Journal of FISH BIOLOGY

Journal of Fish Biology (2017) **91**, 1623–1641
doi:10.1111/jfb.13476, available online at wileyonlinelibrary.com

A field test of the use of pop-off data storage tags in freshwater fishes

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(Received 13 April 2017, Accepted 24 August 2017)

In the present study, pop-off data storage tags (pDST) without any transmitting capabilities were attached to 118 adult salmonids in a 19 000 km^2 freshwater system (Lake Ontario). The 9·3 cm long cylindrical tags were externally attached to fishes using a backpack-style harness, set to record pressure (dBar ≈ depth in m) and temperature every 70 s (and at some key times, every 5 s) and programmed to release from the harness and float to the surface after *c*. 1 year. Recapture of the bright-orange tags for data retrieval relied on members of the public finding tags on shore, or on anglers capturing fishes with tags attached and using the contact information displayed on each tag to mail tags to the research team in exchange for a monetary reward. Thirty-seven tags were found and returned from the 118 released (31%), while 26 of the 118 tags (22%) remained scheduled to pop-off in summer 2017. Of the 37 tags returned, 23 were from wild-caught fishes (out of 88 wild-caught and tagged fishes; 26%) and yielded useful data whereas 14 were from hatchery-reared fishes that were opportunistically tagged and appear to have been unable to acclimate to life in the wild and died days to weeks after release. The field study described here thus demonstrated that pDSTs can be a viable option for collecting large amounts of high-resolution depth and temperature data for salmonids in freshwater systems. Technical challenges, limitations and unknowns related to the use of pDSTs with freshwater fishes are discussed. In addition, pDSTs are compared with alternate electronic tagging technologies and assessed for their potential as a more widespread tool in research on freshwater fishes.

Key words: biologger; Chinook salmon; lake trout; migration; telemetry; thermoregulation.

INTRODUCTION

Depth and temperature are two important dimensions of habitat and behaviour in fishes (Magnuson *et al.*, 1979; Block *et al.*, 2001; Sims *et al.*, 2006; Gutowsky *et al.*, 2013). The central role of temperature in the energetics and fitness of fishes (Brett, 1971; Magnuson *et al.*, 1979) means that a species' behavioural preference for a temperature (or range of temperatures) can be used to define realized thermal niche (Konecki *et al.*, 1995; Huff *et al.*, 2005), providing important context to studies that

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aim to characterize thermal performance curves in laboratory experiments (Forseth *et al.*, 2009; Clark *et al.*, 2013). In many aquatic systems, temperature is also related to depth (*i.e.* distance from the surface) because of thermal stratification. Quantifying species-specific patterns in depth can therefore contribute to a better understanding of behavioural thermoregulation (Azumaya & Ishida, 2005; Sims *et al.*, 2006), trophic and foraging ecology (*i.e.* vertical niche overlap among species or size classes, Stewart & Bowlby, 2009) and inform fisheries assessment and management (Bergstedt *et al.*, 2016).

Fishing has been by far the most commonly used method to assess species-specific depth and temperature distributions (*e.g.* using gillnets or trawls; Olson *et al.*, 1988; Elrod *et al.*, 1996). Recreational anglers can also be surveyed for the depths and temperatures at which they caught fishes (Stewart & Bowlby, 2009). Electronic tags, which include transmitters and data loggers, provide an alternative method for assessing the habitat preferences of aquatic animals (Hussey *et al.*, 2015) and have the potential to provide useful new insight into the habitat use and behaviours of fishes. For example, acoustic telemetry can be used by releasing fishes with temperature or depth-sensing transmitters and either tracking them manually by boat (Ogura & Ishida, 1992; Blanchfield *et al.*, 2005) or by positioning underwater receivers (hydrophones) in areas of interest (Gutowsky *et al.*, 2013). The drawback of this approach is that the fish have to be within the detection range of a receiver for any data measured by the tag to be recorded, which can limit the amount of data generated for each fish tagged and spatially bias the sample, especially in large systems. Pop-up satellite archival tags (PSAT) enable depth and temperature data to be uploaded to the researcher *via* satellite link after programmed pop-off from the animal and, in the marine environment, can also provide a limited amount of coarse positional information (Sims *et al.*, 2009). PSATs are costly, satellite transmission and the quantity of data are often impeded by environmental factors (Fisk *et al.*, 2012) and the tags have to be physically retrieved to obtain high-resolution depth and temperature data because only a binned subset of archived data are transmitted *via* satellite (Thorstad *et al.*, 2013). Another option is the use of non-transmitting data storage tags that are implanted in or affixed to animals such that the animal must physically be recaptured in order to obtain any data; these include depth and temperature loggers (Bergstedt *et al.*, 2016), heart rate loggers (Clark *et al.*, 2009) and accelerometer loggers (Broell *et al.*, 2016), among others.

In many systems, relying on fisheries recaptures is unlikely to yield high numbers of returned data loggers; pop-off data storage tags (pDSTs, without any transmitting functions) may be a useful alternative in such cases. pDSTs are, like PSATs, positively buoyant tags that can be externally attached to aquatic animals and programmed to release after a given date and float to the surface. The release mechanism works by running electric current through a small metal loop that links the tag to the animal; the electric current causes the metal to erode and break. Traditionally, these release mechanisms have only been available for use in the marine environment because of the corrosive properties of salt water (as with PSATs). A data storage tag timed-release mechanism that works in fresh water, however, was recently made available (Cefas, 2015; Cefas Technology; www.cefastechnology.co.uk), although the release unit takes, on average, 2 weeks to erode the metal link rather than the *c.* 30 min it takes the same unit to release in salt water based on laboratory tests by the manufacturer.

pDSTs that record depth and temperature have yet to be used in fresh water, but could be a useful tool for research on freshwater fishes, particularly in systems where some of the alternative methods of obtaining the same information (described above) are not tractable. For example, lake systems with large surrounding human populations (higher likelihood of tags being found) could be conducive to pDSTs that rely on members of the public finding pop-off tags on the surface or on the shore and returning them to the researcher in exchange for a reward. To test the potential use of pDSTs in such a system, non-transmitting pDSTs were attached to salmonids in Lake Ontario (Canada and U.S.A.) over a 3 year period and programmed to release from the fishes and float to the surface 1 year after tag attachment. Members of the public were subsequently relied upon to find and return the tags, in exchange for a monetary reward, so that the tags could be downloaded. The goal of this paper is to report on and evaluate the success of this approach and in doing so provide recommendations to researchers considering using pDSTs in fresh water. First, the tag specifications, along with methods of capture and tag attachment, are described. Next, a report on the success rate of the tag recapture–return–reward programme is given, along with a sample of the resultant data. Finally, the technical challenges and limitations of the approach and the potential for more widespread use are discussed, along with a critical comparison with other electronic tagging technologies.

MATERIALS AND METHODS

DUMMY-TAG RECAPTURE PILOT STUDY

Prior to conducting a full-scale study on live fishes, a small-scale pilot study was carried out to assess the likelihood that popped-off (floating) tags would be found and returned. A total of 100 floating dummy tags were dropped into Lake Ontario at locations *c*. 12–16 km offshore on the Canadian side of the lake (Fig. 1). The dummy tags, made to resemble two different-sized pDSTs (5 and 10 cm long), were built using polyvinyl chloride pipe filled with high-density foam and then coated in either bright orange or pink marine paint along with the attachment of information labels (Fig. 2). The information labels showed the name and contact information for the project lead (A.T.F.), a tag serial number, the name of the research institution (University of Windsor) and '$20 reward'. The dummy tags (25 each of the four colour × size combinations) were dropped into the lake on 5 August 2013 between 0900 and 1100 h at regular intervals along a 4·8 km transect (Fig. 1). Given that the dummy tags recorded no data, members of the public who found tags were not required to return the tags by mail, but were asked to provide the date and location where they found their tag in exchange for a $20 reward per tag.

