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Acoustic telemetry informs conditional capture probability of an anadromous fish

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ABSTRACT

Information on movement ecology and susceptibility to fishing gears is becoming increasingly employed in the management of commercial fisheries. This study combined acoustic telemetry (n = 51 and 52) and a simple passive integrated transponder (PIT) tag (n = 1499 and 1113) mark-recapture study, across two successive years on a commercial river lamprey (*Lampetra fluviatilis*) fishery, to inform exploitation rates and the influence of conditional capture probability on expected catch-per-unit-effort (CPUE). The movements of acoustic-tagged lamprey were used to refine estimates of the number of PIT-marked individuals vulnerable to the fishery. In 2018, this increased the recapture rate estimation by 0.99% and reduced the estimated run size by 152,101 (21.6%; 95% CL, 148,683, 155,688) individuals, with corresponding values of 0.12% and 114,639 (25.0%; 95% CL, 112,900, 116,448) in 2019. Lamprey movements were similar between years, with the number of trap line encounters by individuals between trap lifts used to inform expected CPUE for each lift. Conditional capture probability was mainly dependent on environmental conditions (e.g., river flow) with most trap lifts in the expected CPUE range, although the impacts of behaviour on vulnerability to capture were difficult to disentangle. This study highlights how the incorporation of acoustic telemetry increased the accuracy of, validated, and complemented mark-recapture data, without which management decisions (e.g., quota size) would have been based upon over 100,000 more individuals (27.5% higher than the adjusted run size in 2018 and 33.3% higher in 2019), with potentially severe consequences for the population. These findings demonstrate the importance of understanding fish movement to improve and inform fishery management. The study also presents a framework to quantify conditional capture probability and its influence on CPUE; knowledge that is widely applicable across aquatic systems for management and sustainability of fisheries.

1. Introduction

For centuries, commercial fisheries have exploited marine and freshwater biota; providing food, sport and ornamental trade (Cooke and Cowx, 2006; Britten et al., 2021). Consequently, many fish stocks worldwide are exploited and/or depleted (Anticamara et al., 2011), with overexploitation and collapses of major fisheries raising important concerns about the effects of harvest on fish populations (Worm and Branch, 2012; Zhang et al., 2018). Therefore, many commercial fisheries are managed and regulated using tools such as regulations on the use and structure of fishing gear, spatial and temporal fishing restrictions, size limits for target fish, and limitations on landings (e.g., use of quotas) (Liu et al., 2016). Nevertheless, more advanced fishery management is becoming increasingly common and has resulted in a progressive change from stock-based assessment to incorporating information on movement ecology and susceptibility to fishing gears, including by the use of animal telemetry (Cooke et al., 2016; Crossin et al., 2017; Reis-Santos et al., 2022).

Telemetry has been utilised for fishery management by protecting fish stocks through establishing boundaries (Hussey et al., 2017), Marine

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Protected Areas (MPAs) (Lea et al., 2016) and detecting movements through fishery jurisdictions on a continental-scale (Lédée et al., 2021). Furthermore, telemetry data can be used to inform management decisions by incorporation into catch models (Fielder et al., 2020), for example by informing temporally specific closures to protect bycatch species of conservation importance (Melnychuk et al., 2017). One of the main uses of telemetry in fisheries management is to make solid evaluations of catch proportions (i.e., how large a fraction of a given population is caught in a fishery), with acoustic tracking data an especially useful tool when integrated into mark–recapture models (Dudgeon et al., 2015; Melnychuk et al., 2017; Withers et al., 2019). The precision of parameter estimation, impossible using catch data alone, is improved and enabled, especially when low recapture rates are observed (Dudgeon et al., 2015; Withers et al., 2019), providing calibrated outputs with low bias due to large sample sizes (Mudrak and Szedlmayer, 2019; Withers et al., 2019). Nevertheless, acoustic telemetry is currently an underutilised resource within fisheries management (Lees et al., 2021).

Effective management is especially important when anadromous species are exploited as they must migrate between marine and freshwater environments to complete their life cycles (Lucas and Baras, 2001). These species are susceptible to overexploitation in estuarine and river 'bottlenecks' where migrating fish aggregate and can be exploited intensively, reducing the numbers of individuals reaching spawning habitat and subsequently contributing to future generations (Cooke et al., 2016; Almeida et al., 2021). This is exemplified by the Apalachicola River Gulf Sturgeon (*Acipenser oxyrinchus desotoi* Vladykov, 1955) fishery where stocks have still not recovered 45 years after its closure (Flowers et al., 2020). Moreover, anadromous species often have to pass multiple physical obstacles, such as dams and weirs, to reach spawning habitats. Anthropogenic structures often delay migration and can result in retreat to search for alternative upstream migration routes (Davies et al., 2022), potentially increasing exposure to fisheries located downstream of barriers, as well as reducing the number of adults that reach spawning grounds (Davies et al., 2021). Although weirs are widely employed, directly or indirectly, for exploitation of migratory fishes in rivers (Gudjónsson, 1988; Wolter, 2015), few studies have quantified or determined the mechanism of impact of barriers on exploitation rates in, or performance of, commercial fisheries located downstream.

This study was performed on an exploited population of river lamprey (*Lampetra fluviatilis* [Linnaeus 1758]) in the tidal reaches of a major tributary to a large UK estuary, downstream of the first anthropogenic barrier encountered by immigrating adults. The river lamprey is an anadromous species of high conservation importance that has declined in abundance across its range for several reasons, including exploitation by commercial fisheries and due to migration barriers (Masters et al., 2006; Lucas et al., 2021). Further, river lamprey are semelparous, dying after their only spawning migration (Johnson et al., 2015) and, thus, are particularly susceptible to over exploitation. The overall aim of this study was to incorporate acoustic telemetry data into a simple mark-recapture study, performed across two years, to inform exploitation rates (estimated from recaptures of marked individuals by the fishery) and the influence of conditional capture probability (probability of capture of an individual fish being conditional on the individual fish encountering a trap line) (Guy et al., 2009; Bunch and Stewart, 2020) on expected catch-per-unit-effort (CPUE), a measure of relative abundance. It was hypothesized that the weir would modify lamprey movements and result in increased frequency and duration of exposure to the fishery, resulting in elevated CPUE and increased conditional capture probability, but that river conditions facilitating weir passage would thereby reduce conditional capture probability. Specific objectives were to 1) refine the seasonal exploitation rate and run-size estimates, 2) determine lamprey trap lift and trap line specific recapture rates and the relationship between lift specific CPUE and recapture rate, 3) identify daily, lift specific and seasonal variations in lamprey approach to, passage at, and retreat movement from, the anthropogenic barrier, and 4) establish the relationship between trap line encounters and recapture rate. Our results are discussed in relation to improved fisheries management of migratory fishes, especially for anadromous species in fragmented catchments.

