

REGULAR ARTICLE

Evaluating the behavioural consequences of external pop-off biologging packages on two freshwater fishes

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Abstract

Quantifying the behaviour of animals in the wild can provide important information on their ecology and welfare. External biologgers that ‘pop-off’ to enable tag retrieval have been widely used in marine systems; however, they have only recently been applied to freshwater fishes. As a result, questions remain about the impact that external biologgers have on the behaviour of freshwater fishes. Here, two species of freshwater fish that were previously implanted with acoustic transmitters were recaptured with rod-and-reel and fitted with custom pop-off biologging packages (50 × 30 × 15 mm; 14.7 g) in a small (23 ha) lake. Habitat use and movement behaviour (e.g., cruising, exploratory, stationary) were assessed for each individual for 72 h when pop-off biologging packages were affixed to the fish, and once they were detached from the fish. Acoustically tagged fish in the system that were never equipped with a pop-off biologging package were included as controls. Behavioural impacts of pop-off biologging packages were more evident for Largemouth Bass *Micropterus nigricans* than for Northern Pike *Esox lucius* in water temperatures between 20 and 27°C. Largemouth Bass spent less time in the limnetic habitat and more time close to refuge when pop-off biologging packages were attached compared to controls or when they were detached. Northern Pike spent more time in the limnetic habitat and less time in the semi-complex habitat when pop-off biologging packages were attached compared to controls. Pop-off biologging packages had no impact on the movement behaviour of Northern Pike. Largemouth Bass attached with pop-off biologging packages were stationary for longer compared to controls, or once the pop-off biologging packages were detached. Once the pop-off biologging packages detached, Largemouth Bass movement behaviour resembled the controls, which spent more time cruising and exploring. These results provide important information on behavioural artefacts that can manifest when wild fish are equipped with short-term external biologging packages.

KEYWORDS

acoustic telemetry, biologging, fishing, post-release behaviour, tagging effect

1 | INTRODUCTION

External pop-off biologging packages or similar style packages (e.g., satellite tags) are commonly used in marine systems (Lear & Whitney, 2016; Robichaud et al., 2025; Whitney et al., 2016), yet external pop-off packages are rarely used for freshwater fish (LaRochelle et al., 2025). There are two factors that make the use of external pop-off packages in freshwater challenging: the size of the animal relative to the size of the external tagging packages and a lack of reliable release mechanisms. In marine systems, there are more species that reach large body sizes and can thus accommodate larger tags. Smaller fish are unable to accommodate large external packages since hydrodynamic drag may impact energy expenditure (Lynch et al., 2017; Methling et al., 2011; Tudorache et al., 2014) and swimming performance (Janak et al., 2012; McCleave & Stred, 1975; Peake et al., 1997). The amount of drag caused by external tags is influenced by the shape (e.g., Shorter et al., 2014), size (e.g., Zhang et al., 2020) and location of the tag on the body (e.g., Tudorache et al., 2014). Additionally, time-released galvanic clips that rely on corrosion work poorly (or not at all) in freshwater, making it difficult for the pop-off packages to disconnect from fish and float to the surface for recovery. It is becoming increasingly feasible to use pop-off biologging packages on freshwater fishes as technological advances have allowed for the miniaturization of biologging devices (e.g., Elliot et al., 2023; Raby et al., 2017) and the development of creative release mechanisms (e.g., circular candy; LaRochelle et al., 2024, catgut suture; LaRochelle et al., 2023; Wilson et al., 2026).

Although external pop-off biologging techniques have been used to assess the behaviour of freshwater fishes (e.g., Elliot et al., 2023; LaRochelle et al., 2023; LaRochelle et al., 2024; Raby et al., 2017), the effects that external biologgers have on the behaviour of freshwater fishes are unknown (Jepsen et al., 2015; LaRochelle et al., 2025). Indeed, there is mixed evidence of potential behavioural impacts and energetic costs associated with external tag attachment in fishes. Small external pop-off satellite tags did not have adverse effects on the migration of European Sea Bass *Dicentrarchus labrax* (O'Neill et al., 2018) and Atlantic Salmon *Salmo salar* (Hedger et al., 2017) but did reduce the diving ability of Atlantic Salmon at sea (Hedger et al., 2017). External tags led to a 26% increase in energy use during swimming for European Eels *Anguilla anguilla* (Methling et al., 2011). Echave (2016) observed Sablefish *Anoplopoma fimbria* in a laboratory setting following the attachment of a pop-off satellite package and found no impacts on the normal behaviour of those fish (e.g., feeding, or physical damages) associated with attachment. A general caveat to most tagging effects studies is that they focus on one endpoint (e.g., swimming performance) and often miss potential behavioural implications related to tagging (Shorgan et al., 2026). Understanding the influences that external biologging packages have on the behaviour of freshwater fishes in the wild will provide important considerations for behaviour interpretations in future studies.

Assessing behavioural traits in fish in the wild can provide valuable insight into their welfare (Beitinger, 1990; Huntingford et al., 2006; Iwama et al., 1997). There are fitness and survival

implications depending on the magnitude of behavioural deviation in wild fish (Schreck et al., 1997). Behavioural differences can be observed when swimming capabilities are reduced (Thompson et al., 2008) or when fish engage in hyperactivity (Mäkinen et al., 2000; LaRochelle et al., 2025). Cognitive impairment and disorientation can result in greater susceptibility to predation as abilities to find refuge and avoid predators is reduced (Cooke et al., 2014; Danylchuk et al., 2007). Exploration is energetically costly and potentially increases susceptibility to predation (Mikheev et al., 1997; Mikheev et al., 2010). However, fish must move and explore within their environment to fulfil fundamental living requirements (e.g., food acquisition). Feeding efficacy has previously been reported to increase when searching for food in open limnetic habitats (Mikheev et al., 2010). When faced with predation risk, fish tend to use habitats that are more complex and provide refuge (Eklöv, 1997; Savino & Stein, 1982; reviewed in Mikheev et al., 2010). Alternatively, when fish are willing to engage in more bold behaviours and make themselves risk-prone, they will explore limnetic habitats where refuge offered by complex habitats is not available (Budaev, 1997). This bold behaviour while exploring the limnetic zone is adaptive and can change depending on the situation (Wilson, 1998). Activity levels are generally elevated when fish are in open limnetic zones (Enefalk & Bergman, 2016; Radabaugh et al., 2010) compared to when in complex structures where movement is obstructed, increasing the energetic cost of movement (Brownsmith, 1977; Schooley et al., 1996). Further, stress levels can impact the physiological abilities and cognitive actions of fishes (reviewed in Cooke et al., 2022). Therefore, movement of fish within an aquatic system is a balance between energy mobilization, or the cost of movement and the risk/benefits of moving. Identifying patterns of habitat use and movement behaviour of fish with and without external pop-off biologging packages can provide critical insight into fitness implications when fish are equipped with external pop-off biologging packages.

