zone of Scot's Bay, Nova Scotia and died (Stewart *et al.,* 2017). On the flood tide, particularly above mid-tide, *A. oxyrinchus* could surface with the greatest ease and least risk of stranding. On the ebb-tide, frequent surfacing would be unnecessary because of decreasing pressure on the gas bladder which might mean the fish paid less attention to depth, causing stranding.

When *A. oxyrinchus* migrated to deeper depths in Minas Passage and the Bay of Fundy, the frequency of surfacing events dropped off substantially. In Minas Basin, surfacing frequency probably occurred more often due to the pressure changes fish experienced from the rapidly changing tide depth and the necessity to remain neutrally buoyant above the intertidal substratum for feeding. During off-shore migration, we propose that *A. oxyrinchus* surface less often because they may no longer be feeding and therefore would no longer need to maintain neutral buoyancy above a very specific depth. Also, changing depth when deeper in the water column results in proportionally less pressure change with greater depth (Boyle's Law) and less necessity to change gas bladder volume. *Acipenser oxyrinchus* would only need to add air to their gas bladder periodically upon moving into greater depths. Taylor *et al.* (2016) noted a low frequency of rapid vertical ascents (maximum of 8 per month), which was probably surfacing behaviour, while their archival tagged *A. oxyrinchus* were at greater depths in the Bay of Fundy during November to March while Erickson & Hightower (2007) observed similar behaviour for *A. medirostris* migrating along the west coast of North America.

MiniPAT-tagged *A. oxyrinchus* surfaced from shallow, mid-range and deep depths, demonstrating that surfacing behaviour occurs in a variety of environments. The large proportion of surfacing events beginning at very shallow depths (<5 m), particularly for fish 14P0027, may indicate more of a porpoising behaviour. This was corroborated by a high proportion of relatively low maximum ascent and descent speeds in this depth range ($<1{\cdot}5$ m s^{-1}). *Acipenser fluvescens* have been reported to exhibit porpoising behaviour while swimming upstream during the spawning season (Bruch & Binkowski, 2002). During porpoising, *A. fluvescens* surfaced quickly and broke the water surface only with their heads. Occasionally, they breached completely (Bruch & Binkowski, 2002). We suspect that regardless of the height attained out of the water, the purpose of a surfacing event is probably the same: to quickly add air to the gas bladder to regain buoyancy control.

Breaching behaviour, where a fish partially or completely clears the water, may serve an additional function such as ridding themselves of ectoparasites or unwanted attached commensals. This behaviour has been proposed for bull sharks *Carcharhinus leucas* (Valenciennes 1839) (Curtis & Macesic, 2011), blacktip sharks *Carcharhinus limbatus* (Valenciennes 1839) (Ritter & Brunnschweiler, 2003) and Atlantic salmon *Salmo salar* L. 1758 (Furevik *et al.,* 1988; Stone *et al.,* 2002). *Acipenser oxyrinchus* in Minas Basin are commonly infested with ectoparasites (Munroe *et al.,* 2011), the most prevalent being *Caligus elongatus* (Copepoda; 85%), *Calliobdella vivida* (Hirudinea; 81%) and *Dichelesthium oblongum* (Copepoda; 31%). Fast *et al.* (2009) found lesions associated with *D. oblongum* on *A. oxyrinchus* sampled in the New York Bight, U.S.A. and this was also observed in Minas Basin (Munroe *et al.,* 2011; L. Logan-Chesney, pers. obs.). Long-term infestations of copepod ectoparasites may trigger a reduction in the osmotic capability of *A. oxyrinchus*, directly through tissue damage and indirectly through elevated stress levels (Fast *et al.,* 2009). Irritation caused by *D. oblongum* in particular may prompt *A. oxyrinchus* to breach in an attempt to free themselves of this parasite. Since none of our tagged fish had an infestation of this species or any of the wounds that it causes, we concluded that observed surfacing behaviour of our fish was not related to this factor.

Acipenser oxyrinchus attained relatively high maximum speeds during the ascent into a surfacing event (up to $4{\cdot}17$ m s^{-1}) and on the descent, post-surfacing (up to $3{\cdot}17$ m s^{-1}). These ascent speeds were slightly higher than the maximum ascent speed of 3 m s^{-1} observed for *A. sinensis* (Watanabe *et al.,* 2008). For both our tagged fish, maximum observed ascent speeds were greater than maximum descent speeds. *Acipenser oxyrinchus* are heavy, slow-moving fish and ascending into a breach would probably require its fastest (or nearly fastest) swimming speeds in order to propel itself out of the water. During descent, high speeds attained may simply be the result of remaining kinetic energy, although *A. oxyrinchus* could also be actively swimming to counteract the positive buoyancy from an inflated gas bladder.

Surfacing was a common behaviour for *A. oxyrinchus* occurring in Minas Basin during summer. The most significant factor influencing surfacing frequency was the tidal cycle, with the greatest number of surfacing events taking place during flood tide, above mid-tide. We agree with Watanabe *et al.* (2008) that buoyancy control, by gulping air at the surface, is probably the main purpose for surfacing behaviour in Acipenseridae. Breaching behaviour of *A. oxyrinchus* may serve additional purposes (Sulak *et al.,* 2002), but these possibilities will require further investigation with more sophisticated experimental methods.

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