2. Methods

2.1. Study site and flow data

This study occurred over the authorised fishing season (01-Nov – 10-Dec) during consecutive years, 2018 and 2019, in the Yorkshire Ouse commercial lamprey fishery, north east England (Fig. 1). The Yorkshire Ouse is one of the major catchments of the Humber Estuary, which supports one of the UK's largest river lamprey populations (a designated feature [under the EU Habitats and Species Directive] of the Humber Special Area of Conservation [SAC]) (Foulds and Lucas, 2014). The fishery supplies dead river lamprey to the recreational fishing market in the British Isles (Foulds and Lucas, 2014; Albright and Lucas, 2021). While the Humber fishery is relatively small (removal of ~10 000 – 31 000 lamprey annually between 1995 and 2012 [Foulds and Lucas, 2014] but limited to ~10,000 between 2011 and 2016), it has the potential to impact the local population of this species, which is conservation listed by the EU Habitats and Species Directive Annexes II and V. There is a dearth of knowledge of exploitation rate in the fishery, and potential impacts on the SAC, identified after a review of the fishery following the 2016 season, leading to a suspension of consumptive take from 2017 to 2018 on precautionary grounds. The fishery operates over a 7-km reach downstream of Naburn Weir (O1; 53.893767, −1.098963) and upstream of the River Wharfe tributary confluence (53.844130, −1.129653). Downstream of O1 the river is tidal. Although O1 has a pool-and-weir fish pass, and an elver/lamprey fish pass, the pool-and-weir fish pass was constructed for adult salmonids and the lamprey pass may not be particularly effective in field conditions (Lothian et al., 2020). The full fishery reach was studied, including O1 as well as the reach of river from the release site at R1 (1.54 km downstream of the Wharfe confluence; 53.835363, −1.129775) to the fishery reach.

2.2. Lamprey capture, handling and tagging procedure

River lamprey were captured using 40 Apollo II traps (ENGEL-NETZE, 2022) with modified soft mesh cod ends set across three lines 2.3 km (Trap Line 1; 14 traps), 4.1 km (Trap Line 2; 14 traps) and 5.0 km (Trap Line 3; 12 traps) downstream of O1, which were emptied on seven and six occasions throughout the 2018 and 2019 fishing seasons (01-Nov – 10-Dec), respectively (Fig. 1). These locations were chosen as the river's topography, and reduced tidal current, enabled traps to be fished effectively over tidal cycles, whereas this becomes progressively more difficult further downstream.

Following capture, lamprey were held in aerated, water-filled containers (120 L) treated with Virkon (0.5 g per 120 L; disinfectant, provides protection against fish viruses) and Vidalife (10 mL per 120 L; provides a protective barrier between fish and handling equipment, reducing friction and abrasion). All lamprey were inspected for signs of injury and disease prior to general anaesthesia with buffered tricaine methanesulphonate (MS-222; 1.6 g per 10 L of water); only undamaged individuals were tagged. Prior to tagging, PIT tags (2018 ($n = 1499$) = 32-mm long x 3.65-mm diameter, 0.8 g weight in air; 2019 ($n = 1113$) = 23-mm long x 3.65-mm diameter, 0.6 g weight in air; www.oregonrfid.com) were tested with hand-held detectors. This process was repeated for acoustic tags (2018 ($n = 47$) & 2019 ($n = 52$) = 20-mm long x 7 mm-diameter, 1.6 g weight in air (V7); 2018 ($n = 4$) = 20.5-mm long x 8-mm diameter, 2.0 g weight in air (V8); 69 kHz; www.innovasea.com).

After sedation, the lamprey were measured (total length mm) and weighed (g). Lamprey > 380 mm total length (mean mass: 100.2 g in 2018 & 105.6 g in 2019) were tagged with acoustic and PIT tags, whilst lamprey > 320 mm but < 380 mm (mean mass: 79.2 g in 2018 & 83.1 g

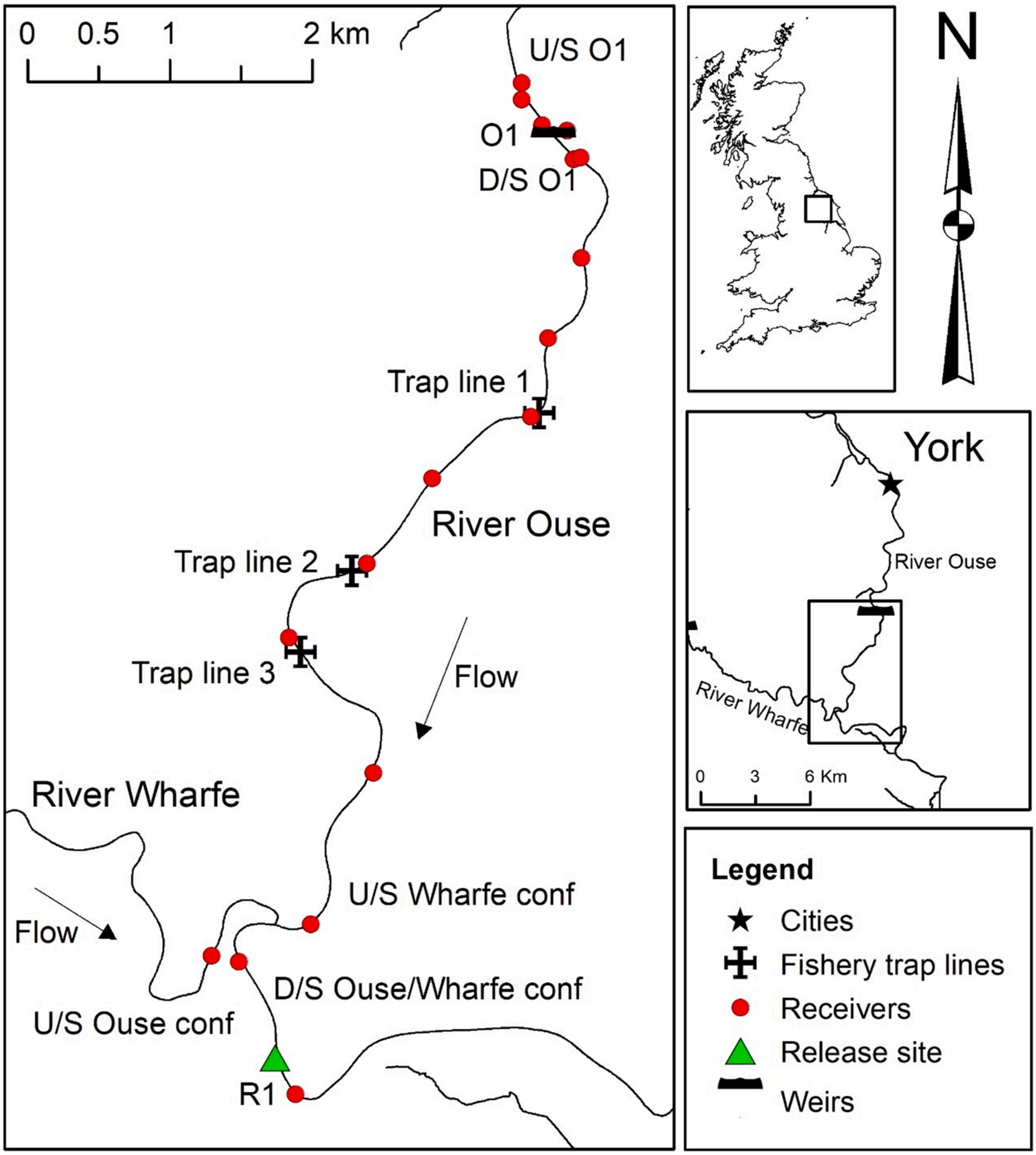

Fig. 1. A map of the commercial Yorkshire Ouse river lamprey fishery reach showing the location of Naburn weir (O1), the River Wharfe, trap lines, acoustic receivers and tagged lamprey release site.

in 2019) were only PIT tagged, with the total tag burden in air not exceeding 3.1% of fish mass, as per Jepsen et al. (2005) and Silva et al. (2017). Tags were implanted into the body cavity through a small mid-ventral incision, anterior to the first dorsal fin and the incision closed with an absorbable monofilament suture for acoustic-tagged fish. After surgery, lamprey were again held in treated and aerated, water-filled containers to recover. Lamprey were tagged in batches on each trap lift (except lift 5 in 2018 [extra lift due to high numbers caught in the fourth lift] and the last lift in each season), with all (2018: $n = 1499$, 2019: $n = 1113$) released at R1 (Fig. 1; Table 1) to examine the exploitation rate of the Yorkshire Ouse commercial lamprey fishery and lamprey movements through the fishery zone prior to each lift and overall.

