



Using a multi-criteria approach to assess post-release recovery periods in behavioural studies: study of a fish telemetry project in the Seine Estuary

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Using a multi-criteria approach to assess post-release recovery periods in behavioural studies: study of a fish telemetry project in the Seine Estuary

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Abstract

Background: Biotelemetry has many advantages for monitoring fish behaviour. However, the accuracy of results can be impacted by changes in fish behaviour following tagging and other forms of human intervention. Different fish take different amounts of time to return to normal behaviour patterns. This recovery period is often difficult to assess. In many studies, it is simply ignored, while in others an assumed duration is used. This assumption is rarely based on objective criteria. To address this challenging aspect of fish telemetry, a multi-criteria stepwise approach was developed based on complementary criteria obtainable through prior knowledge of the normal behaviour of studied species (home range, diel rhythm, homing, shoaling, migration...). It was applied to the case study of an acoustic telemetry project in the Seine Estuary (France) for three estuarine species exhibiting contrasted ecological traits: European eel *Anguilla anguilla* (Linnaeus 1758), thin lipped grey mullet *Liza ramada* (Risso 1827) and bream *Abramis brama* (Linnaeus 1758).

Results: Taking into account the particular traits of the species studied, we used the following three criteria: time to return to core area of activity, time to return to rhythmic activity, and time to return to site of capture. Post-release periods of recovery varied greatly between species. The median value was 10 days for eel, 25 days for mullet, and 1 day for bream. During this period, eels moved very little and the schedule pattern presented a diel rhythm with most detections occurring at night. All mullet exhibited rapid downstream trajectories after release, with larger distances covered during the ebb. Only five individuals returned later to the study site. This behaviour turns out to be not only an effect of post-release stress, but also the result of normal shifts in feeding habitat use by large shoals of mullet. Common bream exhibit very short periods of recovery with strong site fidelity. Most of the individuals of the different species (72%) return to their site of capture.

Conclusions: The approach allows the identification of individual periods of recovery specific to the species and environment being studied. It maximises the amount of conserved data representing normal behaviour and can be implemented with various types of tracking data. Analysis of this period provides additional information about the stress response of species and their associated behaviour.

Keywords: Fish, Telemetry, Behaviour, European eel, Thin lipped mullet, Bream

Background

Biotelemetry and bio-logging are increasingly used to study the behaviour and physiology of fish in their natural

environment, especially their movements, home range, and habitat use. Biotelemetry has an advantage over conventional animal research methods in that it enables undisturbed and continuous monitoring of fish behaviour. This is possibly primarily because transmitters can be attached without causing mortality. This is essential in studies where individuals are released immediately after

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transmitter attachment and awakening, without a controlled recovery period from the tagging procedure [1].

Three methods are commonly used to attach transmitters to fish: external attachment, intragastric insertion, and surgical implantation in the peritoneal cavity. Each method of attachment can have its own short- and long-term effects on fish physiology and behaviour. In most cases, electronic devices are implanted intracoelomically to minimise their effect on cruise speed. Surgical implantation requires numerous processes and an appropriate anaesthesia, but has the benefit of allowing longer-term studies than intragastric insertion [1]. Some of the more recent telemetry devices can be attached to a greater range of size and age classes for both aquatic and terrestrial animals. However, one constraint common to all devices is battery life, especially in the case of very small specimens. In open environments such as large rivers, estuaries, and oceans, accurate detection depends on signal strength. Obviously, transmitting a stronger signal runs down the battery faster. Most behavioural analyses require long-term surveys with numerous detections to analyse rhythms, home range, range shift, transience, etc.

It has long been accepted that fish captured and handled before release tend to be stressed. This stress varies according to species, individual characteristics, water quality and intensity of stressors. A wide range of effects can be observed, such as decreased growth and disease resistance, reduced swimming capability, abnormal feeding behaviour, and stunted reproductive capacity [2]. This has been documented in a number of physiological surveys which monitored physiological responses to stressors (cortisol, lactate, plasma glucose, metabolic rate, etc.) and determined the dynamic of these physiological consequences on manipulated fish compared to controls [3]. Jepsen et al. [4] observed a significant increase in plasma lactate and cortisol in tagged juvenile Chinook salmon (*Oncorhynchus tshawytscha*) 3 h after surgery, compared to control fish. In another study, plasma cortisol levels of gilthead seabream (*Sparus aurata*), 9 days after intracoelomic tagging, indicates a physiological impact but food intake and activity were not affected [5]. Behavioural modifications associated with these physiological dynamics have been mentioned but are restricted to what can be observed in experimental tanks [2]. Physiological studies on stress, restricted to only a few species, mention that the duration of drastic stress is generally several days.

It is, therefore, generally accepted that when fish are captured, their behaviour will change for a certain amount of time following release. These changes can come as the result of several types of stress: capture, handling, anaesthesia, transmitter attachment or insertion. Although experiments conducted on fish in captivity do not replicate the stresses encountered in the wild

(predation or prey capture), they are the most practical method currently available for monitoring survival, tag retention [6] and physiological modifications [7]. While some authors have explicitly tested the effects of tagging on the behaviour of captive tagged and control fish [8], these studies fail to take into account the additional stress experienced by wild fish when they are removed from their natural environment. Also, it is technically very difficult to monitor long-term post-capture behaviour in wild fish at certain life stages (e.g., fish in migration, large specimens). Short-term tagging effects can be measured in the river using a paired release strategy to compare migration behaviour or survival of a tagged group to that of a control group, as shown by Hockersmith et al. [9] for hatchery-reared yearling chinook salmon. In this case, a handling-induced delay was identified, resulting in a downstream movement and a delay of 4–5 days in upstream migration [10]. This post-release period of recovery is complicated to grasp, and is rarely addressed with objective and consensual criteria. Because of this, a litany of different approaches exists relating to behavioural analysis of biotelemetry data. In the literature, some authors do not mention this issue, or consider that there is no post-release period of recovery and start their analysis as soon as the fish are released, while others exclude a certain period of time based on previous studies or on their own criteria.