Biologgers, also known as data storage tags or archival tags, are able to record high-resolution/high-frequency data. There are several different ways that biologgers can be attached or inserted into fish, and they all have varying strengths and weaknesses. For example, biologgers can be placed in the body cavity via surgery (Clark et al., 2010; Reeve et al., 2025), attached on the outside of the fish with a detachable strap (LaRochelle et al., 2021; Louison et al., 2023; Madden et al., 2025; Reid et al., 2025), attached through the dorsal musculature (Algera et al., 2017; Boudreau et al., 2025) or with a pop-off package mechanism (Brewster et al., 2021; Danylchuk et al., 2026; LaRochelle et al., 2023). These tags include one or more sensors and are typically multi-channel such that data from different sensors can be recorded simultaneously (Williams et al., 2020). However, because they are archival tags, it is imperative that the biologgers are recovered if those data are to be collected. On the other hand, acoustic telemetry is a passive technology that records the detection of fish across an acoustic array of hydrophones. Generally, acoustic transmitters are inserted into the body cavity of the fish, requiring surgery and subsequent recovery, yielding a high retention rate (Shorgan et al., 2026). Because data is transmitted to stationary receivers, the transmitters do not

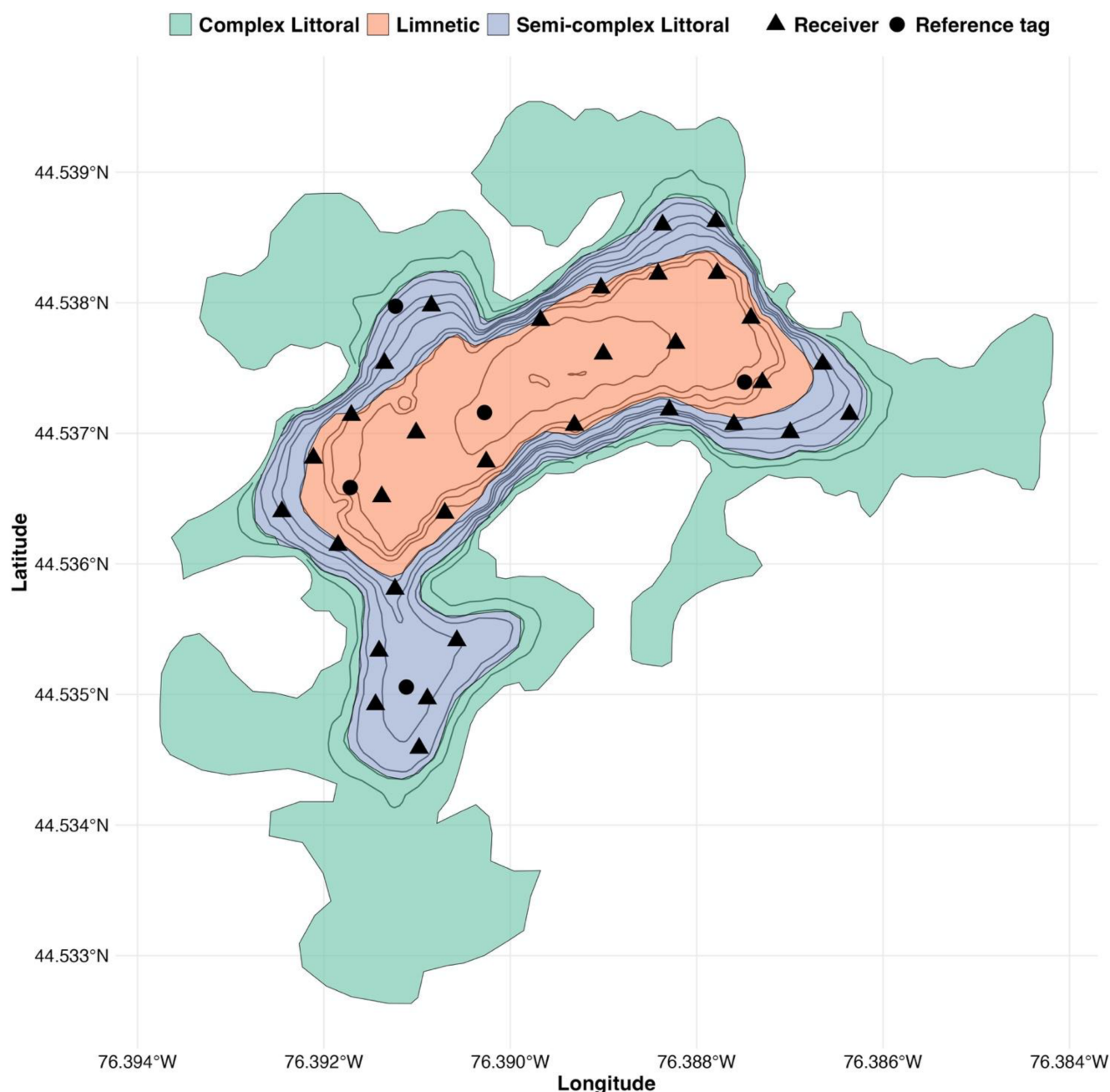


FIGURE 1 Habitat and bathymetry map (2 m contour lines) of Lindsay Lake. The different colours represent the various habitat types in the lake. Black triangles ($n = 32$) indicate the receiver locations, and black points indicate the location of reference tags ($n = 5$).

need to be recaptured or recovered to obtain data (Hussey et al., 2015). However, the acoustic array must cover the majority of the area occupied by the fish, or else there will be no data collected. Both technologies have strengths and weaknesses, which need to be considered when designing a study (reviewed in Cooke et al., 2012).

The objective of this study was to determine if custom external pop-off biologging packages ($50 \times 30 \times 15$ mm; 14.7 g) alter the behaviour of Largemouth Bass *Micropterus nigricans* and Northern Pike *Esox lucius* in the wild. These two species were selected given that previous studies have equipped them with pop-off biologging packages (e.g., LaRocheLle et al., 2023; LaRocheLle et al., 2024;

LaRocheLle et al., 2026; Wilson et al., 2026). Here, we used Largemouth Bass and Northern Pike that were previously tagged with internal acoustic transmitters and equipped them with external pop-off biologging packages. Using fish that were recaptured and recovered from the surgical tagging process provided a unique way to isolate and assess the impacts that external pop-off biologging packages had on the behaviour of fish in the wild. We used high-resolution positions (every 14–18 s) from the acoustic telemetry array to assess habitat use and different movement behaviours (e.g., tortuosity, step length distance and linear displacement). Overall, these findings will provide valuable information on the baseline behaviour of fish

equipped with external pop-off biologging packages that should be considered when contextualizing the behaviour of fish in the wild when similar biologging techniques are used.

2 | METHODS

2.1 | Acoustic tagging

Tagging practices were approved by Carleton University (AUP #110723) and in accordance with the Canadian Council of Animal Care. Lindsay Lake, a small research lake (23 ha) located at Queen's University Biological Station (44°32'14.0" N, 76°23'23.1" W; Figure 1), was equipped with 32 high-residency acoustic receivers (307 kHz HR3; InnovaSea Systems Inc., Halifax, NS, Canada). The receivers were strategically placed, allowing for triangulation of detections that provided the fine-scale positioning of fish using InnovaSea's High Residency system. Each receiver was positioned approximately 75 m from adjacent receivers and approximately halfway down the water column.