FISH CAPTURE AND TAGGING

All fish capture, handling and tagging techniques were separately approved by the University of Windsor Animal Care Committee and by the Ontario Ministry of Natural Resources and Forestry Animal Care Committee in accordance with guidelines provided by the Canadian Council on Animal Care. Three Lake Ontario salmonids were targeted using standard recreational angling techniques: Chinook salmon *Oncorhynchus tshawytscha* (Walbaum 1792), lake trout *Salvelinus namaycush* (Walbaum 1792) and Atlantic salmon *Salmo salar* L. 1758. Some brown trout *Salmo trutta* L. 1758 and rainbow trout *Oncorhynchus mykiss* (Walbaum 1792) that were caught incidentally were also tagged in order to ensure all pDSTs were released within the planned timeframe for the study (Table I). Fishing took place during the spring (April and May) and late summer (September) in 2014 and 2015 and in spring 2016, to avoid peak summer water temperatures and because catch for target species was expected to be highest during these periods based on accounts from charter fishing-boat operators. Fishing in September was generally focused offshore and away from river mouths in order to avoid intercepting and tagging fully mature *O. tshawytscha* that were about to spawn in tributaries. Fishing occurred out of two

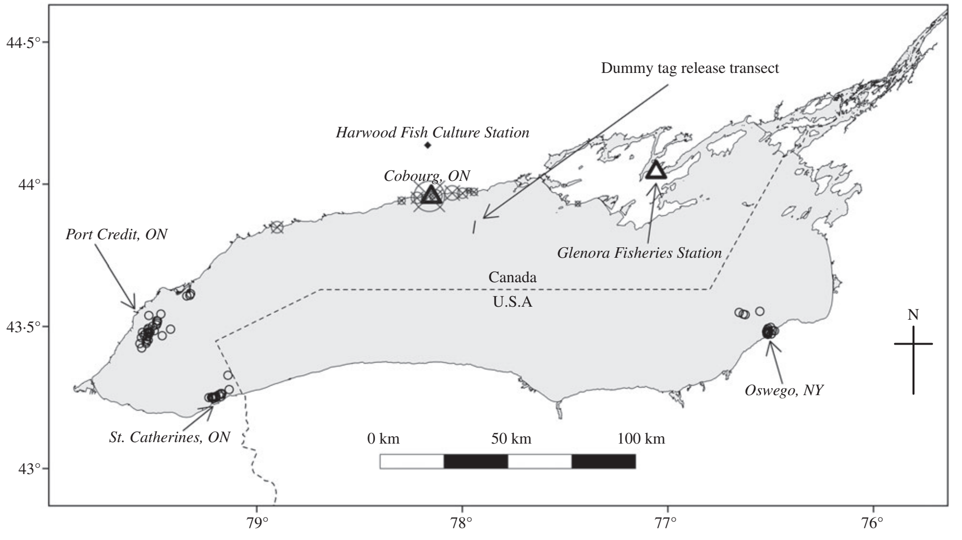

Fig. 1. Map of the study area, showing the locations from which pop-up data-storage tag (pDST)-tagged fishes were released (all species and years: $n = 88$ wild-caught fishes, $n = 30$ among the two hatchery release points, △), the locations of release for the dummy-tag recovery–reporting experiment and the three ports from which fishing took place for tagging of wild-caught fish (Port Credit, Oswego, St Catherine's). The symbols for dummy-tag recoveries (⊗) is proportional to the number of tags: largest symbol = 35 tags, smallest = 1 (locations are approximate). ○, Wild-caught fish capture–release positions.

ports in the western basin of the lake (Port Credit, Mississauga, ON, Canada and St. Catherines, ON, Canada) and one in the eastern end of the lake (Oswego, NY, U.S.A.; Fig. 1). Fishes were caught (locations in Fig. 1) from a boat by trolling at a range of depths (using downriggers that kept lures at a controlled depth) and using a variety of lure types that are typical to salmonid trolling in Lake Ontario, which were equipped with size 2 barbed treble hooks. When fishes were hooked, they were immediately reeled in, which took 1–7 min (median = 3 min), at which point they were landed with a standard (knotted) landing net, de-hooked (5–40 s) and transferred to a water-filled trough for tagging. The trough (Fig. 3) was 86 cm long × 31 cm wide × 15 cm deep, filled with soft foam cut out such that the fish would fit snugly within while allowing for gill movement and for water flow around the head and gills. The tagging trough was continuously supplied by fresh lake water *via* a hose positioned at the front of the trough (towards the fish's mouth). Fishes freely ventilated while in the trough and were exhausted enough from the angling event that they rarely struggled during tagging. Only fishes ≥40 cm fork length (L_F) were tagged (Table I; lengths of each individual in Supporting Information Table SI).

Once in the trough, a pDST was attached to each fish using a custom-designed plastic harness (Fig. 3) similar to the harnesses previously used to attach PSATs to *S. salar* (Lacroix, 2013; Hedger *et al.*, 2017) and European eel *Anguilla anguilla* (L. 1758) (Økland *et al.*, 2013). First, a *c.* 2 mm incision was made below the dorsal fin using a #11 scalpel blade as an entry point for a hollow 11 gauge (3 mm outer diameter) stainless-steel needle. The needle was then inserted through the dorsal musculature, exiting in the same location on the opposite side of the fish. A *c*·10 cm long section of round, clear, *c.* 135 kg (300 lb) monofilament fishing line (2 mm outer diameter) threaded with a plastic washer (1 mm thick, 6 mm outer diameter) and a custom-made plastic bracket [Fig. 3(e)] was then inserted through the dorsal musculature of the fish *via* the sharp end of the hollow needle. The end of the monofilament on the outside of the bracket was pre-crimped [Fig. 3(e)] with an extra piece of monofilament using a stainless steel crimp (designed for crimping 16 mm wire). The needle was removed and the unsecured end of the monofilament (on the proximate side of the fish) was secured to the fish in the same way [plastic washer, bracket and metal crimp; Fig. 3(b)]. A second incision was then made, 3 cm posterior to

FIG. 2. Photo of the two sizes and colours of dummy tags used for the 2013 release experiment that preceded tagging fishes using real pop-up data-storage tags (pDST). Top, pink 5 cm dummy tag; middle, orange 10 cm dummy tag; bottom, orange pDST tag that was found and returned after pop-up.

the first incision, through which the hollow-point needle was used to thread the monofilament attached to the pDST [Fig. 3(c)]. The monofilament was pre-threaded through the metal loop in the timed-release unit (TRU) end of the tag and secured using a pre-threaded stainless steel crimp [Fig. 3(d)]. The surgical tools were wiped clean and sterilized with 95% ethanol between fishes and the tip of the hollow-point needle was kept sharp using a sharpening stone. The harness was secured to the fish with extra space on either side so that the fish could grow without creating extreme pressure against the harness [Fig. 3(d)]. In the first year of tagging (2014, $n = 22$ fishes), stainless steel brackets were used for the harness; the switch was subsequently made in 2015 to plastic to ensure the entire tag–harness complex was positively buoyant (so that it would reach the surface in the event that the entire harness–tag came free of the fish). Simultaneous to the attachment of the tag, a *c*. 0·25*g* clip of tissue was removed from the tip of the dorsal fin, which was stored in RNAlater (Qiagen; www.qiagen.com) and kept on ice for later analyses