When indicated, various types of criteria are used to define this post-release period of recovery or the time at which the fish return to “normal” behaviour. The observation of a known “normal” behaviour is a criterion mentioned by authors. It could be the reintegration of a shoal, with the adoption of shoal behaviour, as observed in bream (*Abramis brama*) by Caffrey et al. [11] and in salema (*Sarpa salpa*) by Jadot et al. [12]. For fish in upstream migration, downstream movements are often observed after release and most authors consider that the post-release period of recovery ends when they resume their upstream migration. Another commonly used criterion relates to shifts in habitat use and establishment of stable areas of concentrated use (core areas within home range). Identifying a vacant location for most of the tracking period, Lyons and Lucas [13] excluded a nine-day period for common bream, considering that it was an anomaly. In another previous study, variations in a home range estimator returned asymptotic values, resulting in a post-release period of recovery of 5 days for sea bream (*Diplodus vulgaris*) [14] and 3 months for *Chorodon schoenleinii* [15]. Another criterion concerns the activity level or the activity pattern. A low activity period followed by greater movement for barred sand bass (*Paralabrax nebulifer*) lead to a post-release period of recovery of 12 h [16].

The duration of this post-release period of recovery therefore varies considerably between species and experiments, and depends on the criteria selected and methods used. Empirically, 1 or 2 weeks are often used as a period which guarantees behaviour similar to wild individuals. As is the case for most rules used in fish telemetry, this comes mainly from salmonid experiments and does not consider specific characteristics (species, size, health condition) or environmental conditions. There is a need for objective criteria to identify a post-release period of recovery or the time when the fish return to “normal” behaviour, thus optimising data analysis in field studies (e.g., movement patterns, home ranges, habitat preferences).

In this study, a stepwise multi-criteria approach was tested using field data from an acoustic telemetry experiment. The experiment was carried out on a number of fish species in the freshwater part of the Seine estuary (northern France, Fig. 1). This approach was based on the

combination of criteria contributing to the appearance of different detection patterns, activity levels, habitat use, or an observed return to known “normal” behaviours (type of movement, rhythmic patterns of activities). The species used to evaluate interspecific and intraspecific responses exhibit contrasting ecological traits: European eel *Anguilla anguilla* (Linnaeus 1758), thin lipped grey mullet *Liza ramada* (Risso 1827) and bream *Abramis brama* (Linnaeus 1758). The European eel and thin lipped mullet are catadromous species that use estuaries during the growth phase of their life cycle, while common bream is a freshwater species that tolerates brackish waters for feeding/rearing [17]. Eels are carnivorous and generally exhibit territorial behaviour (homing) with a strong diel rhythm of activity. Mullet and common bream exhibit shoaling behaviour. Bream in particular can show a homing instinct to return to their parent shoal [11]. These two benthophageous species feed mainly on intertidal mudflats.