Between 4 and 5 May 2023, Largemouth Bass [$n = 24$, 431 ± 32 mm total length (mean $\pm$ SD), 376–495 mm range] and Northern Pike [$n = 19$, 655 ± 59 mm total length (mean $\pm$ SD), 545–735 mm range] were captured by rod and reel and brought to shore for surgical tag implantation using a submerged recovery bag (Dynamic Aqua Ltd., Surrey, BC; 122×31 cm with a mesh of 0.5 cm on both ends). Fish were then transported to a surgery trough lined with a Transcutaneous Electrical Nerve Stimulation unit (TENS Units INC, Largo, Florida, USA) to temporarily immobilize fish during surgery (see Reid et al., 2019). The TENS unit was set to a constant pulse rate of 150 Hz and a pulse width of 300 μ s. Electrical intensity was incrementally increased until fish were immobilized at which point surgery was initiated (Reid et al., 2019; Reid et al., 2024). A tube with fresh recirculating water was placed into the mouth of the fish, allowing for oxygenated water to flow over the gills. To inset the tags in the coelomic cavity, a small (<1 cm) incision was made between the pelvic fins and the cloaca. Fish were equipped with V6-4 $\times$ 307 kHz acoustic transmitters (low power 145 dB, 14–18 s delay, 290-day life, 19.3 mm length $\times$ 6.3 mm diameter, 1.2 g in air; InnovaSea Systems Inc.), as well as a passive integrated transponder (PIT; 12 mm; APT12 Biomark, Boise, Idaho, USA) for identification. The incision was closed with a 3-2-2 surgeon's knot using 3-0 absorbable monofilament PDS II sutures (Ethicon, New Jersey, USA). Surgeries took less than 2 min, and all tools were sterilized with betadine prior to tagging. Fish were then released and allowed to recover for at least 1 month prior to recapture, well beyond the recovery threshold of ~ 200 h identified in the same species and system (Shorgan et al., 2025).

2.2 | Habitat mapping

Habitat types within Lindsay Lake were assigned by creating polygons in RStudio using the *editMap* function from the *mapedit* package

(Appelhans et al., 2026). These polygons were created using the combination of bathymetry and vegetation regime within the lake. Polygons were classified into three categories: complex littoral, semi-complex littoral and limnetic (Figure 1). Complex littoral zone (13.4 ha) was classified as areas that were heavily vegetated (areas with abundant floating vegetation), woody debris or areas that were <1.5 m. Semi-complex littoral zone (4.8 ha) was classified as areas with submerged vegetation or between 1.5 m and <4.8 m. Finally, the limnetic zone (5.1 ha) was classified as the area in the middle of the lake that was >4.8 m without any vegetative structure. These habitats provided various levels of refuge, whereby the complex littoral zone had the greatest amount of refuge, followed by the semi-complex littoral zone; refuge was minimal in the limnetic zone. The acoustic receiver array had an efficient detection range for the limnetic and semi-complex habitats, but detection efficiency was limited in the complex littoral habitat (Figures 2 and 3).

2.3 | Recapture and external tagging

Largemouth Bass ($n = 6$; mean = $426 \text{ mm} \pm 39$ SD, range = 383–481 mm) and Northern Pike ($n = 6$; $586 \text{ mm} \pm 31$, 569–635 mm) were recaptured between 38 and 114 days post-tagging (11 June and 2 September 2023), using rod and reel. Largemouth Bass ($n = 6$; $450 \text{ mm} \pm 20$, 410–460 mm) and Northern Pike ($n = 4$; $713 \text{ mm} \pm 25$, 690–735 mm) that were not recaptured and equipped with a pop-off biologging package were used as controls. Surface water temperature during the angling period varied between 20 and 27°C. Fish were captured on a variety of lures, including bladed jigs, topwater lures and soft plastic lures (rigged with size 1/0 octopus or extra wide gape hooks). All fish were netted and unhooked in <20 s, with total air exposure prior to release being <60 s. All captured fish were then transferred onboard the vessel to a water-filled V-trough where they were scanned for their unique PIT tag.

Each recaptured fish was equipped with a custom floating pop-off biologging package (Figure 4; $50 \times 30 \times 15$ mm; 11 g; casing without biollogger) made from orange dyed Smooth-on Feather Lite™ (Smooth-on, Inc., Macungie, Pennsylvania, USA). The pop-off biologging package consisted of a data storage tag (AXY-5 XS; TechnoSmArt, Guidonia Montecelio, Italy; $20 \times 10 \times 6$ mm; 2.5 g in air) and a radio transmitter (BD-2; Holohil, Carp, Ontario, Canada; 1.2 g in air) used for relocation. These were affixed ventrally between the pelvic fins of Largemouth Bass and pectoral fins of Northern Pike (Figure 5; also see LaRochelle et al., 2023; LaRochelle et al., 2024). Biologging packages were fastened to the fish using two self-locking straps that were secured together using a short (~ 3 cm) piece of 4-0 plain catgut suture (550B, Ethicon, Sommerville, New Jersey, USA), which was used as a dissolvable link. The self-locking straps were then placed into the matching receptacle that was attached to the pop-off biologging package and tightened onto the fish. Pop-off biologging packages would dislodge from the fish when the dissolvable link broke or lost tensile strength, and they would float to the surface for collection.