From the second lift of the study in both years, the entire catch was checked for recaptured (PIT tagged) lamprey using hand-held PIT readers or a bespoke system where lamprey were funnelled through a pipe fitted with a half-duplex (HDX) Oregon PIT detection system. This system recorded the PIT tag code, unique for each tagged lamprey, and was tested using PIT tags passed through the system by hand before processing each run. In the third lift of 2018, repeat testing of captured lamprey identified nine recaptures in 53.15 kg ($n = 709$) of river lamprey using both hand-held and bespoke PIT readers, with all tests showing the bespoke system to be 100% efficient. All lamprey were treated in compliance with the UK Animals (Scientific Procedures) Act (ASPA) (1986) Home Office project licence number PD6C17B56.

2.3. Monitoring equipment

Acoustic-tagged lamprey were tracked using 17 strategically located omnidirectional acoustic receivers (Innovasea (formerly Vemco) VR2W-

Table 1
Number, length (mm) and weight (g) of the river lamprey tagged each trap lift during the 2018 and 2019 fishing seasons.

Date	Total tagged	PIT tagged	Acoustic + PIT tagged	Length (mm ± S.D.)	Weight (g ± S.D.)
07/11/2018	155	148	7	348 ± 26.9	73.5 ± 15.8
14/11/2018	294	282	12	357 ± 22.7	77.6 ± 16.9
21/11/2018	349	338	11	356 ± 23.5	75.4 ± 17.5
27/11/2018	340	329	11	361 ± 21.8	79.5 ± 16.1
05/12/2018	361	351	10	368 ± 22.0	82.8 ± 16.1
10/12/2018	-	-	-	366 ± 21.8	81.7 ± 15.9
2018 Total	1499	1448	51	360 ± 23.5	78.6 ± 16.6
08/11/2019	141	134	7	355 ± 18.6	76.6 ± 13.4
15/11/2019	269	255	14	361 ± 20.9	80.0 ± 14.4
22/11/2019	309	298	11	362 ± 23.3	81.7 ± 16.4
29/11/2019	209	199	10	365 ± 24.0	82.3 ± 17.1
05/12/2019	185	175	10	371 ± 24.9	88.7 ± 17.8
10/12/2019	-	-	-	369 ± 25.7	85.6 ± 18.8
2019 Total	1113	1061	52	364 ± 23.5	82.5 ± 16.8

69 kHz; www.innovasea.com), throughout the commercial river lamprey fishing season (01-Nov – 10-Dec) during both years (Fig. 1; Table 1). Specifically, receivers were located throughout the fishery reach, from R1 to upstream of O1, encompassing all trap lines and the confluence with the River Wharfe. All locations were chosen for effective reception conditions and ensured receiver detection range encompassed the width of the river (tested at installation). The receiver in the River Wharfe was placed so as to record acoustic-tagged lamprey ascending the Wharfe, and was positioned so that it could not detect tags within the main river. Detection efficiency calculations (using three sequential receivers to determine the efficiency of the middle receiver) revealed that all detections between receivers across both study years were 100% efficient. PIT antennas, operated 01-Nov – 10-Dec in both years, were used to quantify the number of PIT tagged lamprey detected in the elver and lamprey pass (2018 and 2019) and pool-and-weir fish pass (2018 only) present on the right hand bank at O1. Extreme flooding events in 2019 damaged antennas and prevented their installation in the pool-and-weir fish pass.

2.4. Data analysis

Acoustic telemetry detection data were processed to determine metrics related to acoustic-tagged lamprey movements, which were then used to inform the movements of PIT-tagged lamprey. The tracking period began when tagged lamprey were released into the fishery on 07-Nov 2018 and 08-Nov 2019, and ended at 12:00 on 10-Dec in both years, when the traps were removed.

A given ‘trap lift’ date refers to all catch and movements from the day of trap deployment until 00:00 on the day of the trap lift. The number caught in the fishery was the actual count of lamprey caught if all the catch was processed or calculated using the formula below if the catch was too large for all individuals to be processed.

1) Numbers caught in fishery (n) = (C_n * 1000) / C_w

where C_n was the catch (kg) on the specific lift, trap line or over the whole season and C_w was the mean weight (g) of all processed lamprey on that lift, trap line or over the whole season. 95% confidence limits were applied to all lifts where not all individuals were processed.As no lamprey were processed for tagging on 02-Dec 2018, weight measurements to determine the number of individuals caught was a mean of lamprey caught on 27-Nov and 05-Dec 2018.Acoustic-tagged lamprey are hereby referred to as ‘tagged’ individuals, whilst PIT-tagged lamprey are referred to as ‘marked’ individuals. Tagged lamprey were classed as available to the fishery between lifts if they were detected in the Ouse between the River Wharfe confluence and O1, classed as vulnerable to the fishery if they were detected on a receiver located at a trap line and classed as vulnerable to a trap line if they were detected on that trap line. Tagged lamprey were also classed as unavailable to the fishery if they were detected on any receiver upstream of O1, on any receiver in the River Wharfe or downstream of R1. The number of tagged lamprey available to the fishery between lifts was used to estimate the total numbers of marked lamprey available to the fishery between lifts. The same process was also used for vulnerability to the fishery as well as availability and vulnerability to each trap line. This was determined by the proportion of tagged lamprey available or vulnerable to the fishery or trap line compared to the number of tagged lamprey released and applying this proportion to the number of marked lamprey released.Full season and weekly recapture rate (similarly utilised by Bunch and Stewart, 2020), and run size through the fishing season were calculated as:

2) Recapture rate (R_s, %) = N_{rs} / N_{as} * 100
3) Run-size during the fishing season (P_s) = (C_t / R_s) * 100

where N_{rs} was the total number of recaptures, N_{as} was the number of marked lamprey at large, either unadjusted or adjusted according to acoustic tracking data, and C_t was the total catch (number of individuals) over the whole fishery or for each trap line.

Trap line specific recapture rates were calculated according to the number of marked lamprey (informed by tagged lamprey) vulnerable to each trap line. Due to the different numbers of traps on Trap Line 3 to Trap Line 1 and 2, trap line specific recapture rates were standardised, by dividing each trap line recapture rate by the number of traps on the line.

Tagged lamprey were considered to have approached and passed O1 when detected sequentially on either receiver immediately downstream and then on any receiver upstream, respectively. Tagged lamprey were present at O1 when detected at either receiver immediately downstream of O1 or until detection upstream or further downstream. A retreat from O1 occurred when a lamprey detected immediately downstream of O1 (either acoustic detection or PIT detection in either fish pass) was subsequently detected further downstream or recaptured. Retreat duration (Davies et al., 2022) was the time elapsed from last detection immediately downstream of O1 before retreating and the first detection back immediately downstream of O1 if returning to the weir or last detection in the study area / end of the tracking period if not returning to O1 for each individual retreat. Retreat distance was calculated the same as retreat duration but for distance moved during retreat movements. Tortuosity of a retreat movement was defined as the distance from either receiver downstream of O1 to the furthest downstream detection location distance, divided by the total distance moved on that retreat, with a tortuosity of 1 representing a straight movement. Using 95% of all successful passage attempts at O1 through the full migration period, 99.3 m^3/s was determined to be the passability threshold for O1 in this study. Wilcoxon Rank Sum tests were carried out to determine the differences between retreat distance between years. The same approach was followed for retreat duration and retreat tortuosity. Kruskal-Wallis tests were also used to determine the differences between lifts in each year for retreat duration, retreat distance and retreat tortuosity. These calculated metrics were non-parametric, thus medians were used in analyses.