TABLE I. Summary of numbers and sizes of fishes tagged for each species across the duration of the study of pop-up data storage tags, separated by wild-caught and hatchery-reared fishes. Details for each individual fish are available in Supporting Information Table SI

Species	Number tagged	L_F at time of tagging (cm, mean ± S.D.)	Number of tags recovered
Wild-caught fishes			
Salvelinus namaycush	40	66 ± 9	7
Oncorhynchus tshawytscha	32	70 ± 15	10
Salmo salar	1	47	0
Oncorhynchus mykiss	10	63 ± 8	4
Salmo trutta	5	53 ± 8	2
Hatchery-reared fishes			
Salvelinus namaycush	10	53 ± 4	4
Salmo salar	20	52 ± 9	10

L_F, fork length.

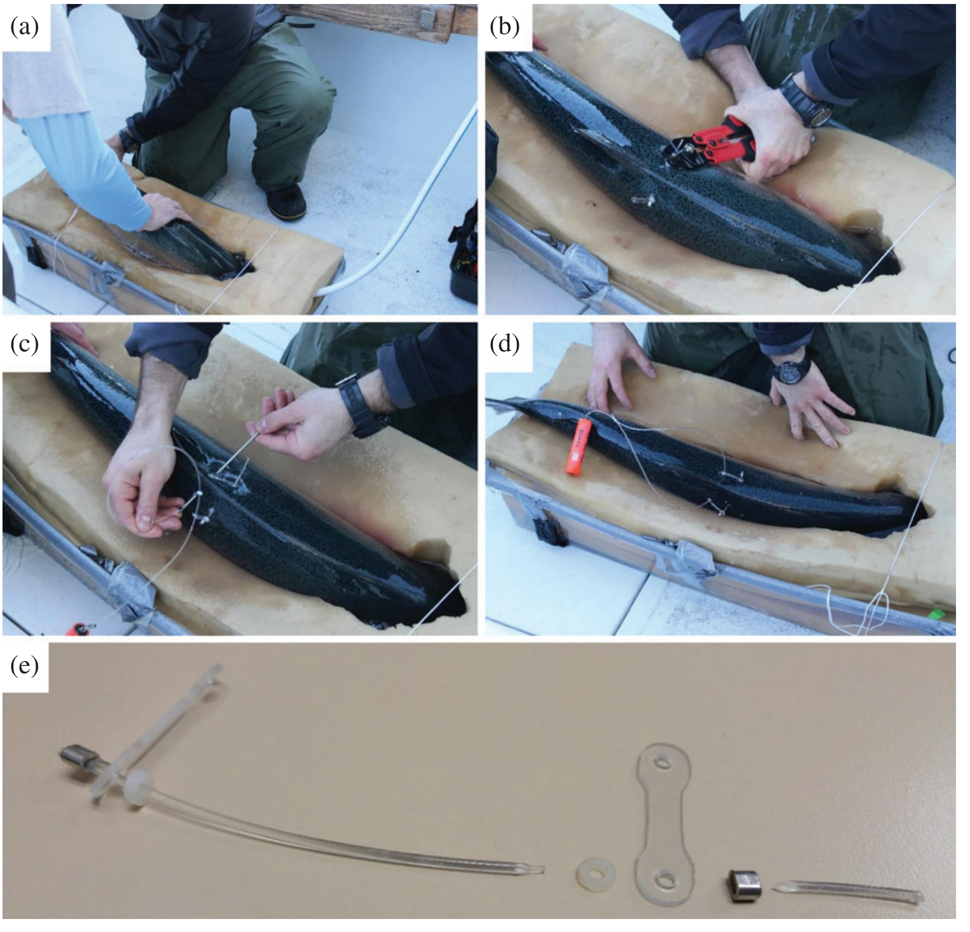

Fig. 3. Photographs of a *Oncorhynchus tshawytscha* undergoing attachment of a pop-up data storage tags (pDST) following capture by angling in Lake Ontario: (a) fish in restraining cradle showing freshwater supply line on right; (b) inserting hollow needle through which to thread ties; (c) ties ready for attaching the pDST; (d) the pDST attached to the harness, ready for release; (e) the parts used for the anterior end of the tag harness.

(data not presented here). The fish was measured (L_F, nearest cm) before release, which occurred 4 min 12 s (median) after the fish was brought on board (range, 2 min 32 s–7 min). A list of all the fishes tagged and released for this study (including dates, locations, species, sizes, *etc*.) is available in Supporting Information Table SI.

Anaesthesia was not used for tagging wild fishes in this study for a number of reasons. In a practical sense, anaesthesia was not required to immobilize the fish for tag attachment because fishes were captured by angling and as a result, were physically exhausted when brought on board. As noted above, fishes remained very still during tagging; instances of fish struggling while tagging occurred were rare and fishes usually did not react to being pierced with the hollow-point needle. A further consideration was the desire to minimize the time required for behavioural recovery and to maximize the survival probability of fishes after release; post-release mortality can occur in salmonids after angling if the fish experiences sufficient physiological disturbance (Ferguson & Tufts, 1992; Donaldson *et al.*, 2011). Anaesthesia (*e.g.* using MS-222) causes ventilation (*i.e.* opercular movement) to become slow, an effect that would probably impair the ability of the fish to repay the oxygen debt incurred during the exhaustive exercise and (brief) air exposure involved in its capture (Clark *et al.*, 2012). An anaesthesia-induced reduction in oxygen delivery to tissues might be particularly detrimental during the moments after cessation of the exhaustion stressor (angling), which is when tagging occurred. Moreover, extended holding of the fishes on board for recovery from angling, onset of anaesthesia and post-tagging recovery from anaesthesia would add substantial confinement stress (Portz *et al.*, 2006). Indeed, there is evidence that holding fishes for an extended recovery period after angling (even if well intended) can increase post-release mortality in salmonids (Donaldson *et al.*, 2011, 2013).

TAG SPECIFICATIONS

The pDSTs used in this study were G5 long-life 20 bar depth–temperature tags with a TRU inside a combination float (Cefas Technology) and were cylindrical, 9·3 cm long, 2·2 cm in diameter (Fig. 2) and weighed 30*g* in air (but were positively buoyant in water). The pDSTs were programmed to log pressure (manufacturer reported precision = 0·08 dBar [≈ depth in m] or better, accuracy: ± 2 dBar [≈ 2 m depth]) and temperature (nearest 0·03125° C; accuracy: ± 0·1° C) every 70 s. Tags were also programmed to have two or three 3 day periods in which logging was increased to every 5 s (*e.g.* immediately upon release, during thermal mixing of the lake in the autumn). The memory capacity of the tags (G5 data storage tags) was 2 MB, which enabled measurements to extend over the course of *c.* 370–380 days with the measurement schedule the tags were programmed to use, while the battery had the capacity to last for 24 months (manufacturer specifications). The TRU (pop-off mechanism) was set to release approximately 1 year after tagging (earliest scheduled release date 1 June, latest 1 September) and, like the G5 data logger, was designed to have a 2 year battery life (Cefas Technology). Each depth and temperature measurement was recorded along with a timestamp (year, month, day, hour, min., s.).