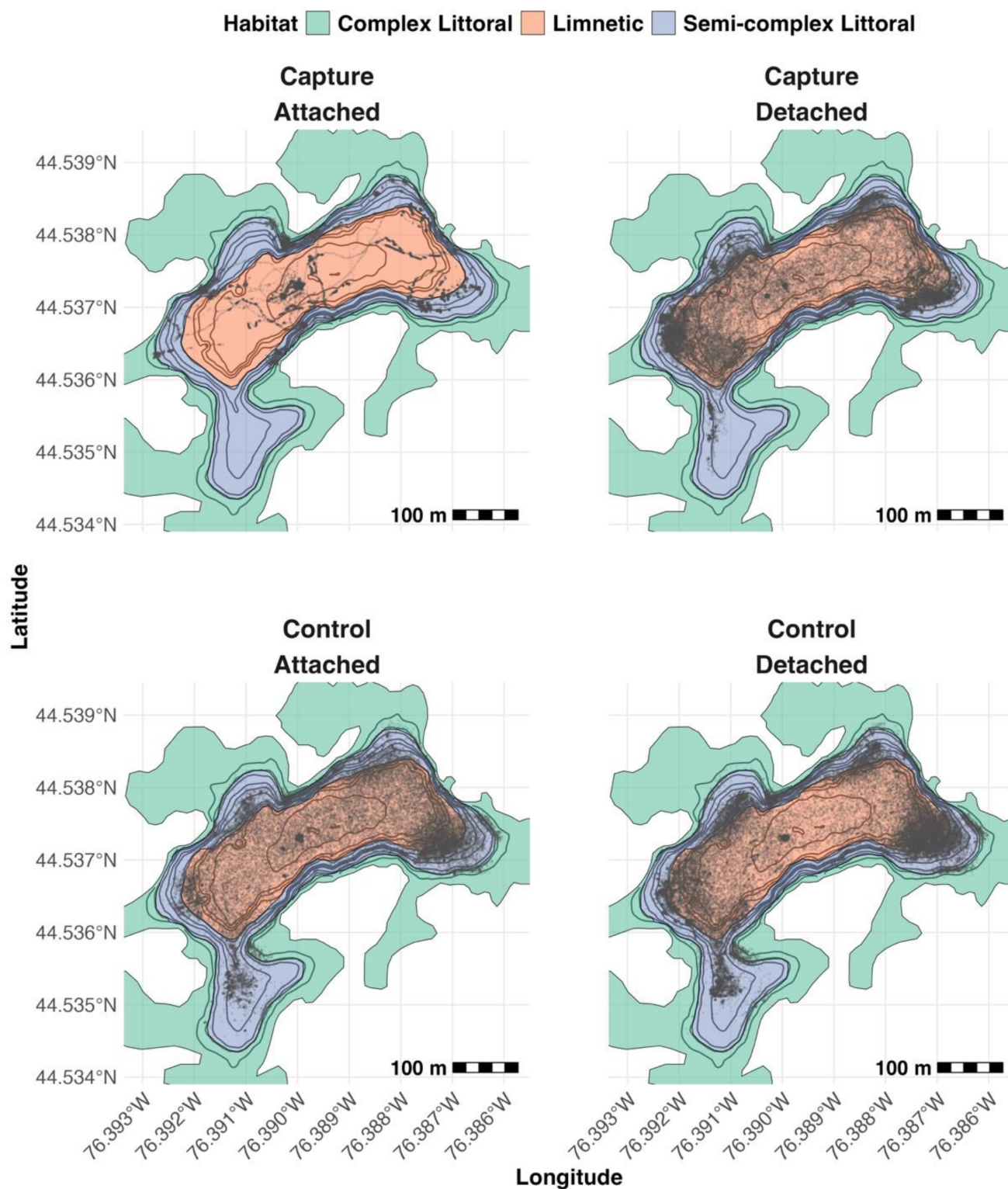


FIGURE 2 Transparent grey points represent the location of captured ($n = 6$) and control ($n = 6$) Largemouth Bass *Micropterus nigricans* while pop-off biologging packages were attached or detached during the same periods. The number of detections is weighted the same between the captured and control fish.

Fish remained submerged during the entire process of affixing the pop-off biologging packages, which took <45 s. Detachment of biologging packages was identified using depth data from the

biologgers. The pop-off biologging package was deemed to be detached from the fish when there was a steady decrease in depth, and the depth remained at 0 m (i.e., the biologist was at the

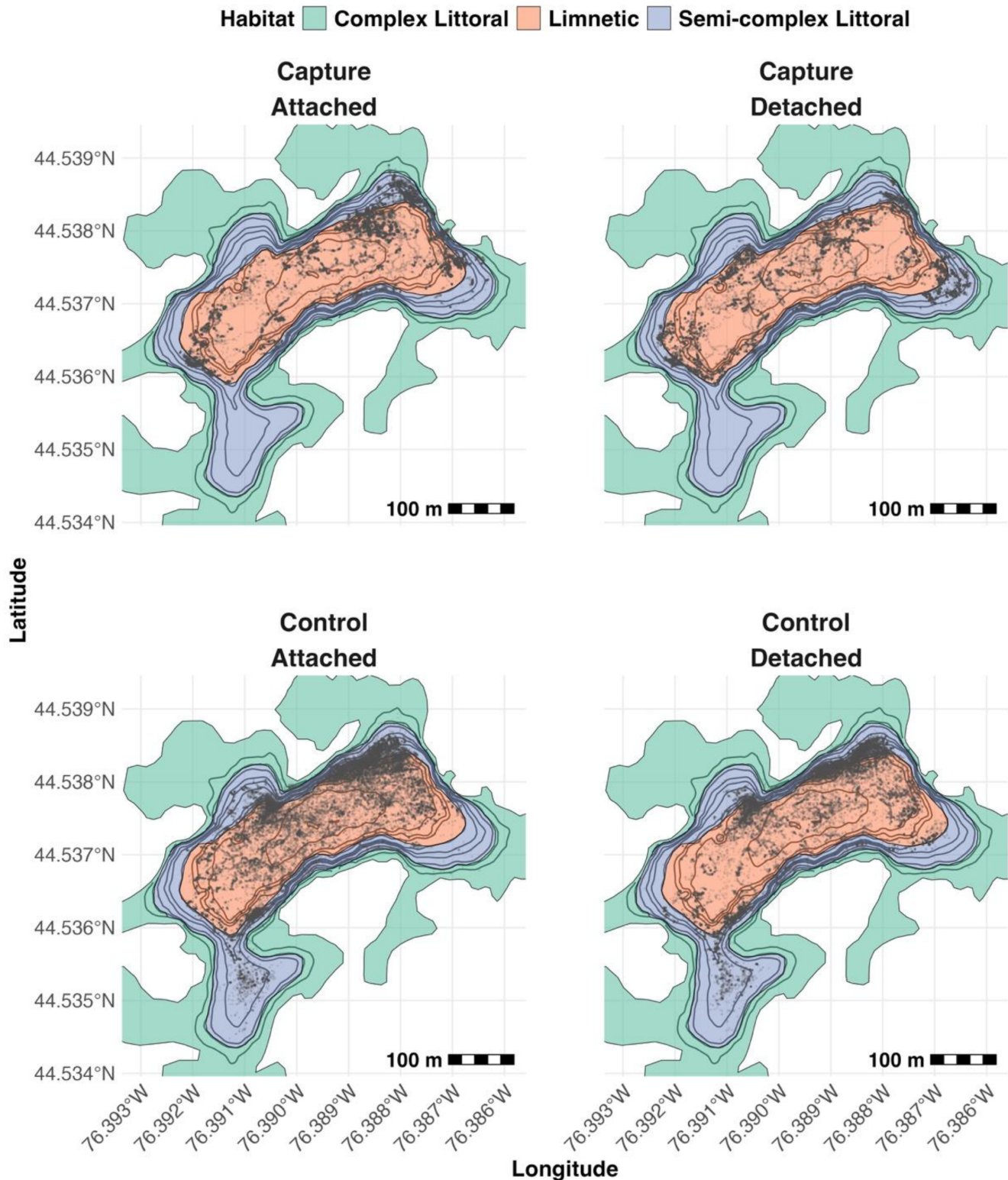


FIGURE 3 Transparent grey points represent the location of captured ($n = 6$) and control ($n = 4$) Northern Pike *Esox lucius* while pop-off biologging packages were attached and detached during the same periods. The number of detections is weighted the same between the captured and control fish.

surface). The last time point prior to the constant decrease in depth was used as the timestamp for being attached to a fish. Pop-off biologging packages had a relative size of 12% of the mean total length for Largemouth Bass and 8% for the Northern Pike.