Tagged lamprey were regarded as having encountered a trap line when they were detected on the receiver located at the trap line, with every detection on the trap line receiver after detection elsewhere classed as a new encounter. Any trap line encounters after approaching O1 were classed as retreat trap line encounters. Relative trap line encounters were the number of specific trap line encounters divided by the number of tagged lamprey vulnerable to each trap line overall, before approaching O1 and when retreating from O1.

Correlations (Spearman's Rank) were used to test for relationships between CPUE and recapture rate per trap line, combining data across the two seasons (2018 and 2019) to increase the sample size. The same approach was used to test for relationships between recapture rate and trap line encounters per vulnerable lamprey to each trap line overall, on first encounter and retreat from O1.

All statistical tests were carried out using R Statistical Software (version 4.0.2; R Core Team, 2020) whilst all other data analyses and graphical representations were performed in Microsoft Excel (Microsoft Corporation, 2018).

2.4.1. River flow data

River level flow (15-min interval; m^3/s) data were obtained from the Environment Agency gauging station at Skelton, River Yorkshire Ouse (15.0 km upstream of O1) to determine annual mean daily discharge (m^3/s) during the commercial river lamprey fishing season (01-Nov – 10-Dec) (Fig. S1). Non-parametric Wilcoxon Rank Sum tests compared the difference in median daily discharge during the commercial river lamprey fishing season (01-Nov – 10-Dec) between 2018 and 2019. The median daily discharge (01-Nov – 10-Dec) was significantly different between the two study years ($W = 295$, $p = <0.001$), with 2018

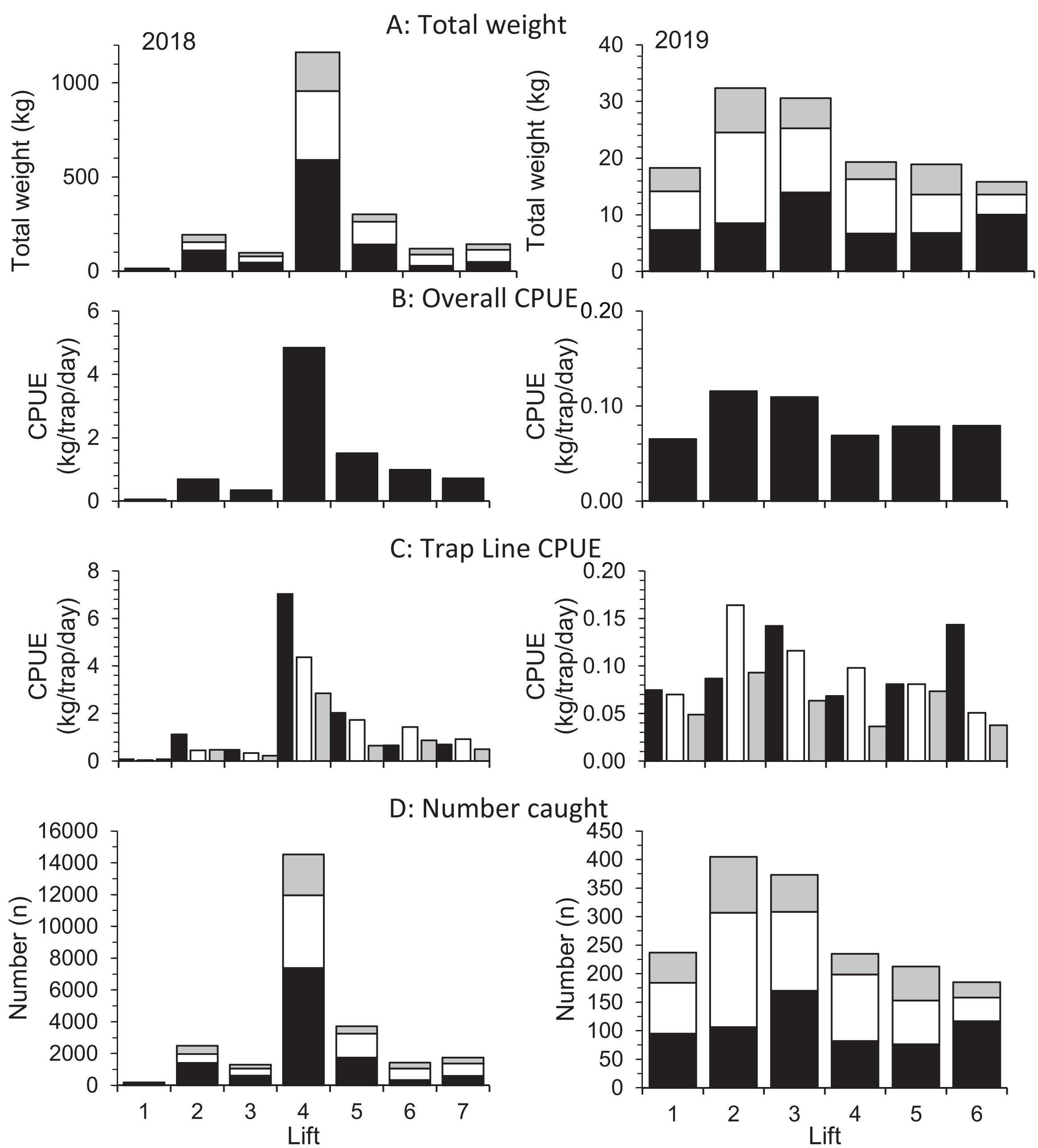

Fig. 2. Commercial fishery catch data of total weight (kg) caught (A), overall Catch Per Unit Effort [CPUE] (B), trap line CPUE (C) and the number of individuals caught (D) for Trap Line 1 (black), Trap Line 2 (white) and Trap Line 3 (grey) per lift during the 2018 and 2019 commercial lamprey fishing seasons. Note the differences in y-axis scale between 2018 and 2019.

(28.3 m^3/s) significantly lower (W = 20,339, p = <0.001) and 2019 (108.9 m^3/s) significantly higher (W = 8465, p = <0.001) than the long-term median (53.7 m^3/s). Indeed, the former was the third driest in the last 20 years, after 2003 and 2017, while the latter was the fourth wettest in the last 20 years, after 2000, 2009 and 2015 (Fig. S1).

3. Results

3.1. Catches, recaptures and run size estimates

3.1.1. Catches

Catches varied between years, with the total in 2018 (2031.64 kg) fifteen-fold higher than in 2019 (135.31 kg) (Fig. 2). In 2018, catches were highest at Trap Line 1, whereas in 2019 they were highest at Trap Line 2, although Trap Line 1 catches were similar (Fig. 2). Trap Line 3 had the lowest catches in both years (Fig. 2). During 2018, catches and CPUE varied dramatically between lifts and both were low across all lifts in 2019 (Fig. 2); the largest lift specific catch coincided with a flow increase not large enough to exceed the passability threshold of O1 (99.3 m^3/s) (fourth lift; Fig. S2, A).