TAGGING AND RELEASE OF HATCHERY-REARED FISH

A primary objective of the study for which the pDSTs were being used was to assess the vertical–thermal niche overlap between *S. salar* and other salmonids, in order to inform ongoing efforts to restore *S. salar* populations in Lake Ontario (McKenna & Johnson, 2005; Stewart *et al.*, 2014). Owing to their low density in the lake, however, it was only possible to capture and tag one *S. salar* (in spring 2016) in the 3 years of tagging. Thus, in order to attempt to fulfil the objectives of the study *S. salar* that had been hatched and reared inside fish-hatchery facilities were experimentally tagged and released. The first such effort occurred on 12 May 2015, when 10 *S. salar* and 10 *S. namaycush* were transported from Codrington Fisheries Research Facility (44° 08′ 48·6″ N; 77° 48′ 14·9″ W) to the shore of Lake Ontario (Cobourg, ON, Canada; Fig. 1) for tagging and release. Fishes were netted from their holding tanks at the hatchery and transported 44 km (*c.* 40 min) in well-aerated hatchery water (*c.* 10° C), to the lakeside where they were tagged and released using the same tagging methods described above for wild-caught fishes.

A further 10 *S. salar* were tagged with pDSTs at the Harwood Fish Culture Station (Fig. 1) on 30 March 2016 ($n = 7$) and on 6 April 2016 ($n = 3$) and released from the Glenora Fisheries Station (Glenora, ON, Canada; Fig. 1) on 7 April 2016 following a post-surgery monitoring period (8 days for those tagged 30 March, 1 day for the three tagged 6 April). These 10 *S. salar* were experimentally double-tagged: acoustic transmitters (Vemco V13 transmitters, 13 mm diameter, 36 mm length, 11*g* mass in air, 6*g* in water, Vemco Amirix; www.vemco.com) were surgically implanted into the body cavity in addition to external attachment of the pDST. The acoustic transmitters were implanted opportunistically for release of the *S. salar* into an already-existing array of underwater acoustic telemetry receivers in the area of release (the Bay of Quinte; telemetry data not reported in this paper). The surgery for these *S. salar* followed typical best practices (Wagner *et al.*, 2011) and, unlike the other 108 fishes to which pDSTs were attached, involved the use of anaesthesia. Briefly, *S. salar* were placed into a 20 l bath (in a 45 l container) of 100 mg l^{-1} MS-222 buffered with 200 mg l^{-1} $NaHCO_3$ until they lost equilibrium and their ventilation patterns slowed (which took 3–5 min) at which point they were transferred to a smooth, V-shaped surgery trough in the supine position. The transmitter was inserted through a *c*. 2 cm incision in the ventral side of the *S. salar*, which was closed using three sutures (size 0 monofilament PDS II absorbable sutures, 36 1/2 circle reverse cutting needle; Ethicon; www .ethicon.com). After transmitter insertion, the *S. salar* was flipped over into the prone position for attachment of the pDST as described above. During surgery (8–13 min total duration) the gills were continuously irrigated with a well-aerated maintenance dose of anaesthetic (50 mg l^{-1} MS-222, 100 mg l^{-1} $NaHCO_3$). Following surgery the *S. salar* was placed in an 80 l cooler (filled with well-aerated water) for recovery (*c*. 20 min) before being returned to a flow-through holding tank for prerelease monitoring. All *S. salar* recovered well from the surgery, evidenced by the fact that they were actively swimming around the holding tank similarly to non-tagged conspecifics. *Salmo salar* were transported by road (108 km, *c*. 90 min, in a well-aerated 1600 l transport tank) from Harwood Fish Culture Station to Glenora Fisheries Station where they were released (7 April 2016).

TAG RECOVERY, DOWNLOAD AND DATA PROCESSING

Once fishes were released, tag returns relied on anglers or other members of the public finding tags and contacting the research team (by e-mail or telephone). To raise awareness of the project, tag–return reward posters and business cards were circulated *via* the relevant fisheries management agencies and awareness was further increased by giving presentations at stakeholder meetings, including a large (>200 attendees) symposium of those involved in the Lake Ontario salmonid fishery (competitive and recreational anglers, guides, fisheries agency members). Those who reported finding a tag were asked for the date and location where they found their tag (or caught their fish with a tag, in some cases) and the serial number on the tag. Tags were found in one of three ways: still attached to a fish, on the shore but with the harness still attached, indicating that the fish probably died and the entire harness subsequently came free of the carcass or on the shore, popped-off normally (no harness attached, pop-off metal link burned off). Monetary rewards of $100 (Canadian or U.S.A.) were provided as incentive–compensation. Tags were downloaded using the same USB-to-serial connection device that was used for programming and launching tags. pDSTs that were at liberty and recording for a full year (full memory bank) each generated >670 000 lines of data.

RESULTS

DUMMY-TAG RECAPTURE EXPERIMENT

Among the 100 dummy tags released, 73 were found on shore and reported by members of the public, with recaptures occurring 2–36 days after the tags were released offshore (median = 5·6 days). A further three calls were received about tag recaptures, but we were unable to re-connect with those callers to obtain dummy-tag IDs or dates–times of recapture. All recaptures occurred on the north shore of Lake Ontario (Fig. 1), with the majority in or near Cobourg, ON. The straight-line distance between two furthest-apart recaptures locations was 118 km.

RECAPTURE AND DOWNLOAD OF TAGS

Among 88 wild-caught and tagged fishes, 23 tags were found and returned (26%), with a further 20 of 88 scheduled to release from fishes in summer 2017 (Fig. 4). Using only tags scheduled to have already popped-off from wild-caught fishes (*i.e.* by September 2016), 13 of 58 have thus far been returned (22%). Although sample sizes are limited, the rate at which tags attached to wild-caught fish have been found and returned has been significantly lower than for the hatchery-reared fish [26 *v*. 47%; binomial regression, effect of group (hatchery *v*. wild) on recapture probability;