2.4 | Acoustic telemetry monitoring

Fine-scale positing estimates for both species were created using the Innovasea High Residency system using hyperbolic positions based on

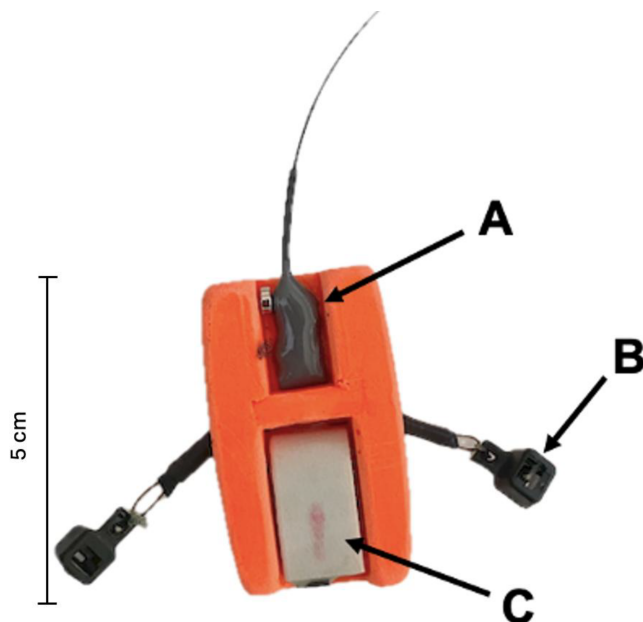


FIGURE 4 Custom floating pop-off biologging package used to assess the behaviour of fish in the wild. This package contains a radio transmitter (a), an internal data storage tag (b) and receptacles for self-locking straps (c) used to affix the biologging package to fish.

the timing of detections (Smith, 2013). Five reference transmitters were used to calculate the estimated horizontal position error (HPE; Figure 1), which was used as an estimated positional error for each fish position (Smith, 2013). HPE was calculated using the horizontal distance between a synthesized position [i.e., measured HPE in m - (HPEm)] of reference tags and the known receiver location. Based on the HPEm from the reference tags, we removed all detections with an HPE > 1.5 (Smith, 2013). This HPE cut-off had a mean HPEm of 1.8 m, with 99% of the measured errors being below 5.8 m. Two-dimensional positions had a median interval of 16 s.

To avoid confounding impacts from the angling event on the behaviour of fish, only fish that retained their pop-off biologging packages until after behavioural recovery from angling were used in the analyses (LaRochelle et al., 2026). Based on previous results on behavioural recovery, Largemouth Bass that retained pop-off biologging packages for 9.5 days and Northern Pike that retained pop-off biologging packages for 9 days were used. Of the fish used for this study, Largemouth Bass retained their pop-off biologging packages for a median duration of 245 h (± 67 SD), and Northern Pike retained pop-off biologging packages for a median duration of 281 h (± 83 SD).

Habitat use by each fish was determined by calculating the total number of minutes each fish spent in the complex littoral, semi-complex littoral and limnetic zones, or the amount of time not positioned for each hour of the 144-h monitoring period (72 h with the pop-off biologging package attached, 72 h after detachment). The total time both fish species were not positioned within the array was also included as an undetected period to account for the period that the fish were not being positioned within the array. Control fish were not separated into the attached and detached periods. Given

the high detectability of fish in the middle of the lake (Figures 2 and 3), fish that were not detected were assumed to be in the complex littoral zone. The proportion of time per hour that fish were not positioned was also included in the pop-off biologging package status variable for modelling. Positions of fish for each hour were only included if they were positioned within 5 min of the previous positioning. Movement was assessed across all hours during the monitoring period by calculating the step length, net displacement and the tortuosity for each individual and hour. Total step length was calculated by summing the distance between consecutive points for each hour, providing the overall movement. The net displacement was calculated as the distance between the initial and final locations of the animal within a given hour. Finally, tortuosity was used to determine how direct or indirect the movement behaviour (i.e., straightness or sinuosity; Bovet & Benhamou, 1988; Benhamou, 2004; Postlethwaite et al., 2013) of the fish was during each hour. For tortuosity, values near 1 suggest straighter swimming paths, while values nearing 0 represent swimming paths that are more tortuous. The tortuosity was calculated as a ratio by dividing the net displacement by the total step length for each hour for each fish.

2.5 | Statistical analysis

All statistical analyses were performed in R version 4.5.1 (R Core Team, 2025) via R studio (2025.05.1.153; Posit team, 2025). Plots were created using the *ggplot2* package (Wickham, 2016). Pairwise comparisons were used to assess differences between the pop-off biologging package status (i.e., attached, detached and control) for each model using the *contrast* function from the *emmeans* package (Lenth, 2025). Significance threshold was $\alpha = 0.05$ for all models and post-hoc testing.

Proportion of time among habitats was modelled for both species with generalized linear models with a beta regression distribution using the *glmmTMB* function from the *glmmTMB* package (Brooks et al., 2017). For both the Largemouth Bass and Northern Pike, generalized mixed effects models were fit with the interaction of pop-off biologging package status (i.e., tag attached, detached and control) and habitat type (i.e., undetected, complex littoral, semi-complex littoral and limnetic) as fixed effects. These models also included fish ID as a random effect to account for repeated measures of individuals.

We then used k-means clustering to identify and classify different behaviour types based on the tortuosity, step length displacement and net displacement of both species. The same three behaviour types were identified (cruising, exploring and stationary) and used across both species for the analyses. Cruising consisted of long linear displacements with little tortuosity (i.e., straight swimming), exploring was identified when fish had a short net displacement, but a long step length and high tortuosity (i.e., several turns in a localized area), and stationary was identified with minimal net and step length displacement. To assess if the identified behaviour types (e.g., cruising, exploratory and stationary) from the k-means clustering differed across the status of pop-off biologging packages (e.g., attached, detached, control), three separate generalized linear mixed models were fit using



FIGURE 5 Release photos of a Largemouth Bass *Micropterus nigricans* (a) and a Northern Pike *Esox lucius* (b) with a pop-off biologging package affixed between their pectoral fins.

TABLE 1 Pairwise comparisons of the proportion of time spent in habitats between the different periods of pop-off biologging attachment of Largemouth Bass *Micropterus nigricans* and Northern Pike *Esox lucius*.