3.1.2. Recaptures and run size estimates per season

In 2018, 54 marked lamprey were recaptured (three were also tagged), mostly in Trap Line 1 (n = 24), followed by Trap Line 2 (n = 18) and Trap Line 3 (n = 7), with five from an unknown trap line (Table 2). The movements of tagged lamprey were used to estimate the number of marked lamprey vulnerable to exploitation (21.6% [323 individuals] lower than the number released), which consequently increased the recapture rate by 0.99% and reduced the run size estimate by 152,101 (21.6%; 95% CL, 148,683, 155,688) individuals (Table 2). In 2019, four marked lamprey were recaptured (Trap Line 1 = 1, Trap Line 2 = 2, Trap Line 3 = 1) and the movements of tagged lamprey were used to estimate the number of marked lamprey vulnerable to exploitation (25.0% [278 individuals] lower than the number released). Consequently, this increased the recapture rate by 0.12% and reduced the run size estimate by 114,639 (25.0%; 95% CL, 112,900, 116,448) individuals (Table 2).

Table 2
The number of acoustic tagged and PIT-marked lamprey released and adjusted according to availability and then vulnerability to being exploited and the resulting impact on recapture rate (number of recaptures) and run size estimates (95% confidence interval) using the numbers caught (95% confidence interval) in 2018 and 2019.

	Released	Available to be exploited	Vulnerable to being exploited
2018			
Tagged lamprey	51	45	40
Marked lamprey	1499	1323	1176
Recapture rate (n = 54)	3.60%	4.08%	4.59%
Numbers caught (lower-upper)	25,404 (24,833–26,003)	25,404 (24,833–26,003)	25,404 (24,833–26,003)
Run size (lower-upper)	705,196 (689,346–721,824)	622,232 (608,246–636,904)	553,095 (540,663–566,136)
2019			
Tagged lamprey	52	41	39
Marked lamprey	1113	878	835
Recapture rate (n = 4)	0.36%	0.46%	0.48%
Numbers caught (lower-upper)	1648 (1623–1674)	1648 (1623–1674)	1648 (1623–1674)
Run size (lower-upper)	458,556 (451,600–465,791)	361,554 (356,069–367,258)	343,917 (338,700–349,343)

3.1.3. Trap line specific recapture rate

In 2018, the numbers of tagged lamprey encountering each trap line decreased upstream, adjusting the number of marked lamprey vulnerable to each trap line (Table S1). Consequently, the adjusted recapture rate per trap according to the number of traps per trap line was 0.16% for Trap Line 1, 0.11% for Trap Line 2 and 0.05% for Trap Line 3. In 2019, all trap lines were encountered by the same number of tagged lamprey and the adjusted recapture rate according to the number of traps per trap line was 0.01% for Trap Line 1, 0.02% for Trap Line 2 and 0.01% for Trap Line 3.

3.1.4. Intra-season variations in recapture rate

In 2018, marked lamprey were recaptured in four of the six lifts, mostly at Trap Line 1 (n = 16) during the fourth lift (Fig. 3). The largest number vulnerable to be exploited was 421 (prior to seventh lift), and the highest lift specific adjusted recapture rate according to vulnerability was 15.40% (fourth lift) (Fig. 3). In 2019, recaptures only occurred on three lifts, the largest number of lamprey vulnerable to be exploited was 247 (prior to the fourth lift) and the highest recapture rate according to vulnerability to being exploited was 1.29% (fifth lift) (Fig. 3). Trap line specific CPUE and recapture rate per trap line according to vulnerability was positively correlated across both fishing seasons (Spearman's rank correlation, S=2997.9, rho=0.5, p = 0.003) (Fig. S2, C).

3.2. Approach, passage and retreat at O1

3.2.1. Lamprey specific approach and retreat from O1

In both years, the majority of tagged lamprey that approached O1 did not retreat (2018 = 65.7% and 2019 = 65.8%) but the most retreats by any individual in 2018 was 6 and four in 2019 (Fig. S3). The median retreat distance was similar between 2018 (maximum = 9.14 km) and 2019 (maximum = 7.36 km), as was the cumulative retreat distance (Table S2), but the number of lamprey and the total numer of retreats at each trap line varied between years (Fig. S3). Tagged lamprey spent a similar total retreat duration from O1 in 2018 and 2019 (Table S2). Of the 54 recaptured marked lamprey in 2018, 14 (25.9%) had previously been detected on the PIT antennae in the fish passes at O1 (caught during retreat); recaptures during retreat from O1 were only observed during the fourth and fifth lifts.

3.2.2. Temporal variations in approach, passage and retreat at O1

Overall, 35 (68.6%) tagged lamprey approached O1 during the 2018 lamprey fishing season (01-Nov – 10-Dec) and 12 (34.3%) of these passed, compared to 38 (73.1%; approached) and 23 (60.5%; passed) in 2019 (Fig. 4). More tagged lamprey were present immediately downstream of O1 during 2018 (up to 20) than 2019 (up to 13) (Fig. 4). Retreats occurred on 13 different days during both seasons, resulting in vulnerability to the fishery on 11 (2018) and 10 (2019) different days. Tagged lamprey ascended O1 on only five different days in 2018 compared to 11 in 2019; ascents were limited to elevated flows (>99.3 m^3/s) except for one tagged lamprey on 25-Nov in 2018 (34 m^3/s). The duration, distance and tortuosity of lamprey movements during retreat from O1 was similar between weeks within years (Fig. S4; Table S3) and between years (Fig. S4; Table S2).