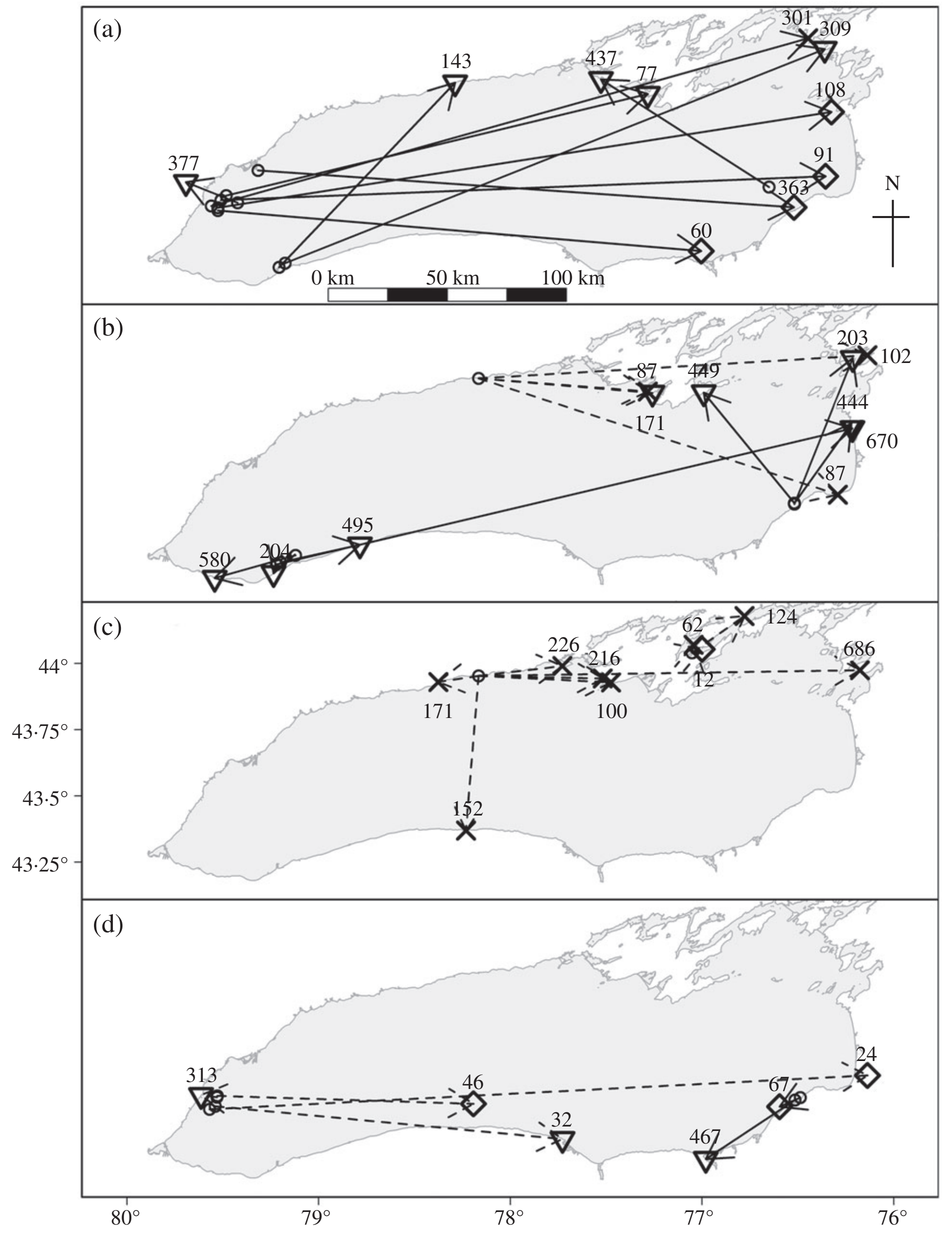

FIG. 4. Maps showing the release and recapture locations for the 37 pop-up data storage tags (pDST) that were recaptured: (a) *Oncorhynchus tshawytscha*, (b) *Salvelinus namaycush*, (c) *Salmo salar*, (d) *Salmo trutta* (——) and *Oncorhynchus mykiss* (_ _ _). The numbers adjacent to each recapture location give the number of days from release to the reported recapture date. ○, Tagged fish release point; ×, Tag returned with harness attached; ◇, Fish recaptured with tag attached; ▽, Tag popped-up, without harness. (a)–(c) ——, Release–recovery vector for wild-caught and _ _ _, hatchery-reared fish.

TABLE II. Month during which tags released from the fish (popped up) and reached the surface, for tags where the time of reaching the surface could be clearly confirmed by examining the depth and temperature data recorded by the tag. *N.B*. Among the 23 wild-caught fishes for which tags were found, seven fishes were recaptured by anglers (no pop-up), while the pop-up date could not be confirmed for a further five fishes because the memory bank was full for those tags before they reached the surface ($n = 11$ known pop-up dates)

	Number of tags confirmed reaching the surface							
Group	May	June	July	Aug.	Sep.	Oct.	Nov.	Dec.
Hatchery-reared fishes	1	2	3	1	0	2	1	1
Wild-caught fishes	0	1	1	1	6	1	1	0

$Z_{1,116} = -2{\cdot}13$, $P < 0{\cdot}05$]. Compared with the hatchery-reared fishes (apparent rate of mortality of 100%, see below), the rate of mortality appears to have been low among wild-caught and tagged fishes (8·7%). Only one tag was found with an attached harness (from an *O. tshawytscha* tagged in 2014), while one *S. namaycush* was found to have died based on an examination of its depth recordings (the tag was later found without an attached harness). In both cases, these two mortality events occurred long after release: 148 and 311 days after release for the *O. tshawytscha* and *S. namaycush*, respectively (12 February 2015 for the former, 3 March 2016 for the latter). For the limited number of tags for which the date when they surfaced could be confirmed (tags that popped-off on schedule finished recording and had full memory banks before reaching the surface), there were no major differences between wild-caught and hatchery fish tags in terms of the temporal distribution of pop-up timing (Table II), although pop-up of tags from wild-caught fishes was relatively concentrated in the month of September. Among the 23 tags, eight popped-off or were broken free of fish prematurely (recovered long before scheduled release date) and seven were recaptured by anglers who caught the fish with a tag still attached. Thus, only the remaining 8 of 23 tags were found after recording a full year of data and having popped-off on schedule. In some instances, however, it was expected that tags would be found before a full year elapsed. For example, based on their size at the time, many of the *O. tshawytscha* that were tagged in spring 2016 will have spawned (or attempted doing so) and subsequently died in the autumn of 2016 in one of Lake Ontario’s tributaries. For example, one such tag was found adjacent to the mouth of the Ganaraska River (Port Hope, ON) in mid-September, 2016. The metal loops that attached the pDST to the harness (and erode when scheduled to do so) are small enough that they could conceivably be broken by sufficient mechanical stress.

Among 30 pDSTs that were deployed on hatchery-reared fishes, 14 were recovered and returned for download (47%), which included 10 of the 20 released in 2015 (due for pop-off in 2016) and 4 of 10 among those released in 2016 (due for pop-off in 2017). Most of these tag returns (10) came *via* tags with harnesses still attached. Two of the 14 fishes were caught in a commercial fishery gillnet 1 and 12 days after release, respectively (both were *S. salar* tagged in 2016), with the tags still attached. A 15th tag was confirmed as having been found (harness attached) among the hatchery *S. salar* released in spring 2016, but was never returned for download. An examination of the depth and temperature data from the harness-attached tag returns confirmed that those fish died after release. Harness-attached tags were found on shore after having