Species	Habitat	Comparison	z ratio	Standard error (SE)	p-value
Largemouth Bass	Undetected	Attached-detached	10.143	0.074	<0.001
		Attached-control	1.388	0.038	0.347
		Detached-control	-12.315	0.022	<0.001
	Complex littoral	Attached-detached	2.581	0.048	0.027
		Attached-control	-1.651	0.032	0.225
		Detached-control	-5.130	0.028	<0.001
	Semi- complex littoral	Attached-detached	-6.250	0.036	<0.001
		Attached-control	3.188	0.041	0.004
		Detached-control	11.516	0.055	<0.001
	Limnetic	Attached-detached	-11.519	0.027	<0.001
		Attached-control	-5.609	0.029	<0.001
		Detached-control	9.607	0.051	<0.001
Northern Pike	Undetected	Attached-detached	-1.800	0.042	0.170
		Attached-control	4.726	0.048	<0.001
		Detached-control	5.537	0.054	<0.001
	Complex littoral	Attached-detached	0.397	0.042	0.917
		Attached-control	-0.064	0.038	0.998
		Detached-control	-0.488	0.033	0.877
	Semi-complex littoral	Attached-detached	3.803	0.052	<0.001
		Attached-control	-0.541	0.038	0.851
		Detached-control	-4.271	0.033	<0.001
	Limnetic	Attached-detached	-3.478	0.039	0.002
		Attached-control	-8.114	0.027	<0.001
		Detached-control	-3.900	0.035	<0.001

Note: Bold rows represent comparisons that are significantly different.

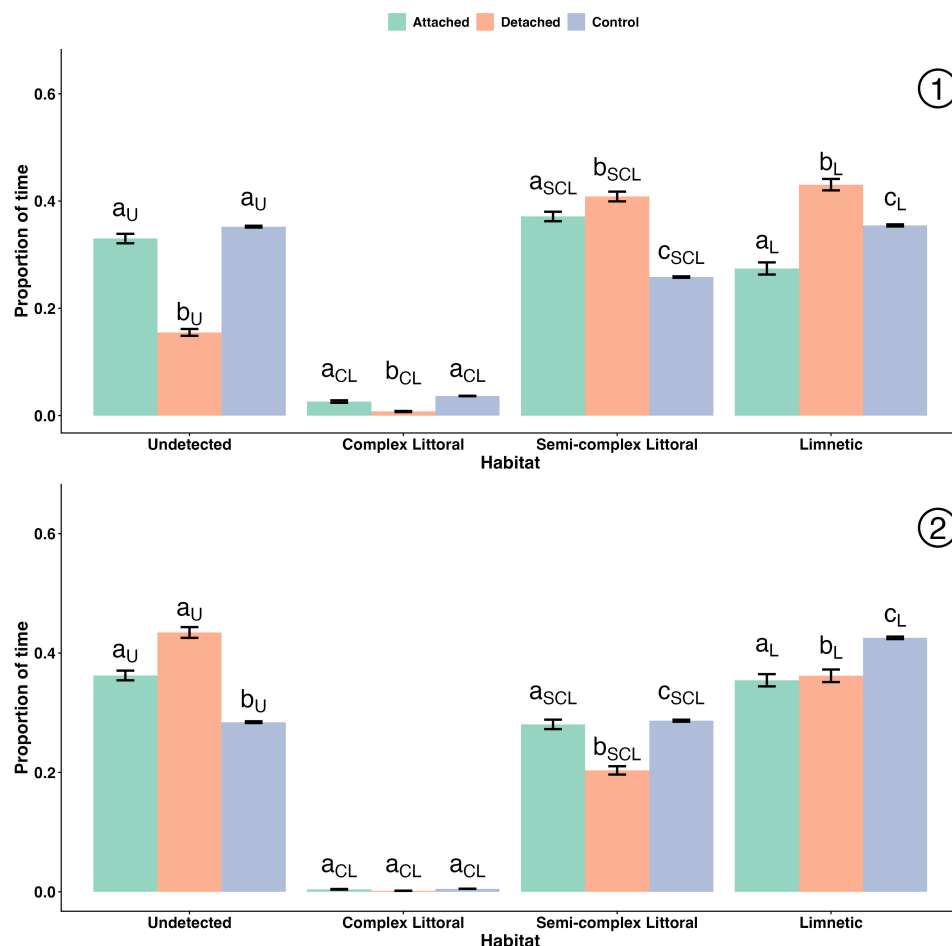
the *glmer* function from the *lme4* package (Bates et al., 2015). All models were fit with pop-off biologging package status as the fixed variable, and fish ID as a random variable to account for the repeated measures on individual fish. These models used a binomial distribution because the data consisted of counts for each fish across the hours of the monitoring period. For each fish at each given hour, the behavioural type identified was assigned a 1, while a 0 was assigned to the other behaviour types for that fish in that given hour. This method allowed us to calculate the proportion of time spent engaging in the different behaviour types.

3 | RESULTS

3.1 | Largemouth bass

Pop-off biologging package status influenced the proportion of time that Largemouth Bass spent in different habitats ($\chi^2 = 498.060$, $df = 6$, $p < 0.001$). Habitat use of Largemouth Bass shifted substantially once the pop-off biologging packages were detached (Table 1; Figure 6-1). Generally, when pop-off biologging packages were attached to Largemouth Bass, they spent more time near refuge

FIGURE 6 Proportion of time ($\pm$ standard error) that Largemouth Bass *Micropterus nigricans* (1) and Northern Pike *Esox lucius* (2) spent in different habitats based on their pop-off biologging status (i.e., attached, detached or control). Dissimilar letters represent significant differences in the proportion of time spent in a habitat. Subscripts on the letters are used to represent which habitat group the letters belong to.



compared to the controls or when the tags were detached (Figure 6-1). Largemouth Bass spent significantly more time in the limnetic and semi-complex littoral zone once pop-off biologging packages were detached, compared to when they were attached (Table 1; Figure 6-1). Similarly, control Largemouth Bass spent more time in the limnetic habitat and less time in the semi-complex habitat compared to when the pop-off biologging packages were attached. When equipped with a pop-off biologger, Largemouth Bass went undetected at a similar rate as the control Largemouth Bass, but was significantly more than when the pop-off biologging packages were detached (Table 1; Figure 6-1).

Movement behaviour analyses revealed clear differences between control Largemouth Bass and the Largemouth Bass that were attached with pop-off biologging packages. The movement behaviour of Largemouth Bass changed once the pop-off biologging packages were detached and was similar to that of the control Largemouth Bass once detached (Figure 7-1). The pop-off biologging package status had a significant influence on the cruising behaviour ($\chi^2 = 55.534$, $df = 2$, $p < 0.001$), exploration behaviour ($\chi^2 = 9.350$, $df = 2$, $p = 0.009$) and stationary behaviour ($\chi^2 = 34.211$, $df = 2$, $p < 0.001$) of Largemouth Bass. Control Largemouth Bass spent significantly more time cruising (53% more) compared to Largemouth Bass attached with pop-off biologging packages, and control Largemouth Bass spent significantly less time stationary (Table 2; Figure 7-1).