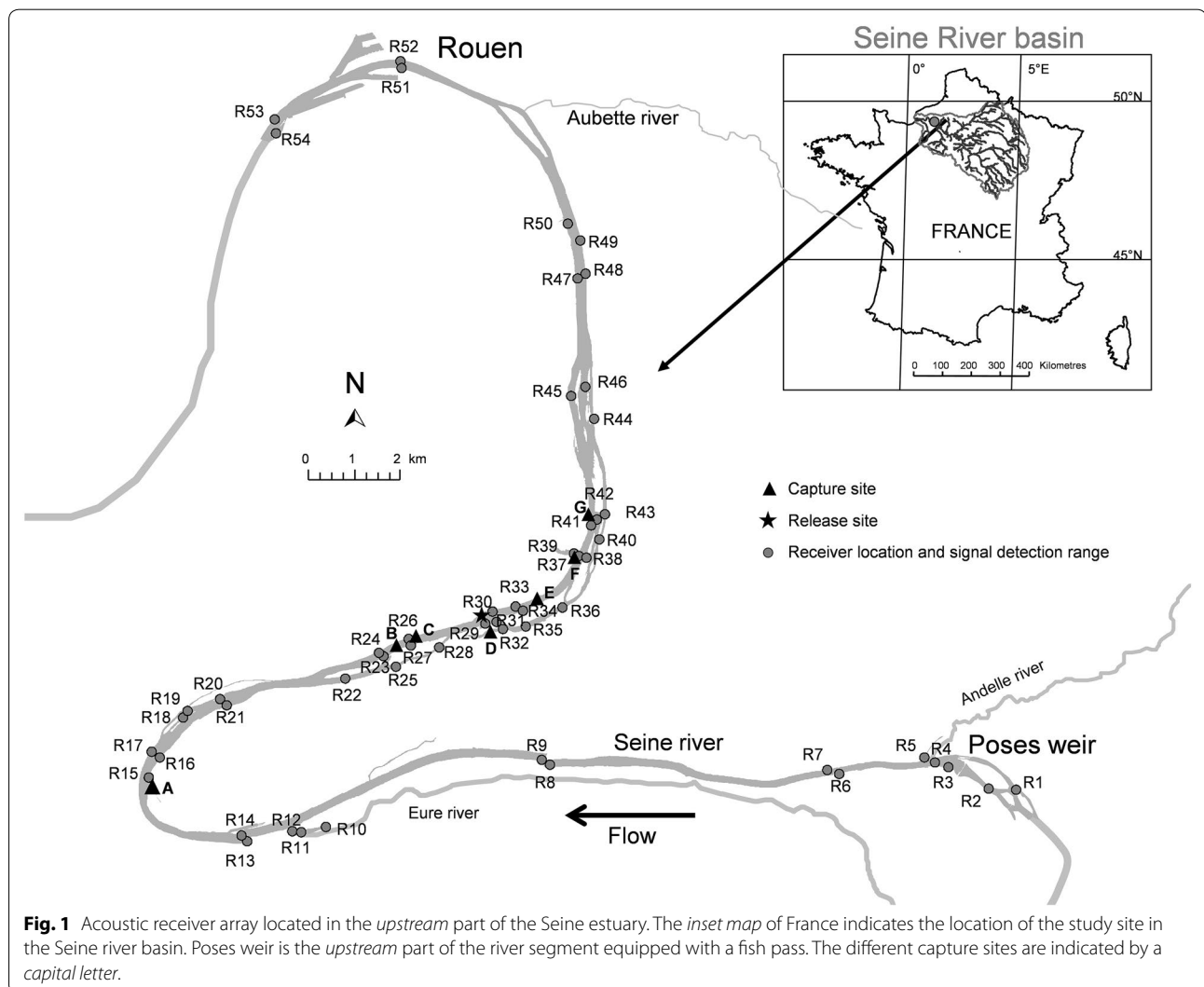


Fig. 1 Acoustic receiver array located in the *upstream* part of the Seine estuary. The *inset map* of France indicates the location of the study site in the Seine river basin. Poses weir is the *upstream* part of the river segment equipped with a fish pass. The different capture sites are indicated by a *capital letter*.

Methods

Study site and environmental data

The study site is located in the tidal freshwater part of the Seine River basin (North France); 120–160 km from the sea and 202 km downstream of central Paris (Fig. 1). The upstream limit is Poses weir, the first obstacle from the sea, which is equipped with a fish pass, enabling some species such as mullet and eel to move upstream. There are a number of meanders, with high hydraulic diversity (main channel, secondary channels and hydraulic annexes) and several shelters in banks. Fishing activity is limited to a few recreational anglers. The experiment was carried out in June–August 2009. During this period, the Seine discharge varied between 162 and 379 m³ s⁻¹ (DIREN Ile de France and Banque hydro), water temperatures were between 18.4 and 24.3°C and oxygen concentration values varied between 2.5 mg l⁻¹ and 12.8 mg l⁻¹ (at 12 h) (Fig. 2).

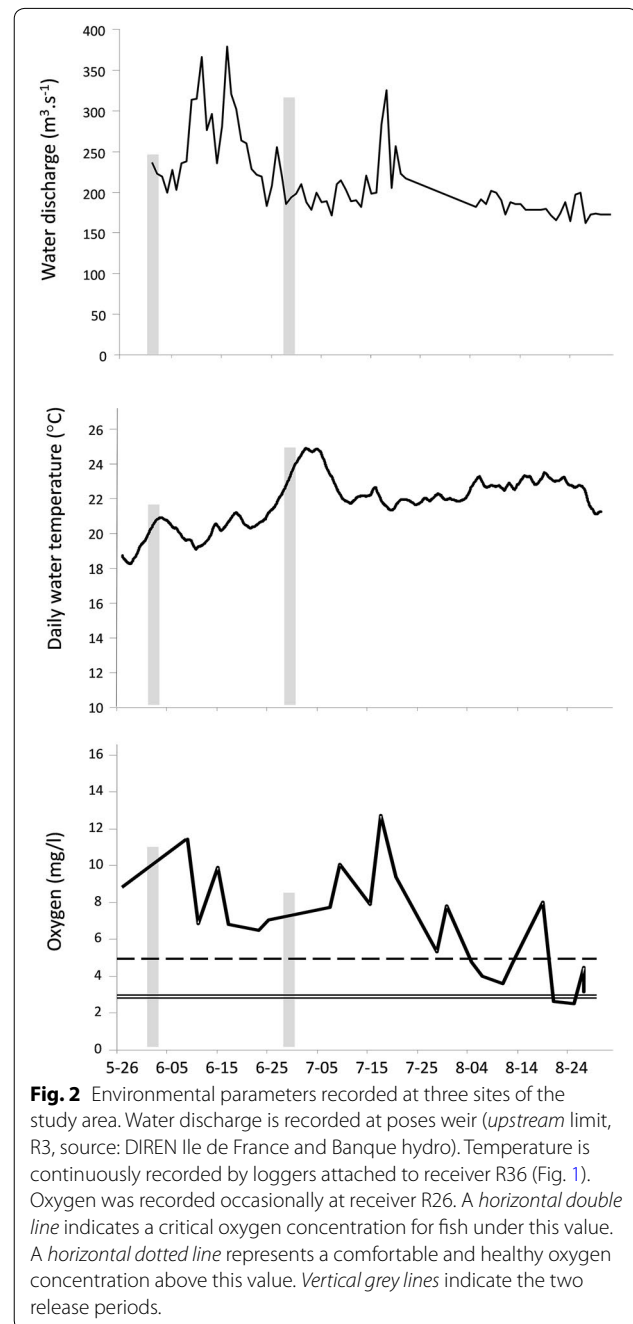
Fish tagging

Preliminary tagging test

As recommended by Rogers and White [18], the potential effect of surgically attaching transmitters was tested. The behaviour and health of captive European eel and thin lipped mullet carrying transmitters were monitored and compared to captive untagged fish. European eel and thin lipped mullet, acclimated for over a month at the experimental station of Saint-Seurin-sur-l'Isle, were divided into two groups: a control group and a tagged group. We selected eel and mullet specimens weighing over 80 g. This equates to a length of more than 200 mm (Fork length) for mullet (age >2+) and more than 350 mm (total length) for eel (>6+).

Manipulations and surgery were carried out from the 3rd to the 4th of March 2009 on 10 eels (430–530 mm) and 3 mullet (225–270 mm). They were stocked in two closed-circuit tanks of 4 m³, filled with brackish water (salinity of less than 7‰). Temperatures were kept at 18–19°C and pH at 6.5. Tagged and control fish were held together to check for environmental effects. Tagged and control fish were visually identified in tanks with brightly-coloured pearls placed in the anterior part of the dorsal fin. Over a period of 1 month, tagged and control fish were monitored daily for mortality and behaviour and weekly to check the healing process. At the end of the monitoring period, fish were weighed and checked for lesions and healing of tagging wounds.