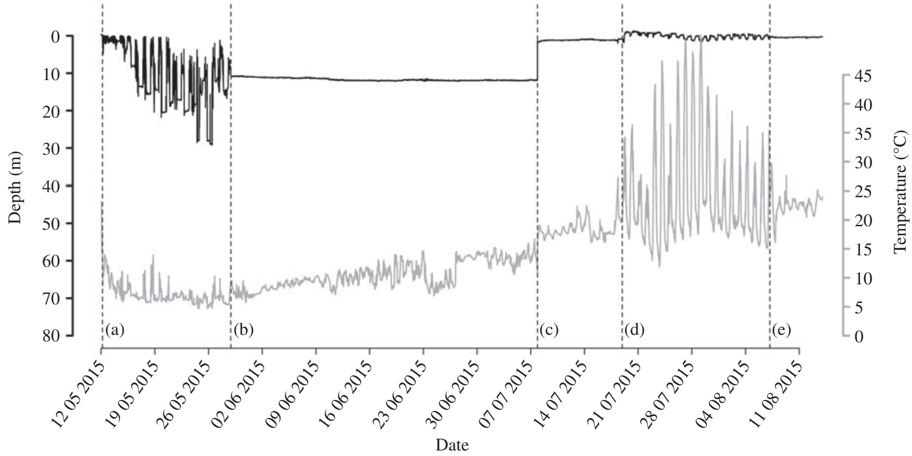

FIG. 5. Raw depth data from a pop-up data-storage tags (pDST; ——) that was attached to a hatchery-reared *Salmo salar* in May 2015 and subsequently found with the plastic harness still attached. Key events in the timeline of this tag are shown (⋮): (a) release; (b) the mortality event, after which the fish's carcass and the tag are on the lake bed nearshore at 10 m depth; (c) the tag and harness come free of the carcass and float to the surface; (d) the tag washes onto dry land and starts to experience more substantial daily fluctuations in temperature (——) and pressure; (e) the tag is found. The extreme highs in temperature after the tag reached the shoreline may be explained by a combination of microclimate in the location where the tag was resting, direct exposure to sunlight and heat absorption or a greenhouse effect within the float of the tag during exposure to direct sunlight (air temperatures >40° C have not been recorded in Ontario, but air temperatures are measured in the shade for meteorological purposes, not in direct sunlight).

registered constant depths (presumably on the lake bottom) for a period of 25–217 days (median = 66 days) before coming free of the fish's carcass, floating to the surface at a median rate of 7·8 m min^{-1} (range, 2·3–11·5 m min^{-1}; Fig. 5). The apparent time elapsed between release and mortality in the hatchery fishes for which the time of mortality could be estimated based on depth recordings ranged from 3·4 to 42·8 days (median = 14·3 days, $n = 12$). The apparent depth of the lake at the locations where hatchery-reared fishes died (based on the depth the tags sank to) ranged widely, from 2·6 to 139 m (median = 33·4 m). Tags returned before their scheduled pop-off date were downloaded and re-programmed for re-use in additional fishes.

Cumulatively, the 37 tags that were returned generated over 14 million lines of data, although this figure includes data recorded by tags not attached to fishes. For instance, tags that came free prematurely continued recording data while at the surface, on shore and *en route* to the University of Windsor *via* courier. In nearly every case, a manual examination of the data made it clear when the tag came free of the fish, when the fish died (or both), or was recaptured, allowing the data to be trimmed to include only data points recorded for tags attached to fish, which resulted in a dataset 9 million lines long. The maximum depth recorded in the entire dataset was 218 m (recorded by a *O. tshawytscha* in early March 2016). As expected, the high-frequency (every 70 s) at which measurements were made provides a glimpse at within-individual variation that would not be evident without the use of electronic tags, particularly during times of the year when few data are typically collected using fishing surveys (for a sample, see Fig. 6).

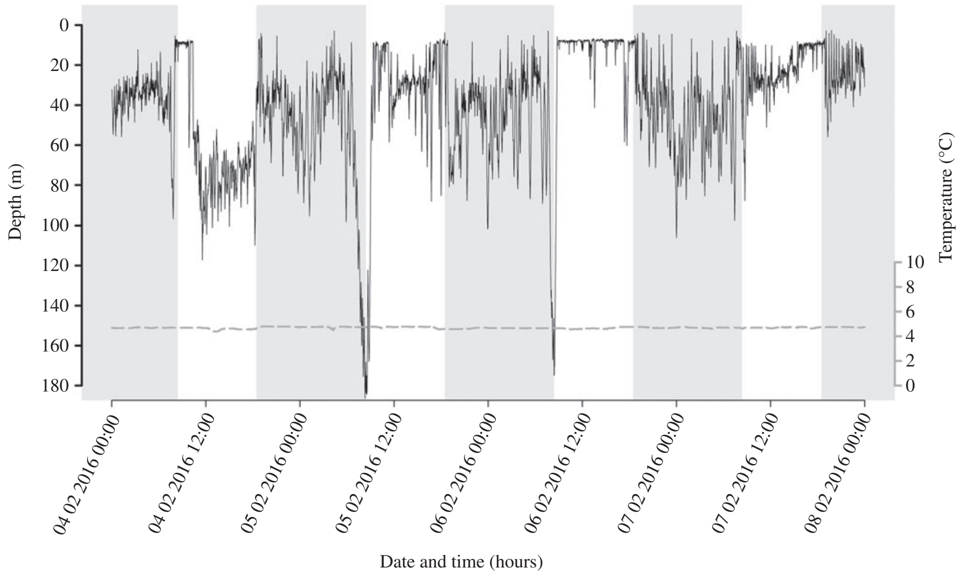

FIG. 6. A sample of data showing the depths and temperatures recorded by a pop-up data-storage tags (pDST) attached to *Oncorhynchus tshawytscha* over the course of 4 days in February 2016 (——). Sunrise and sunset times were obtained using the function sunriset in the maptools package in R (Bivand & Lewin-Koh, 2016) and are based on coordinates in the middle of Lake Ontario (43° 37′ 32·7″ N; 77° 54′ 18·9″). ▮, The period from sunset to sunrise; - - - -, temperature.

DISCUSSION

TAG RETURN RATES AND VIABILITY OF THE METHOD

With 37 tags retrieved among 118 released on fishes (23 of 88 wild-caught fishes; 26%), the large-scale field study reported on here demonstrated that pDSTs are a viable way of collecting detailed information on the depths and temperatures selected by salmonids in Lake Ontario. Some of these tag returns (14 of 37), however, were from hatchery-reared fishes that evidently died at some point after release and hence did not contribute particularly useful data. The overall rate at which pDSTs were found and returned for download was low (31%) in comparison with the rate of 73% observed in the 2013 dummy-tag pilot study. Interestingly, the actual rate of return for wild-caught fishes was lower (26%) than for tags attached to hatchery-reared fishes (47%). It is only possible to speculate about the causes of this discrepancy. The locations and times at which tags reached the surface and the shore could have explained part of the difference among the two groups. There is limited ability, however, to assess these differences (but see Table II) because the actual (realized) pop-off date is only known for 11 fishes from each of the two groups; several tags had full memory banks before they reached the surface, precluding identification of release times. In other cases, fishes were recaptured before their tag popped-off.