Stationary behaviour was reduced by 51% when pop-off biologging packages were detached from Largemouth Bass compared to when the pop-off biologging packages were attached. Largemouth Bass also spent 71% more time stationary when attached with a pop-off biologging package compared to controls. The exploration behaviour of Largemouth Bass increased significantly after the pop-off biologging packages were detached (increase of 96%), and when attached with the pop-off biologgers, they spent significantly less time (97% less) exploring compared to controls. Once the pop-off biologging packages were detached, Largemouth Bass behaved similar to control Largemouth Bass (Table 2, Figure 7-1).

3.2 | Northern pike

Pop-off biologging package status influenced the proportion of time that Northern Pike spent in different habitats ($\chi^2 = 236.599$, $df = 6$, $p < 0.001$). Habitat used by Northern Pike changed significantly once the pop-off biologging packages were detached (Table 1; Figure 6-2). When Northern Pike were equipped with a pop-off biologging package, they spent a similar amount of time in the undetected state as when the pop-off biologging packages were detached. However, control Northern Pike spent significantly less time undetected compared to when the tags were attached or detached (Table 1). Control

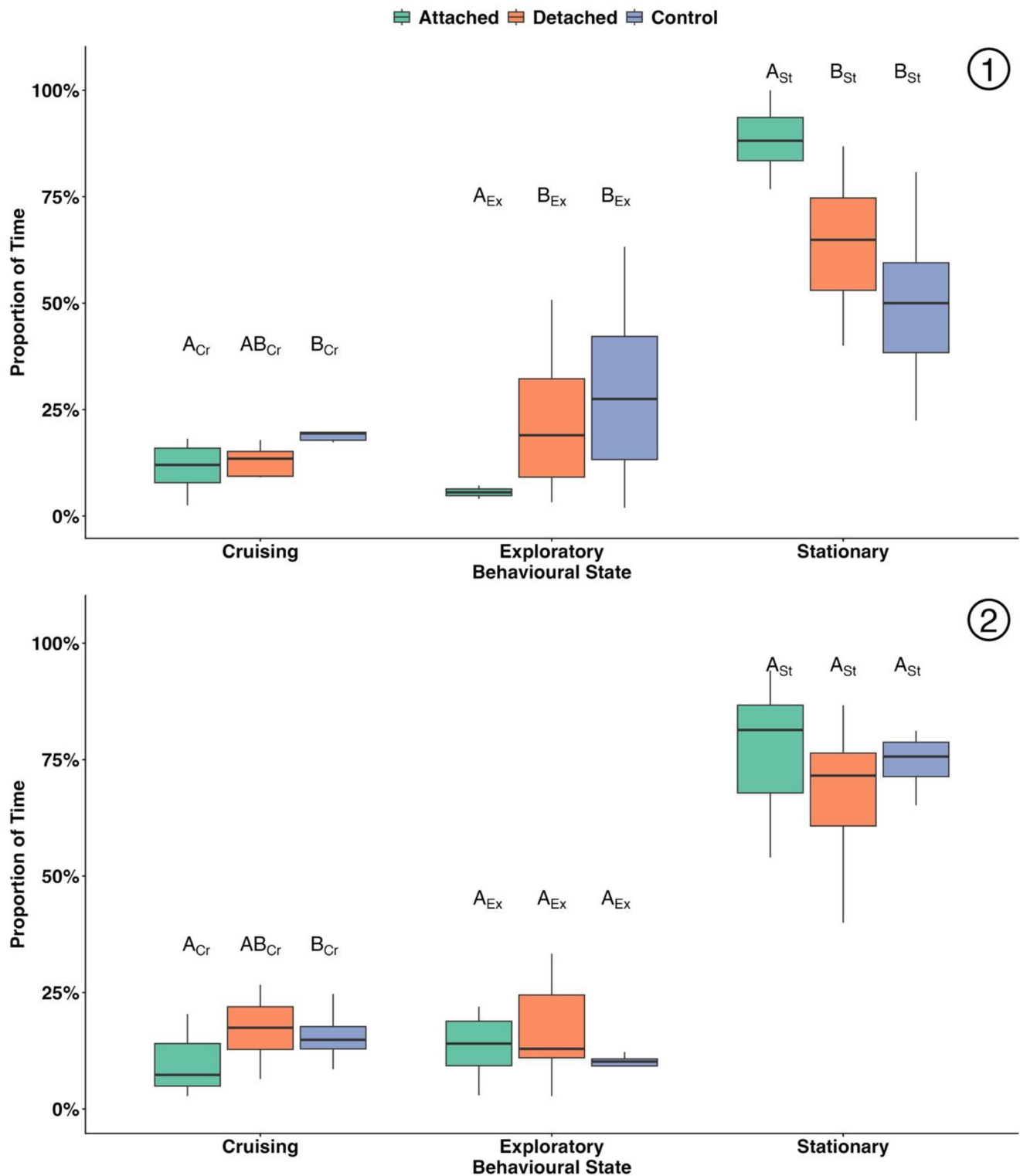


FIGURE 7 Proportion of time that Largemouth Bass *Micropterus nigricans* (1) and Northern Pike *Esox lucius* (2) spent engaging in the different behaviour types (cruising, exploring, stationary) while pop-off biologging packages were attached (72 h), after they were detached (72 h) and controls that were not equipped with pop-off biologging packages (144 h). Behaviour types were classified with k-means clustering, whereby cruising behaviour was identified with long linear movements, while exploratory behaviour consisted of long step lengths, with high tortuosity and smaller linear distances. Short step lengths and small net displacement were classified as stationary behaviour. Dissimilar letters represent significant differences in the proportion of time engaging in the specific behaviour. Subscripts on the letters are used to represent which behaviour type the letters belong to.

TABLE 2 Pairwise comparisons of movement behaviour types across the pop-off biologging package status (e.g., attached, detached and control) for Largemouth Bass *Micropterus nigricans*.

Species	Behaviour type	Comparison	z ratio	SE	p-value
Largemouth Bass	Cruising	Attached-detached	-2.139	0.148	0.082
		Attached-control	-3.032	0.120	0.007
		Detached-control	-1.297	0.178	0.397
	Exploratory	Attached-detached	-5.829	0.025	<0.001
		Attached-control	-4.024	0.034	<0.001
		Detached-control	-0.141	0.557	0.989
	Stationary	Attached-detached	7.075	1.160	<0.001
		Attached-control	5.074	3.340	<0.001
		Detached-control	1.245	0.608	0.427

Note: Bold rows represent comparisons that are significantly different.

Northern Pike spent significantly more time in the limnetic and semi-complex habitats compared to when the pop-off biologging packages were attached or detached. Once the pop-off biologgers were detached, Northern Pike spent significantly less time in the semi-complex habitat and more time in the limnetic habitat compared to when the pop-off biologging packages were attached (Table 1, Figure 6-2). Finally, pop-off biologging packages did not significantly influence the movement behaviour of Northern Pike. Neither the exploratory behaviour ($\chi^2 = 5.596$, $df = 2$, $p = 0.061$), stationary behaviour ($\chi^2 = 0.244$, $df = 2$, $p = 0.885$), or the cruising behaviour ($\chi^2 = 4.319$, $df = 2$, $p = 0.115$) of Northern Pike differed when equipped with pop-off biologging packages compared to the controls or when the packages were detached (Figure 7-2).