3.3. Trap line encounters

In total, there were over twice as many trap line encounters by

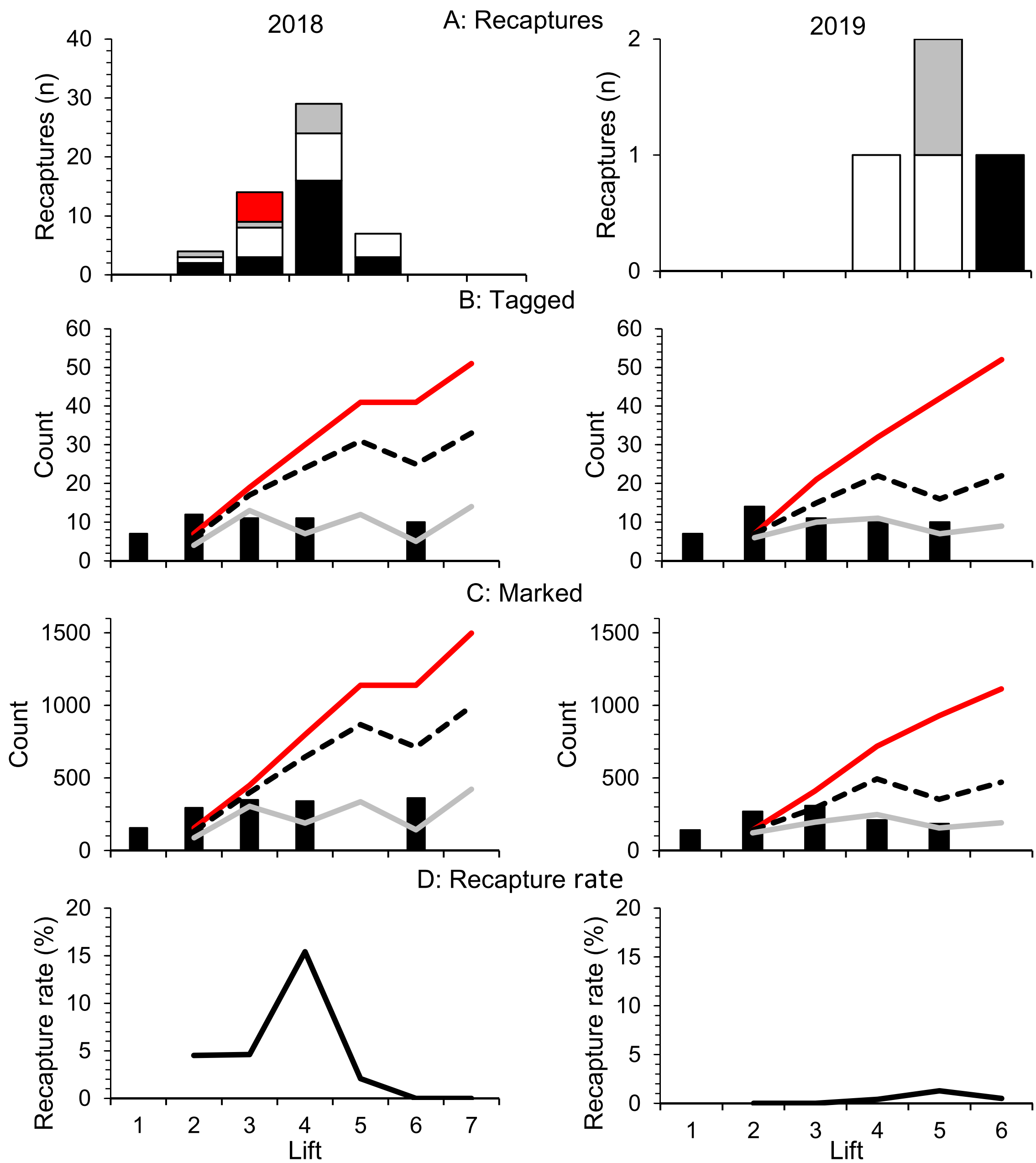

Fig. 3. The number of recaptures in Trap Line 1 (black), Trap Line 2 (white), Trap Line 3 (grey) and unknown (red) (A), the number of tagged (B) and marked (C) lamprey released after each lift (black, bar), the cumulative number released (red, line), available to the fishery (dashed line) and vulnerable to the fishery preceding that lift (grey, line), and the adjusted recapture rate according to vulnerability to the fishery (D) on each lift of the commercial lamprey fishing season (01-Nov – 10-Dec) in 2018 (left) and 2019 (right).

tagged lamprey in 2018 ($n = 401$) than 2019 ($n = 169$), of which 114 (28.4%; 2018) and 40 (23.7%; 2019) were during retreat from O1 (Fig. S3). In 2018, the most encounters occurred at Trap Line 2 ($n = 209$), whereas it was Trap Line 1 in 2019 ($n = 70$) (Fig. S5). The proportion of trap line encounters during retreat was inversely correlated with distance from O1 and was higher in 2018 than 2019, although there were variations between weeks (Fig. S5). Trap line specific recapture rate was positively correlated to relative trap line encounters across both fishing seasons overall and when retreating from O1, but not before approaching O1 (Fig. S6; Table S4). Moreover, in 2018, Trap Line specific recapture rate was positively correlated to relative retreat encounters (Fig. S6; Table S4).

Most trap line lifts were in the expected recapture rate range according to the number and relative number of trap line encounters overall, before approaching O1 and when retreating from O1 (Fig. 5). However, lamprey at Trap Line 1 had a higher conditional capture probability than expected on one occasion, while the recapture rate was lower than expected according to the number and relative number of trap line encounters on several occasions overall (Fig. 5).

4. Discussion

Acoustic telemetry was utilised to refine and accurately measure recapture/exploitation rates, reducing estimated run sizes. Consequently, the value of acoustic telemetry for fisheries management was highlighted, without which > 100,000 more individuals (27.5% higher than the adjusted run size in 2018 and 33.3% higher in 2019) would have been included in quota calculations, increasing exploitation

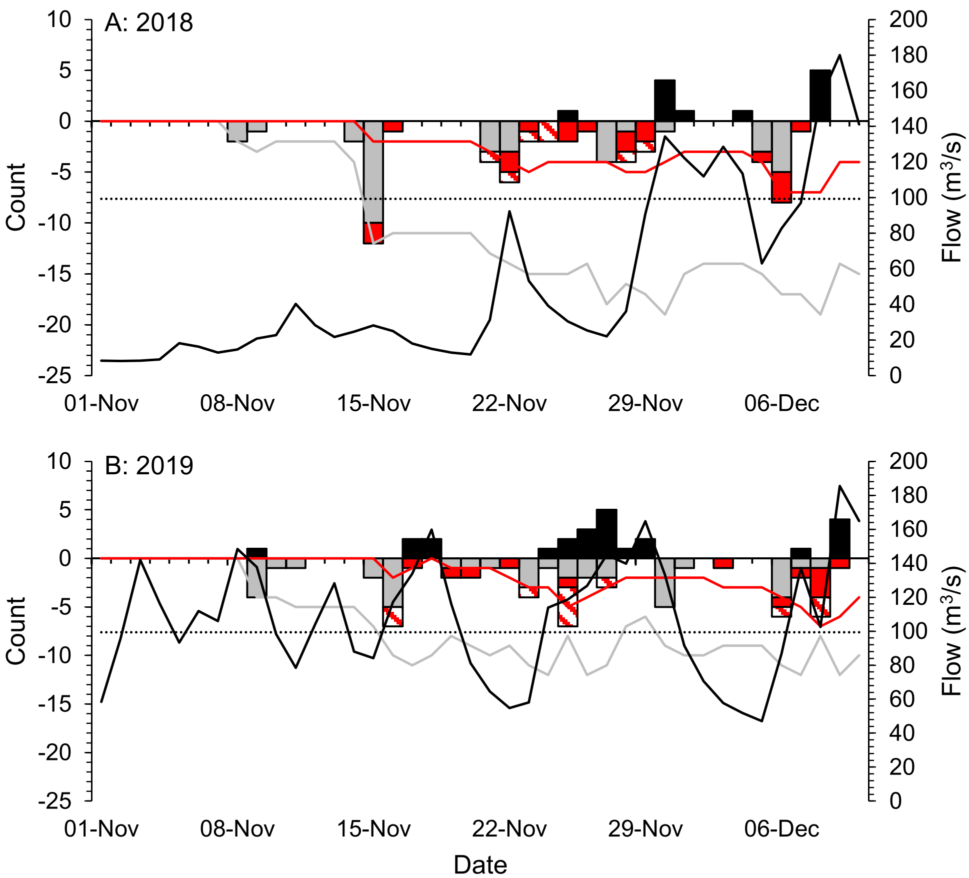

Fig. 4. The daily number of tagged lamprey that first approached barrier O1 (grey bar, negative), retreated from O1 that did (red bar, negative) or did not become vulnerable to the fishery (red diagonal lines bar, negative) and passed O1 (black) as well as the cumulative numbers present at (grey line, negative) and retreating from (red line, negative) O1 with mean daily discharge (m^3/s; black line) and O1 passability threshold (99.3 m^3/s) at Skelton Gauging Station on the Yorkshire Ouse from 01-Nov – 10-Dec in 2018 (A) and 2019 (B).

beyond what may be sustainable, with potentially severe consequences (Zhang et al., 2018; Almeida et al., 2021). Moreover, acoustic tracking revealed lamprey movement and subsequent trap line encounters, informing conditional capture probability and how managers can utilise this information in the future. Here we discuss how lamprey movement, environmental conditions and trap effectiveness influenced vulnerability to capture and the implications for management and conservation.