Causes other than spatiotemporal differences may have contributed to the lower recapture rate for tags from wild-caught fishes as compared with those from hatchery-reared fishes and the dummy-tag experiment. The hatchery-reared fishes all appear to have died within days or weeks of release (based on the tags that have been found). The poor survivorship among these fishes is attributed primarily to the difficulty they probably faced learning to forage in novel environment and with live (motile) prey. It must be acknowledged, however, that stress caused by transport and tagging, along with the burden of the external tag, may have played some role in the failure of these fishes to acclimate to the wild. The relatively higher rate of return for tags from these hatchery-reared fishes that died may have been facilitated by the fact that the harness remained attached to the pDST while at the surface or on shore. A tag on shore with an attached harness may have made these tags easier for shore-walking members of the public to see, or reduced the speed at which the tags became buried under sand or rocks in the shorelines. It was notable that one tag (from a wild-caught fish) was found in August 2015 after having popped-off prematurely on 29 September 2014. That tag therefore spent nearly a year, including a full winter, on the beach (Sodus Bay, NY, U.S.A.) and when it was found part of the float was chipped off and all of the orange paint had faded or chipped away. Based on those observations, it seems likely that the probability of tags being found on shore decreased considerably over time because of the tags becoming less visible *via* gradual mechanical or UV damage to the orange paint, or because of the tag becoming buried under rocks, sand or other debris. Aside from that one instance, however, all other returned tags had still retained all or nearly all of their bright orange paint. One clear difference between the dummy-tag experiment and the actual pDSTs is that it is known with 100% certainty that all dummy tags reached the surface (they were simply released onto the surface of the water). Moreover, they were all released (and presumably reached shore) in mid-summer, when the likelihood of recapture is probably at its peak due to high human activity around the shoreline. It also involved a high number of tags making landfall within a relatively concentrated area and period of time, which resulted in some members of the public finding multiple tags on the same day, and local word-of-mouth about the tags, all of which were probably a consequence of all tags having been released in the same part of the lake and within hours of each other. On the other hand, the pDSTs would have reached the surface relatively sporadically in time and space and each tag would have surfaced in a relatively independent event as compared with the 100 dummy tags that were released in the same event. It is possible that some number of pDSTs attached to fishes simply never reached the surface, either because they were impeded from floating upwards by some underwater structure, or because of malfunction of the TRU. The battery for the TRU, however, is built to last in excess of 2 years, so even if the time required for the metal link to sufficiently erode (enabling release) were 5–10 times longer than advertised (2 weeks in tap water at room temperature based on trials by Cefas Technology), tags should have reached the surface eventually.

Among the seven tags that were returned *via* recaptured fish, one report was received of a *S. trutta* suffering visible injuries from the harness (tagged and recaptured in 2014) that involved open wounds seemingly caused by tension or movement of the harness. It is not clear, however, whether the injuries existed before the fish's encounter with the angler who, while netting the *S. trutta* onto his boat, might have caused the injuries. The damage may also have been caused by the *S. trutta* being foul-hooked on the tag harness. No other reports of ill effects of the tags on fishes were given among the seven recaptured (tagged) fishes and the fact that many fishes were evidently able to survive throughout winter and the following summer (based on an examination of data from the tags) indicated that the tags did not necessarily prevent them from being able to survive, feed and grow. For example, one *O. tshawytscha* tagged near Port Credit (Fig. 1) in September 2015 was recaptured 363 days later and 226 km away, outside the mouth of the Oswego River (Oswego, NY, Fig. 1) and was visibly (based on a report from the angler) in excellent condition, filled with eggs and had approximately tripled in mass since being tagged a year earlier (*c.* 3·3 kg at tagging based on its L_F, *c.* 10 kg at recapture).

OPTIONS FOR MAXIMIZING TAG RECAPTURE AND RETURN

Were the attachment and release of pDSTs on Lake Ontario fishes to become a more routine research technique, there are some approaches that could be used to increase the likelihood of tag recapture. It now seems obvious that maximizing the likelihood of tag recapture should be prioritized over having the tag attached for a longer amount of time. For example, it would be preferable to have two fewer months of data on a fish (*e.g.* tag pop-up in July instead of September) were that to meaningfully increase the recapture rate. Presumably, having a tag on the shore for a greater portion of the summer would increase the likelihood of recovery. Moreover, it would be useful to conduct an experiment to estimate the realized time (and range of times) required for the release mechanism to work across a range of depths and temperatures in Lake Ontario water, which of course differs somewhat in its properties from the tap water used to generate the 2 week release time estimate (*e.g.* pH, ion concentrations, organic compounds, microbiota). The mechanical stress placed on the metal link of the tag by the fish's movement was probably responsible for some variation in release times; this is particularly relevant for the tags that surfaced several months before they were scheduled to do so. An expanded or prolonged pDST study may also benefit from an increased investment into outreach and communication efforts, perhaps along with an increase in the tag return reward, both of which might encourage more active searching of Lake Ontario's shorelines by members of the public.

Attaching a global positioning system (GPS) transponder or radio transmitter to each pDST as a means of locating and retrieving popped-up tags are two obvious ways of increasing the number of tags that are retrieved for download. The option of using GPS was explored prior to the start of this study and was ultimately avoided because adding a GPS transponder would further increase the size of the tag, the increased cost per tag would be substantial, GPS transmissions from such tags can be unreliable (Fisk *et al.*, 2012; Thorstad *et al.*, 2013) and because of the increased time and expense that would be involved in searching for and retrieving tags. The addition of a radio transmitter would be of limited use in a large system like Lake Ontario and would require focused searching (with a handheld radio receiver) of areas of the lake's shoreline predicted, based on lake circulation models or existing recapture data, to be areas of high encounter probability. In a smaller lake, however, where periodic searches of the entire shoreline with a radio receiver are plausible, the addition of a small radio transmitter could result in increased tag recovery rates.

LIMITATIONS, BIASES AND ALTERNATE METHODS

Aside from difficulties in retrieving the tags, an obvious limitation with the use of pDSTs is the effect of the tag on the behaviour of the animal, which is largely unknown.

Tagging effects are a necessary consideration for any electronic tagging study with wild animals. The pDSTs used in the present study are relatively large compared with the (typically smaller) internal or external tags (transmitters or data loggers) often used in freshwater fishes that do not require the addition of a float and a TRU (the pop-off mechanism). In instances where tagging effects are a concern or if using smaller animals for which the (relatively large) external tag application used here would be inappropriate, internally-implanted tags would probably be the best alternative. For example, the depth–temperature loggers used in this study (Cefas G5; Cefas Technology) without the associated float or TRU are only 12 mm in diameter and 35·5 mm long (*v.* 22 mm diameter, 93 mm long for the entire pDST) and could be internally implanted or externally attached, though this would require physical recapture of the fish [= 8% tag return rate (7 of 88 wild-caught fishes) for Lake Ontario based on the data here]. Also available are the LAT1000 series of archival tags offered by Lotek Wireless (Newmarket; www.lotek.com), which are small enough to be implanted into the body cavities of many freshwater fishes and have previously been used to assess depth and temperature in salmonids in Lake Huron (Bergstedt *et al.*, 2016). That study relied on commercial and recreational fisheries recaptures of lake whitefish *Coregonus clupeaformis* (Mitchill 1818) and *S. namaycush* that were internally implanted with the data loggers and externally marked with orange dart tags bearing a reward message and phone number, of which 147 were recaptured out of 808 fishes tagged (18%; Bergstedt *et al.*, 2016). The tags used in that study had a lower memory capacity than the Cefas G5 tags used in the present study and offered a resolution that progressively decreased based on deployment time (1 year of recording = data recorded at 16 min intervals *vs.* every 70 s with the tags used in the present study; Bergstedt *et al.*, 2016). For illustrative purposes, the same data set from Fig. 6 is plotted to show what it would look like were the sampling rate decreased from every 70 s to 15 or 30 min (Fig. 7). This demonstrated (Fig. 7) that the lower sampling frequencies generally underestimate the extreme values and miss a number of vertical movements, but nevertheless capture a useful and representative sample. Weighing higher resolution (Cefas G5 tags) *v.* lower resolution sampling (Lotek LAT1000 tags or longer-term deployments of the tags used here) would depend on study objectives and whether fish recapture–return rates would be expected to be high enough to enable internal tag implantation.