No statistical differences were observed for eel (no mortality) and mullet (one tagged and one control died). For mullet, active behavior of fish swimming in shoals was observed from the day after surgery for both tagged and control fish. Eels were hidden together under cages, likely fleeing from the light. Feeding recovery



was observed 3 days after tagging. The stitches held as expected and wound healing was completed without persistent acute inflammation. Tag retention was good, with only one observed tag loss for a mullet. Results from this tagging test in captive conditions suggest that the protocol used to tag individuals has no obvious effects on survival, food recovery, swimming behavior and growth, and can be used to carry out field behaviour studies on individuals of comparable size.

Fish capture and field tagging

All fish were captured within the study site. Their different locations were recorded using a Global Positioning System (A–G locations in Fig. 1). Eel were captured using fyke nets put out during the night and hauled in the morning, while mullet and bream were captured during day time with gill nets (mesh size 20 and 25 mm) that were hauled in within an hour. Fish were removed carefully from the nets to minimise capture injury and stress and transferred rapidly to a recovery tank. Their status was checked before being handled.

The procedure for surgically implanting coded acoustic transmitters was based on the recommendations of Bridger and Booth [1] and [19] and was tested during the preliminary tagging test. Handling and surgery were performed by trained and experienced staff during two periods (2/06 to 4/06 and 29/06 to 2/07). A total of 21 European eels, 20 thin lipped mullet and 10 common breams were anaesthetised using a 0.03–0.1 ml l⁻¹ eugenol solution [20]. At stage-4 of anaesthesia (total loss of swimming motion with weak opercular motion [21]), fish were weighed, measured and placed on a V-shape surgical board with a circulation of water with a light sedative. The ventral part of the fish was dried slightly using a sterile compress, then disinfected with Betadine® (10% povidone–iodine). The transmitter, which had been previously disinfected with ethanol and dried, was implanted by incision into the intraperitoneal cavity and an antibiotic treatment (amoxicillin, 0.025 ml/individual) was injected in the abdominal cavity. As recommended by Winter [22], no transmitters weighing more than 2% of a fish out of water weight were used. The incision was closed with two simple interrupted monofilament sutures with surgeon's knot (sterile Ethicon monofilament) [19] and a hydrophobic antifungal cream was applied. The surgical procedure took less than 5 min per fish. Fish were placed in an oxygenated tank during the recovery period. After full recovery (20–30 min.), the fish were released into the estuary at a single release site (Fig. 1) to test the homing capacities of species. For the second release period, anaesthesia was adapted to higher air (23°C) and water temperatures (Fig. 2).

Acoustic monitoring array

VEMCO acoustic receivers (VR2W) and coded acoustic transmitters operating at 69 kHz with 147 dB power output (<http://www.vemco.com>) were used to monitor individual movements. The timing and duration of the study were based on the expected battery life of the transmitters (minimum 45 days warranty by the manufacturer). Each tag (V7, 7 × 18 mm, 1.0 g in water) transmits a unique acoustic numerical code that is randomly produced in the intervals of 45–90 s. The detection set-up

was subject to a field test before the study started [23]. In December 2008, passive submersible acoustic receivers (Vemco VR2W-69 kHz) were anchored in different parts of the study area. Transmitters (V7) were placed at a known distance from the receiver for 15 min. The distance between receiver and transmitter was increased in increments of 50 m, from 50 m to 500 m. Based on these trials, the maximum distance at which a signal was detected at least 50% of the time was estimated at 100–150 m. These distances were used to design the longitudinal and lateral monitoring array, as well as planning the deployment of receivers.