Despite an almost identical, both spatially and temporally, sampling effort between years, catches were 15 times higher during 2018 (2031.64 kg) than 2019 (135.31 kg), and there were large variations in catch between lifts in 2018. Crucially, based purely on CPUE, as was occurring prior to this investigation, the lamprey population (during the fishing season) in 2019 would be considered very small, i.e. 6.7% of 2018, and may have led to further fishing restrictions. However, the recapture rate, and the associated estimate of exploitation rate, was also low in 2019 and thus the unadjusted population estimate 458,556 (95% CL, 451,600–465,791) was 65.0% of the 2018 value of 705,196 (689,346−721,824). Indeed, the low catch in 2019 was probably more indicative of when and how river lamprey move through the exploited reach, and passage conditions at O1 influencing their vulnerability to capture, rather than due to a low abundance.

Historically, the percentage of the Yorkshire Ouse lamprey fishery catch caught during the current authorised season (01-Nov – 10-Dec) between 2000/01–2008/09 represented a mean of ~55% of the total catch over the unrestricted season (September to February), whilst the catch prior to 01-Nov accounted for a mean of 17%, although in many years scientific sampling or commercial fishing did not start until early October (Masters et al., 2006; Foulds and Lucas, 2014; R. Noble, unpublished). The Yorkshire Ouse experienced some of the highest river levels ever recorded during October 2019 and thus a considerable proportion of the lamprey population may have already migrated through the exploited reach prior to the commencement of the fishing season. Conversely, the large catch in 2018 could be interpreted as an excessive rate of exploitation that could also lead to fishing restrictions, but mark-recapture revealed that was not the case. Moreover, high CPUE with low recapture rates during specific lifts were likely indicative of an influx of lamprey into the exploited reach rather than excessive exploitation. Altogether, this study further demonstrates the difficulty of attempting to regulate a fishery using catch and effort alone and the utility of incorporating mark-recapture or other measures of fishing mortality, as others have found (Michielsens et al., 2006; Kuparinen et al., 2012).

Conventional mark-recapture studies cannot account for fish location once released and so, in this study, acoustic telemetry was incorporated to provide information on fish movement through the fishery to inform the proportion of individuals available for capture, and vulnerable to exploitation. Consequently, exploitation rates from a previous conventional simple mark-recapture study on the same fishery (i.e. 12.0% after correcting for external tag loss [Masters et al., 2006]) may be erroneous. This is further supported by Dudgeon et al. (2015) where Cormack–Jolly–Seber models showed that acoustic telemetry data resulted in at least tenfold higher recapture rates than catch data during the same time period. Greater precision in survival estimates were also obtained, which for one dataset were inestimatable using catch data alone (Dudgeon et al., 2015). Mudrak and Szedlmayer (2019) also utilised acoustic telemetry to increase the precision and allow the calculation of calibration estimates of mortality for a red snapper (*Lutjanus campechanus* [Poey, 1860]) fishery in the Gulf of Mexico, without which conventional simple mark-recapture would have been inaccurate.

Previous laboratory studies by one of the authors utilising the tagging method described found no PIT tag loss in a sample of river lamprey (n=60) over a 5-month period (M. Lucas, unpublished), and other lamprey species studies have revealed high PIT tag retention (Moser et al., 2017; Simard et al., 2017). Thus, tag loss was probably

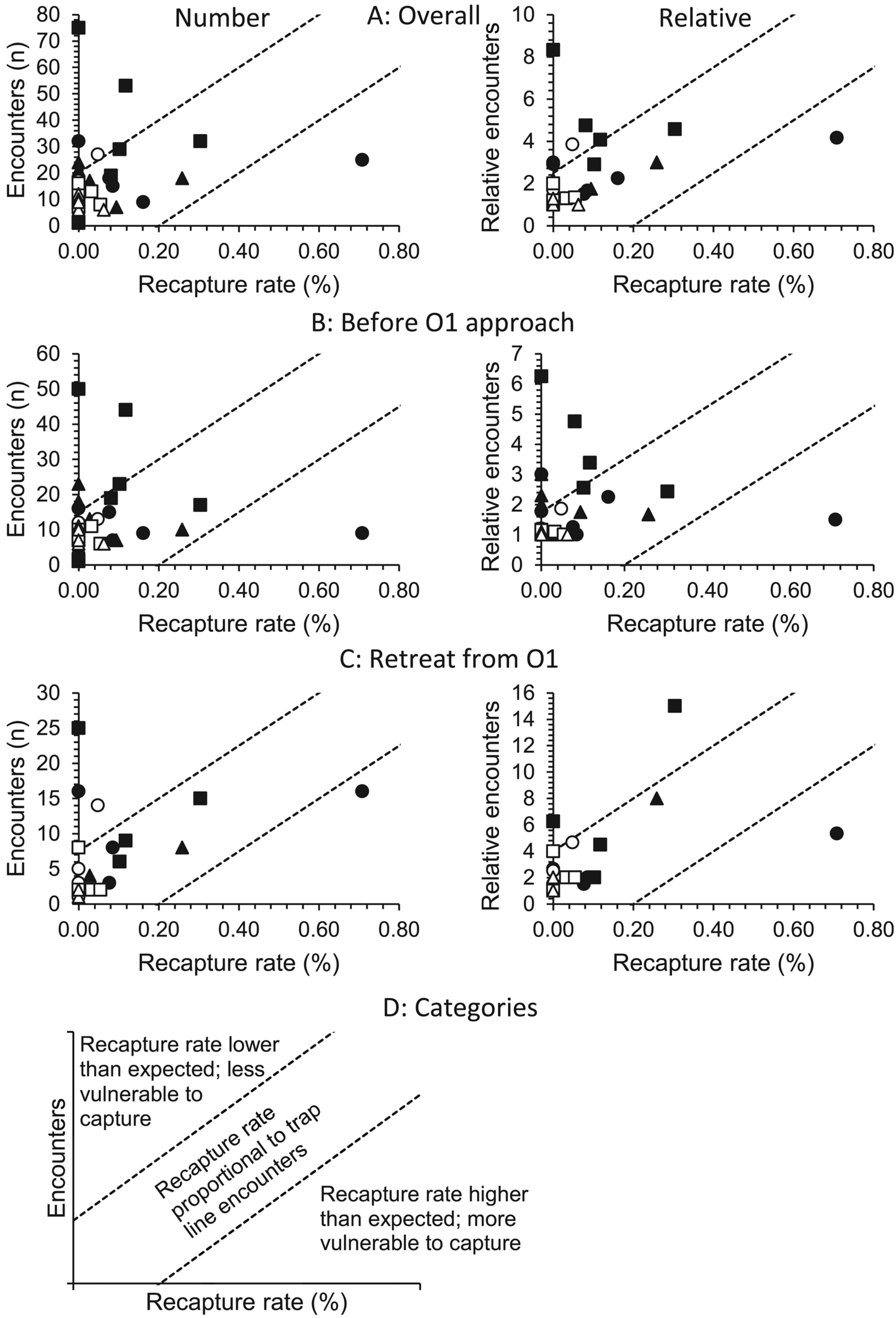

Fig. 5. Recapture rate adjusted according to vulnerability (%) against the number of (left) and relative number of trap line encounters (right) overall (A), before approaching barrier O1 (B), and when retreating from O1 (C) at Trap Line 1 (circle), Trap Line 2 (square) and trap Line 3 (triangle) per lift in the 2018 (black) and 2019 (white) commercial lamprey fishing seasons with the category of expected values (D).

extremely low in this study. Nevertheless, there are potential behavioural changes associated with tagging and handling effects for many anadromous species that could limit the conclusions drawn from this study (Frank et al., 2009). These are usually diagnosed as "fallback" in published studies, due to the inherent difficulty of determining differences between tagged and untagged individuals (Frank et al., 2009). However, river lamprey have been shown to re-engage in their original spawning movements within one hour of release post-tagging by Jang and Lucas (2005) and although not for river lamprey, Close et al. (2003) showed that adult Pacific lamprey (*Entosphenus tridentatus* [Richardson, 1836]) tagged with radio tags did not significantly differ behaviourally to untagged individuals. Previous studies have also tracked acoustic-tagged river lamprey with little to no impact of tagging or handling on behaviour (Lucas et al., 2009; Tummers et al., 2016; Silva et al., 2017). Furthermore, all tagged river lamprey in this study were detected moving upstream (towards spawning habitat) after release.