4 | DISCUSSION

Although there have been studies that have assessed the impacts of external tagging (reviewed in Jepsen et al., 2015), fewer have assessed the behaviour of fish in the wild with external biologging packages. We used fine-scale positions of fish that were previously tagged with acoustic transmitters, equipped with external pop-off biologging packages and compared their behaviour with and without those external biologgers. This unique opportunity to assess tag effects on the behaviour of fish provides valuable insight that is worth considering in future studies using external tagging methods when assessing the behaviour of fish in the wild. Overall, we found clear evidence that external pop-off biologging packages influenced the behaviour and habitat use of both Largemouth Bass, and only habitat use of Northern Pike. Largemouth Bass spent greater time in habitats that were more complex and provided more refuge when attached with an external pop-off biologging package. Once the external pop-off biologging packages were detached from the Largemouth Bass, they spent more time in the limnetic zone of the lake. Largemouth Bass spent more time stationary when equipped with an external pop-off biologging package, and only after the pop-off package was detached did they spend more time cruising and exploring, similar to controls. When equipped with pop-off biologging packages, Northern Pike spent more time in the semi-complex habitat compared to after the

tagging package detached. Interestingly, control Northern Pike spent even more time in the semi-complex habitat compared to when the pop-off packages were attached, possibly suggesting that the influence of pop-off packages on the normal behaviour of Northern Pike is not as biologically meaningful. The overall movement behaviour of Northern Pike was unaffected by the attachment of the external pop-off biologging package.

Habitat complexity has an important influence on the ability to acquire food and seek refuge from predators (Mikheev et al., 1997; Mikheev et al., 2010). The habitat type used when the external pop-off biologging package were removed suggests that the fish may feel they are at greater risk of predation (e.g., from mammals or avian predators) when the external pop-off biologging packages are attached and feel more 'comfortable' to explore open habitats once the pop-off biologging packages are detached. Feeding efficacy increases with decreasing habitat complexity (Eklöv, 1997; Savino & Stein, 1982), suggesting that being able to use the open limnetic habitat frequently is important for food acquisition. The shift in habitat used with and without an external pop-off biologging package is an indication that behavioural trends changed from vulnerable, frightened or defensive in the complex habitat areas to more of a risk-prone behaviour (e.g., bold and exploratory) where they were actively searching for forage in the limnetic zones. Although fish are able to feed in semi- to complex habitats, the efficacy of capturing prey is typically reduced (Eklöv, 1997; Savino & Stein, 1982). Ultimately, anything that could reduce the feeding efficacy of fish by not engaging in actively seeking prey (e.g., equipped with the external pop-off biologging package) could have negative implications for the fitness of fish.

External tagging methods have the potential to create excessive drag that can impact swimming performance, energy expenditure and oxygen consumption of fish (reviewed in Jepsen et al., 2015). Tag burden from external tagging methods reduces critical swimming speeds of fish (McCleave & Stred, 1975; Peake et al., 1997), decreases time to exhaustion (Mellas & Haynes, 1985) and increases oxygen consumption (Steinhausen et al., 2006). However, the influence of tag burden is size-specific, and not all fish are impacted to the same degree (Gray & Haynes, 1979; Sundström & Gruber, 2002). There was evidence that the external pop-off biologging packages used in this study had an impact on the movement of Largemouth Bass, whereas

the movement of Northern Pike was not influenced. This is likely due to Northern Pike having a larger body size compared to Largemouth Bass, and thus could accommodate the extra drag from the external pop-off biologging package. The increase in cruising and exploratory behaviour of Largemouth Bass after the external pop-off biologging packages were detached suggests that their swimming performance might have been influenced by the attachment of the external pop-off biologging packages. Largemouth Bass likely needed to expend more energy to move around the environment and became exhausted faster when equipped with external pop-off biologging packages. Finally, swimming performance is vital for avoiding or evading predators (Walker et al., 2005) and capturing prey (Borla et al., 2002; Budick & O'Malley, 2000; Higham et al., 2007; Rice & Westneat, 2005). Therefore, negative impacts on fitness could occur for Largemouth Bass when external pop-off biologging packages are given, as the swimming performance (i.e., movement behaviour) of fish was impeded.

Future research should aim to identify the body to external tag ratio or other aspects of tag design (e.g., shape influences on drag) that do not cause biologically meaningful differences in the behaviour of fishes, building on the existing evidence base (see Jepsen et al., 2015). The current study suggests that larger-bodied fish (e.g., Northern Pike) were marginally impacted by the attachment of the external pop-off biologging packages, yet the results do not provide evidence of how larger fish in marine systems or migratory species would be impacted by the attachment of external biologging packages. With such small nuances in the behaviour of Northern Pike in our study, it is unlikely that these packages would have much of an effect on larger fish species, although that has yet to be tested. The approach we used to test tagging impacts associated with external attachment was unique and took advantage of a small, high-resolution whole-lake telemetry array capable of positioning tagged fish with high levels of precision and accuracy. Similar arrays are not overly common, such that it is not often that the approach used here could be applied elsewhere. Nonetheless, it has merit where such opportunities exist.

As more studies use external biologging methods to assess the behaviour of fish in the wild, it is important that the interpretation of the results considers the impacts that biologgers have on the habitat use and movement behaviour of fish. We found that habitat use and movement behaviour of fish differed when equipped with external pop-off biologging packages. The swimming activity of Largemouth Bass is likely being underestimated when using external tagging methods, while the swimming activity of Northern Pike is presumably more accurate. Because habitat use was influenced by the presence of the external pop-off biologging package, determining if fish are using those habitats because of an acute stress (e.g., catch-and-release) event will be challenging, but critical for determining the extent of the acute stress event. Being able to disentangle tagging effects from acute stress-induced behavioural differences will be important for the interpretation and contextualization of results in future studies. Finally, given the changes in habitat use and movement behaviour that occur from carrying external pop-off biologging packages, unnecessarily long

attachment periods should be avoided. In similar contexts to this study (e.g., fish of small to moderate body size), external pop-off biologging packages should only be attached to fish for the period of time that fish are behaviourally impaired from the capture, or an acute stress event, to avoid any negative impacts the pop-off biologging packages could have on the fitness of fish.

AUTHOR CONTRIBUTIONS

Conceptualization: L.L., S.J.C.; data curation: L.L., M.B.S., G.D.R.; data collection: L.L., M.B.S., G.D.R.; formal analysis: L.L., G.D.R., J.W.B.; visualization: L.L., G.D.R., J.W.B.; funding acquisition: S.J.C., G.D.R., A.T.F.; writing—original draft: L.L.; and writing—review & editing: L.L., S.J.C. A.J.D., G.D.R., J.W.B., M.B.S., A.T.F.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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