The dataset generated by the methods described in this paper, like many based on electronic tagging studies, is large enough (>14 million lines based on 37 fishes and growing) to pose technical challenges relating to data management, analysis and visualization. The use of database software becomes necessary with such a dataset (in this case, postgresQL was used), as does the use of R (www.r-project.org) or some other script-based approach to visualizing and analysing data. Fortunately, a rapidly increasing number of ecologists have the necessary knowledge (or access to resources) needed to undertake such analyses. High temporal resolution depth and temperature data like those generated here will, in addition to providing the best knowledge to date on the depth and temperature distributions of salmonids in Lake Ontario, enable novel insights into fish behaviour. For example, the data will provide insight into within-individual, within-species and among-species variation in behaviours, knowledge that often cannot be gleaned by traditional methods (*e.g.* gillnet surveys). There may also be opportunity to examine the behavioural reactions of fishes to environmental perturbations like extreme weather events, though such an analysis would have to focus on lake-wide weather systems (*e.g.* high or low pressure systems) because the horizontal position of

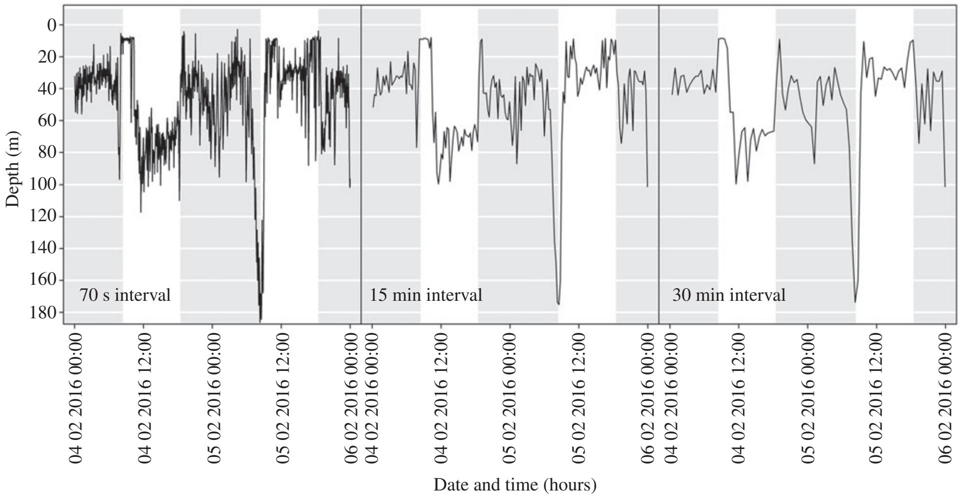

FIG. 7. A comparison of three data sampling intervals from pop-up data storage tags (pDST, ——) for a 2 day section of data from a *Oncorhynchus tshawytscha* (first 2 days of the time series shown in Fig. 6). (a) Raw data at 70 s intervals; (b) sub-sampling data points every 15 min and (c) sub-sampling data points every 30 min. Sunrise and sunset times were obtained using the function sunriset in the maptools package in R (Bivand & Lewin-Koh, 2016) and are based on coordinates in the middle of Lake Ontario (43° 37′ 32·7″ N; 77° 54′ 18·9″). ▮, The period from sunset to sunrise.

the fishes within the lake (latitude and longitude) is not provided by these tags. Indeed, the lack of positioning information is arguably the main drawback of using pDSTs (though this can be overcome by double-tagging the fish with an internal acoustic transmitter) and will limit the extent to which the vertical behaviours observed in the data can be interpreted.

The best available information on the effects of external DSTs on the vertical behaviour of salmonids comes from a recent paper in which data were compared between *S. salar* equipped with backpack-attached PSATs against *S. salar* with smaller, internally implanted DSTs (Hedger *et al.*, 2017). In that study, *S. salar* tagged with small internal tags (38·5 mm long × 12·5 mm wide cylindrical tags made by Star-oddi; www.star-oddi.com) effectively served as controls against which to compare data obtained from PSATs that were comparable in size (120 mm long × 32 mm maximum diameter) and attached similarly to the pDST in the present study (Hedger *et al.*, 2017). The *S. salar* equipped with PSATs survived at rates comparable to 'controls' and exhibited nearly identical overall depth and temperature distributions (Hedger *et al.*, 2017). There were notable differences in behaviour, however; PSAT *S. salar* tended to make deep dives (to >100 m) less frequently, dived to shallower maximum depths and made their ascents and descents more slowly during dives; all based on tags (PSATs and internal DSTs) logging every 30 min (Hedger *et al.*, 2017). That study occurred in the marine environment and as such, maximum dive depths were commonly >300 m (with both tag types; Hedger *et al.*, 2017), whereas dives >100 m were uncommon in the present study presumably partly owing to physical restrictions as much of Lake Ontario is shallower than 100 m. Nevertheless, it seems unsurprising that a large, buoyant, external archival tag would, to some extent, affect vertical behaviour. In addition to the possible effect of the tag's buoyancy, the tag's hydrodynamic drag would increase the cost of transport (energy use m^{-1} travelled), particularly at high swimming speeds. For example, in *A. anguilla* swimming at 0·3–0·9 body lengths s^{-1} in a swim tunnel, the external attachment of a PSAT increased the minimum cost of transport by 26% (Methling *et al.*, 2011). The tag design used in this study (Fig. 2) involved flat rather than rounded ends and so was less hydrodynamic than standard PSATs, which may have resulted in an even greater addition to cost of transport than estimated for *A. anguilla* carrying PSATs (Methling *et al.*, 2011). It has consequently been recommended to the manufacturer that the ends of the tag be re-designed to a more rounded shape. It is perhaps partly because of added hydrodynamic drag and cost of transport that the growth rates were somewhat less for PSAT-tagged *S. salar* in the Hedger *et al.* (2017) study than in *S. salar* tagged with internal DSTs. Consequently, deciding whether to use pDSTs in place of other electronic tagging approaches requires that the potential behavioural effects of pDSTs be weighed against the study objectives and the relative cost (per datum) of different methodological options (*e.g. v.* acoustic telemetry, internal DSTs, or some combination of methods).

The authors would like to extend their thanks to N. Foxcroft (Moby Nick Fishing Charters, Mississauga, ON, Canada) and to E. Lantiegne (Fish Doctor Charters, Oswego, NY, U.S.A.) for their assistance with capturing and tagging fishes. Additional assistance in the field was provided by J. Lewis, S. Dogru, N. Hussey, B. Graham, N. Sopinka, B. Metcalfe, B. Johnson, J. Fisk, D. Raby, C. Taraborelli, S. Larocque, J. Buckley, R. Green, A. Barkley, B. Nawrocki and D. Favato. J. Mumby and A. Todd provided assistance with the dummy-tag recapture experiment. Thanks to J. Ruegg at Normandale Fish Culture Station and to B. Rosborough at Harwood Fish Culture Station for providing and coordinating access to hatchery-reared *S. salar*. Research funds were provided by a grant from the Great Lakes Fishery Commission, with further support from the Ontario Ministry of Natural Resources and Forestry and from the University of Windsor. A.T.F. is supported by the Canada Research Chairs Program. G.D.R. is supported by a post-doctoral fellowship from the Natural Sciences and Engineering Research Council of Canada.

Supporting Information

Supporting Information may be found in the online version of this paper:
Table S1. List of fishes tagged with pop-up data storage tags (pDST).

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