The large variations in catches between years and within 2018 were likely a consequence of variations in river level. Environmental conditions play a major role in migration timings of anadromous fish (Lucas and Baras, 2001; Smith, 2012), and have been shown to influence fisheries for these species (Arlinghaus et al., 2015). Masters et al. (2006) showed the Yorkshire Ouse commercial lamprey fishery to have a quadratic relationship between CPUE and discharge. Similar was found here with small catches during periods of low flow that were not conducive to river lamprey migration, as exemplified during the first three lifts in 2018. Catches were also small when elevated river level drowned out O1, as exemplified during 2019 when there was a far higher passage rate (60.5%) than in 2018 (34.3%), and on the last lift of 2018. Although bottom traps can fish ineffectively during high flows because they become debris filled or twist in the flow, the telemetry data here support the conclusion that during high flows traps caught fewer lamprey because, at least in part, they were less readily available. Catches were highest after periods of elevated flow that were sufficient to attract lamprey into the fishery reach but could not leave, via passage at O1. There were also differences in catches between trap lines, possibly due to variations in river topography. This is supported by Bravener and McLaughlin (2013) who suggested that spatial heterogeneity of aquatic ecosystems caused fish interactions with traps to vary based on topography at the trap location, due to traps being passive and reliant on habitat features to increase the likelihood of encounter and, thus, trapping success.

While spatial and temporal differences in catch can be broadly attributed to variations in river level, they were also likely a consequence of how lamprey moved through the fishery, including during retreat from O1, and the efficiency of the traps. In some cases, lamprey had a higher conditional capture probability, presumably due to traps fishing more efficiently or lamprey actively seeking refuge, whilst in others the conditional capture probability was lower, presumably due to traps fishing inefficiently or lamprey not actively seeking refuge. Elsewhere, sea lamprey (*Petromyzon marinus* L.) behaviour has been shown to affect trapping efficiency in the St. Marys River (Bravener and McLaughlin, 2013), with low trapping success attributed to individuals not encountering traps, not entering upon encounter, not remaining at the trap, or not returning upon departure. Although these findings are a reflection of intrinsic variability in the data, ultimately, they highlight that the processes that determine lamprey vulnerability to capture are hard to disentangle.

Despite statistically similar retreat movements between years, tagged lamprey retreated further in 2018 than 2019, and the cumulative retreat distance per individual was greater in 2018 than 2019, and thus likely influenced their vulnerabilty to capture. Anadromous species that approach barriers have been shown to do one of three things: switch from a migratory state to a sedentary state, seek refuge and "wait" for favourable passage conditions (Kirk and Caudill, 2017); retreat and search for alternative migration routes around the obstacle (Rooney et al., 2015; Holbrook et al., 2016) or ascend the barrier if passage conditions allow (Tummers et al., 2016; Lothian et al., 2020). Consequently, lamprey seeking refuge during retreats are more likely than those searching for alternative passage routes or spawning tributaries to inadvertantly seek refuge in traps. Lamprey fisheries are known to take advantage of lamprey refuge-seeking behaviour in the way they operate and the types of traps often used (Almeida et al., 2021). This potentially explains the higher than expected recapture rate according to trap line encounters on lift 4 at Trap Line 1 in 2018, which corresponded with the highest proportion of retreat trap line encounters at Trap Line 1, the largest number of retreat recaptures (n=8; 50% of all recaptures in that lift) and consequently, the largest recapture rate (and catch). Since only 45.7% of tagged fish that reached O1 in 2018 went on to be detected on the PIT arrays, the estimates of known retreat recaptures of marked lamprey are likely to be much lower than the actual values. Thus, the susceptibility of retreating lamprey to capture is potentially much higher than shown.

4.1. Conclusions

Overall, this study demonstrates the importance of understanding fish movement to inform management. Worldwide, important fisheries, such as those for grouper, snapper and sharks, are data-limited (Amorim et al., 2019; Retnoningtyas et al., 2021) and thus require managers to make decisions based on incomplete or potentially inaccurate data, further adding to the inherent difficulty in managing sustainability (Sutherland, 2001). Acoustic telemetry provides an opportunity for improved fisheries management to better protect threatened fish stocks, such as those for sharks (Worm et al., 2013) and salmon (Healey, 2009), during conditions when they are most vulnerable to being exploited and help contribute to their conservation. Telemetry data should be used to gather a holistic understanding of the fishery and species ecology, including migratory patterns and immigration into and emigration out of the fishery area to establish whether temporal restrictions or other remediation techniques, like trap and transport of a proportion of the catch (Lusardi and Moyle, 2017), are required. Additionally, telemetry-derived behaviour characteristics can accurately establish the need for spatial restrictions such as no-take zones / protected areas (Lea et al., 2016; Hussey et al., 2017), but can also be useful to address bycatch issues, such as those in shark sanctuaries (Ward-Paige, 2017). For example, in our study, a no-take zone within 3 km of O1 would encompass Trap Line 1, and thus would have reduced the adjusted recapture rate from 4.59% to 2.55% in 2018 and from 0.48% to 0.36% in 2019 if removed to protect retreating lamprey. Further, information on trap line interactions is vital, when used in conjunction with CPUE data, to inform expected catch and determine the health and status of the fishery. Altogether, this study further highlights how the incorporation of acoustic telemetry increases the accuracy of, validates, and complements mark-recapture data, but also reveals a framework to quantify conditional capture probability and its influence on CPUE; knowledge that is widely applicable across multiple different aquatic systems and vital for worldwide management and sustainability of fisheries.

CRediT authorship contribution statement

Jubb, W. M: Writing – original draft, Formal analysis, Project administration, Visualization, Data curation, Investigation, Methodology, Software. **Noble, R. A. A:** Writing – original draft, Supervision, Project administration, Visualization, Investigation, Methodology, Validation, Resources. **Dodd, J. R:** Writing – review & editing, Visualization, Investigation, Software, Validation, Resources. **Nunn, A. D:** Writing – review & editing, Visualization, Investigation, Validation. **Lothian, A. J:** Writing – review & editing, Visualization, Investigation, Software, Validation. **Albright, A. J:** Writing – review & editing, Visualization, Investigation. **Bubb, D. H:** Writing – review & editing, Visualization, Investigation. **Lucas, M. C:** Writing – review & editing, Project administration, Visualization, Methodology, Validation, Conceptualization, Resources. **Bolland, J. D:** Writing – original draft, Supervision, Funding acquisition, Project administration, Visualization, Investigation, Methodology, Validation, Conceptualization, Resources.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data Availability

Data is currently in the process of being uploaded to the European Tracking Network (ETN).

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.fishres.2023.106737.

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