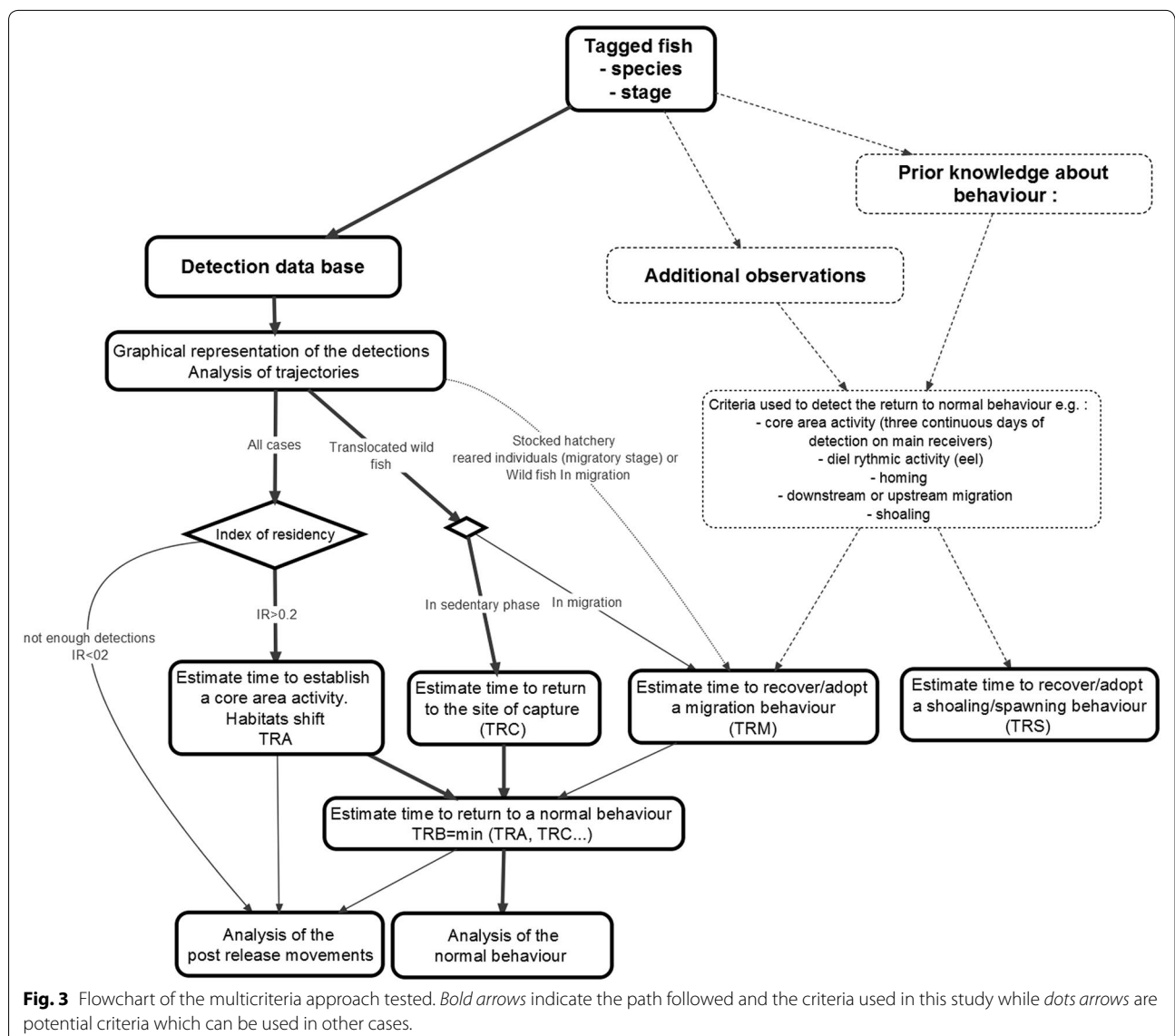
Fifty-four VR2W receivers were placed along the 45 km length of the Seine River and at confluence with tributaries to record the passage of tagged fish (Fig. 1). Two receivers were placed upstream of Poses weir, and a further downstream of Rouen (Fig. 1). Receivers were distributed around the release site. Special care was taken to ensure that islands in the middle of the river did not interfere with reception. Receivers were organised in pairs, located on each side of the main channel, with an overlap in their detection range, to avoid fish passing undetected (net swimming speed below 3 m s⁻¹). In secondary channels and oxbows, only one receiver was necessary due to their smaller widths. Some receivers were moved to other positions at the end of the first month to increase the density of receivers in the segments where individuals were detected.

Data analysis

Multi-criteria approach

A multi-criteria approach was used to estimate a threshold date on which behaviour was considered to have returned to “normal”. The steps for completing the multi-criteria approach are summarised in a flowchart, containing both the processes applied in this study and some potential processes that could be used in other studies (Fig. 3). The criteria adopted in this study are based on existing knowledge about normal behaviour of tagged species.

First, a detection database was constructed. The fields in this database were fish number, date and time of detection and the coordinates of the receiver detecting the individual (Lambert-93 on RGF93 France Map Projection). Receivers were also identified by their distance (in metres) from the most downstream point of the study site map. To provide a visual representation of individual fish detected by different receivers, we used individual detection plots (Fig. 4). This approach highlighted when individuals were present along the monitored area. This was a form of residency analysis, as mentioned by Ohta and Kakuma [24]. An initial identification of the range of longitudinal upstream and downstream movements also



provided information on rarely detected individuals or individuals leaving the study site.

Detection data were used to compute individual trajectories. To avoid multiple detections of the same fish at the same time by overlapping receivers, an application written in the R language was used to smooth trajectories (Comprehensive R Archive Network, <http://cran.r-project.org>). Detections were smoothed using a time period of 3 min (which corresponds to the mean time taken by a fish to cover a distance equal to twice the detection range of a given receiver). These weighted positions are equivalent to short-term centres of activity, as well as being appropriate for the study of long-term fish movement patterns and home ranges [25]. The weighted positions were used to map fish multi-segment trajectories using

Hawth's Analysis Tools for ArcGIS® [26]. A few segments were modified to fit river shapes.

Site fidelity during the study period was evaluated with a residency index (IR) calculated as the number of days with detections by at least one receiver over the number of days of tracking. This index varies between 0 (no residency) and 1 (full time resident) [27]. For individuals with an IR below 0.2 (<12 days of detection), we only carried out minimum graphical analyses of behaviour after release (Fig. 3). For each individual with IR >0.2, days of detection by each receiver were divided by days of potential detection (percentages). The days of potential detection are the shared period between the effective detection period for each receiver and the fish tracking period. In the graphical representation, receivers were organised

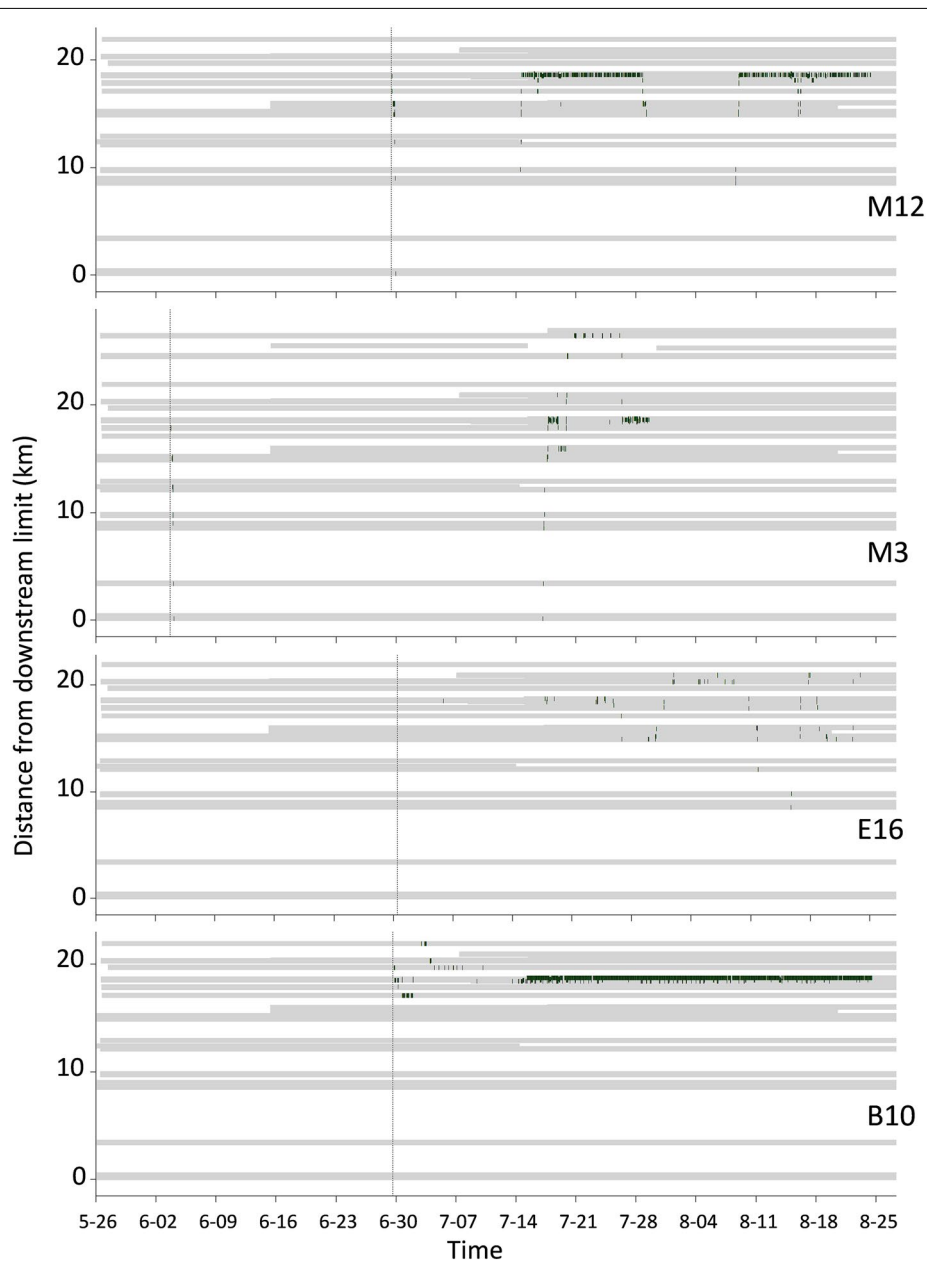


Fig. 4 Individual spatio-temporal detection plots for some individuals of the three species. European eel (E16), thinlip grey mullet (M3, M12) and common bream (B10); with their release date (vertical dotted line). Grey lines indicate detection period for each receiver.

in decreasing order of percentage, providing the number and distribution of the main receivers, which are indicators of fish residency. For each fish trajectory, the first three consecutive days of detection by one (or by pairs) of the main receivers were identified, based on the criterion selected by Kawabata et al. [15]. In the Kawabata study, changes in the combinations of receivers detecting fish were taken as an indication of a shift in core area of activity (high density of use). The beginning of this period

was potentially an indicator of a core area of activity or stable home range being created. By comparing this with the date of release, it was possible to arrive at a time to establish a core area of activity (TRA) (Fig. 3). In some cases, particularly when fish left the study zone, or swam out of the area of detection, we determined an overestimated TRA value (indicated with a less than sign).

In addition, because individuals were not released at their site of capture, the multi-segment trajectory and

individual detection plots were analysed (1) to calculate the longitudinal distance between release and capture sites, (2) to note the possible return to the site of capture, and (3) to calculate the time taken to return to the capture site (TRC, Fig. 3).

Finally, using values of TRA and TRC, we created a third value, Time to Return to normal Behaviour (TRB), which is the smaller of either TRA or TRC. In other studies, with the case of potential additional criteria indicating a return to normal behaviour, TRB could serve as a compromise between different “times to return” (Fig. 3).

Statistical tests

Equality of distribution for the number of days of detection and TRB was tested between species and between the two periods of tagging using the approximate Kruskal–Wallis test. This was followed by a post hoc non-parametric multiple comparison test (NDWD). The null hypothesis that the distributions were the same was rejected at p value <0.05 . All statistical tests were performed with R packages “Coin” for approximate tests (Monte Carlo resampling).

Results

Multi-criteria approach

Table 1 summarises the number of tagged fish, their general biometrical characteristics, and the number of days during which they were detected. Intraspecific size ranges are quite narrow, but this corresponds to different individual ages: eel (6–10 years) [28], mullet (8–15/20 years) [29], bream (4–12/16 years) [13, 30]. The number of days of detection is not significantly different between the two periods of tagging ($p = 0.67$) but is significantly higher for eel and bream than for mullet ($p < 0.01$; Fig. 5). There is a significant intraspecific variability for bream. The median residency index (IR) is 0.46 for eel; 0.63 for bream and 0.05 for mullet; indicating higher site fidelity for bream with most of the individuals staying in the study site (Table 2). All mullet left the study site at least temporarily, leading to a residency index between 0.25 and 0.61 for the five fish which returned (Table 2).

Main receivers were identified for each individual. An example is shown for each species (Fig. 6). For eel E6,

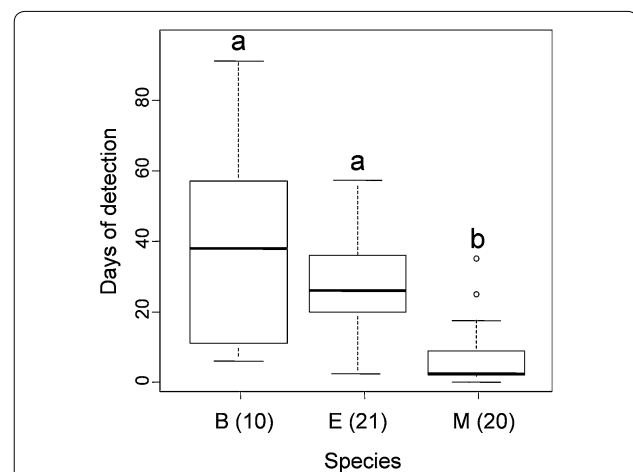


Fig. 5 Box-plots of the days of detection by at least one receiver for all tagged fish grouped by species. European eel (E), thinlip grey mullet (M) and common bream (B). Number of fish in brackets. Species with different superscript are significantly different at $p < 0.05$ (Wilcoxon rank sum test).

the main receivers are one pair of receivers, one on each side of the channel. The high number of receivers which detected mullet M12 reflects the species’ wide-ranging downstream and upstream movements. The main receivers correspond to settlement habitats. One to three pairs of receivers archived a high proportion of the detections for bream B2. For most of the main receivers identified, the percentage of detection was higher than 40% of the potential detection period, with some reaching 90–100%. With these main receivers, rhythmic activities were identified for eels using detection plots (Fig. 7).

There is intraspecific and interspecific variability in TRA values (Table 2). The median value for TRA is 12 days for eel, 36 days for mullet, and 1 day for bream. Most of the individuals (72%) return to their site of capture (individual examples are shown in Fig. 8). The median value of TRS is 5 days for eel, 37 days for mullet, and 1 day for bream. For bream, the two individuals that were translocated 8.5 km downstream did not return to their site of capture. The resulting TRB is significantly higher (Wilcoxon rank sum test, $p < 0.05$) for mullet than for bream (Fig. 9).

Post-release movements

We chose the median TRB value for each species to separate detection datasets and create individual trajectories for post-release recovery period. These are illustrated in Fig. 8 with characteristic species patterns. Individual M12 exhibited a 1–3 days downstream trajectory, leading it out of the study site. Fifteen days later, this individual returned to its site of capture, using the same secondary

Table 1 General characteristics of species tracked in the study area

Species	N	TL (mm) Median (min–max)	BW (g) Median (min–max)
<i>Liza ramada</i>	20	485 (400–525)	1,325 (935–1,680)
<i>Anguilla anguilla</i>	21	405 (348–475)	101 (81–164)
<i>Abramis brama</i>	10	405 (230–475)	1,108 (215–1,495)

N number of fish, TL total length, BW body weights.

Table 2 Characteristic of the 29 fish used to test the multi-criteria approach

Fish ID	TL (mm)	BW (g)	Tagging period	Capture site	Release to capture (m-direction)	Days of detection (days)	IR	TRA (days)	TRC (days)	TRB (days)
E1	435	139	3-Jun	C	1,800-u	20	0.35	<36	No return	<36
E2	348	84	3-Jun	C	1,800-u	23	0.40	<12	<12	<12
E3	450	164	3-Jun	C	1,800-u	40	0.70	5	5	5
E4	405	130	3-Jun	C	1,800-u	42	0.74	13	13	13
E6	440	156	3-Jun	C	1,800-u	57	1.00	4	4	4
E7	385	99	3-Jun	E	1,070-d	27	0.47	<28	No return	<28
E8	432	142	3-Jun	E	1,070-d	16	0.28	16	1	1
E11	381	96	3-Jun	E	1,070-d	27	0.47	<35	No return	<35
E12	349	81	30-Jun	B	2,300-u	29	0.51	5	5	5
E13	435	153	30-Jun	B	2,300-u	47	0.82	<7	4	4
E14	385	101	30-Jun	B	2,300-u	26	0.46	<17	5	5
E15	473	163	30-Jun	B	2,300-u	36	0.63	2	25	2
E16	415	96	30-Jun	B	2,300-u	28	0.49	17	31	17
E17	370	89	30-Jun	G	3,200-d	24	0.42	33	No return	33
E19	450	146	30-Jun	G	3,200-d	21	0.35	10	25	10
E20	384	101	30-Jun	F	2,300-d	37	0.65	5	5	5
E21	413	142	30-Jun	F	2,300-d	26	0.46	11	46	11
B2	395	1,030	2-Jun	D	600-l	92	1.00	1	1	1
B3	440	1,355	3-Jun	D	600-l	57	1.00	1	1	1
B4	240	219	3-Jun	D	600-l	51	0.89	1	1	1
B5	370	775	29-Jun	D-O	600-l	58	1.00	2	25	2
B6	440	1,400	29-Jun	D-O	600-l	25	0.44	2	2	2
B8	230	215	29-Jun	A-O	8,500-u	16	0.28	<40	no Return	<40
B10	415	1,185	29-Jun	A-O	8,500-u	54	0.95	1	no Return	1
M1	490	1,261	3-Jun	D	600-l	14	0.25	<36	37	37
M3	500	1,410	3-Jun	D	600-l	15	0.26	<44	44	44
M9	510	1,653	4-Jun	A-O	8,500-u	19	0.33	<40	40	40
M12	525	1,610	29-Jun	D-O	600-l	35	0.61	<15	15	15
M15	510	1,545	29-Jun	A-O	8,500-u	25	0.44	<25	25	25

E eel, B bream, M mullet. Capture sites are indicated in Fig. 1. TL total length, BW body weight, IR residency index, TRA time to establish a core activity area, TRC time to return to the site of capture, TRB time to return to a normal behaviour, U upstream, d downstream, l lateral, A-O, D-O site A and D in the oxbow.

channel at the end of the path (Fig. 8). This individual is typical of the five mullet that were detected after 2–6 weeks spent downstream, hence the low number of days of detection observed and high values for TRB. Before leaving the study site, these five mullet exhibited rapid and straight downstream trajectories (such as fish M12, Fig. 8); with larger distances covered during the ebb (median sum of distances covered during ebb: 13.7 km and during flow tide: 3.3 km). They returned to the study site with a rapid upstream movement using mainly flow tide.

The post-release movements of eels were very scarce. There were little or no detections, as shown by the four individuals in Fig. 7. For E6 (Fig. 8), there were both downstream and lateral movements, before the individual returned to its site of capture. At the end of this period, 76% of the individuals were detected by receivers

close to their capture site (Fig. 7). To reach their site of capture, fish E3 travelled 1,800 m upstream, while fish E20 travelled 2,800 m downstream. When detected, the schedule pattern presented a clear diel rhythm, similar to the natural behaviour of this species [31], i.e., movements during the night (95% of the detection was recorded between 7 pm and 2 am GMT).

The post-release trajectories of bream were generally short because of low TRB values. After swimming a short distance downstream, B2 (Fig. 8) spent time on the right bank of the channel before returning to the oxbow. The analysis of hours of detections during the day after release showed that 98% of the detections were distributed in two peaks: one between 11 am and 5 pm (38%) and the second between 10 pm and 3 am (46%), indicating rhythmic activity.

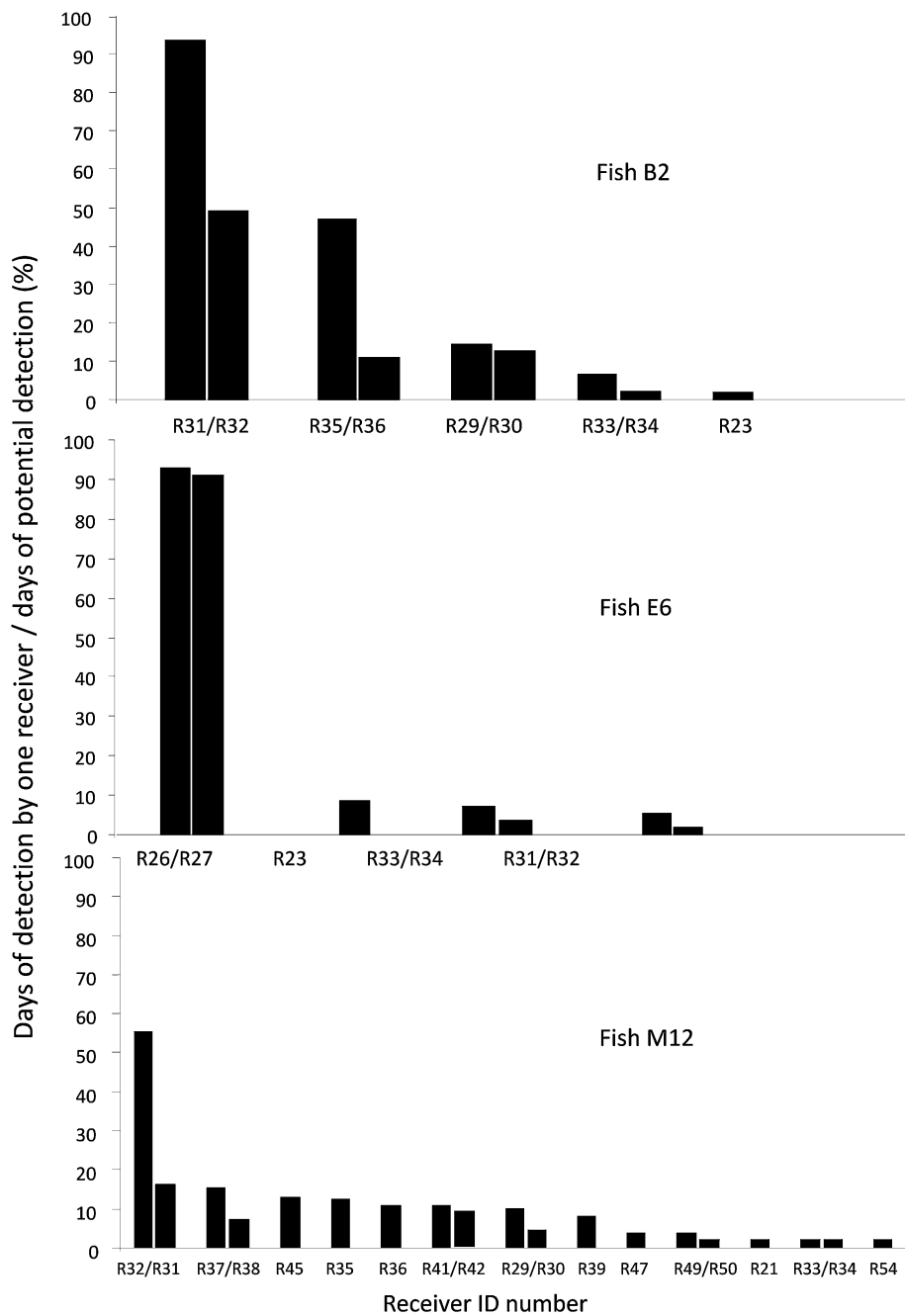


Fig. 6 Days of detection by each receiver as a percentage of days of potential detection. Receivers are organised by decreasing percentages and by pairs when they occur.

Discussion

Multi-criteria approach

By identifying a time to return to normal behaviour, it was possible to obtain an overview of expected recovery in fish released immediately after tagging. Using this approach, data indicative of natural fish behaviour can be separated from those resulting from obvious stress. If the

recovery period is known for each individual, researchers can be sure of analysing behavioural data that lead to unbiased conclusions [1].

One interesting feature of the multi-criteria approach is that it produces an individual TRB, suited specifically to the species and environment being studied. This value indicates individual responses to stress caused by

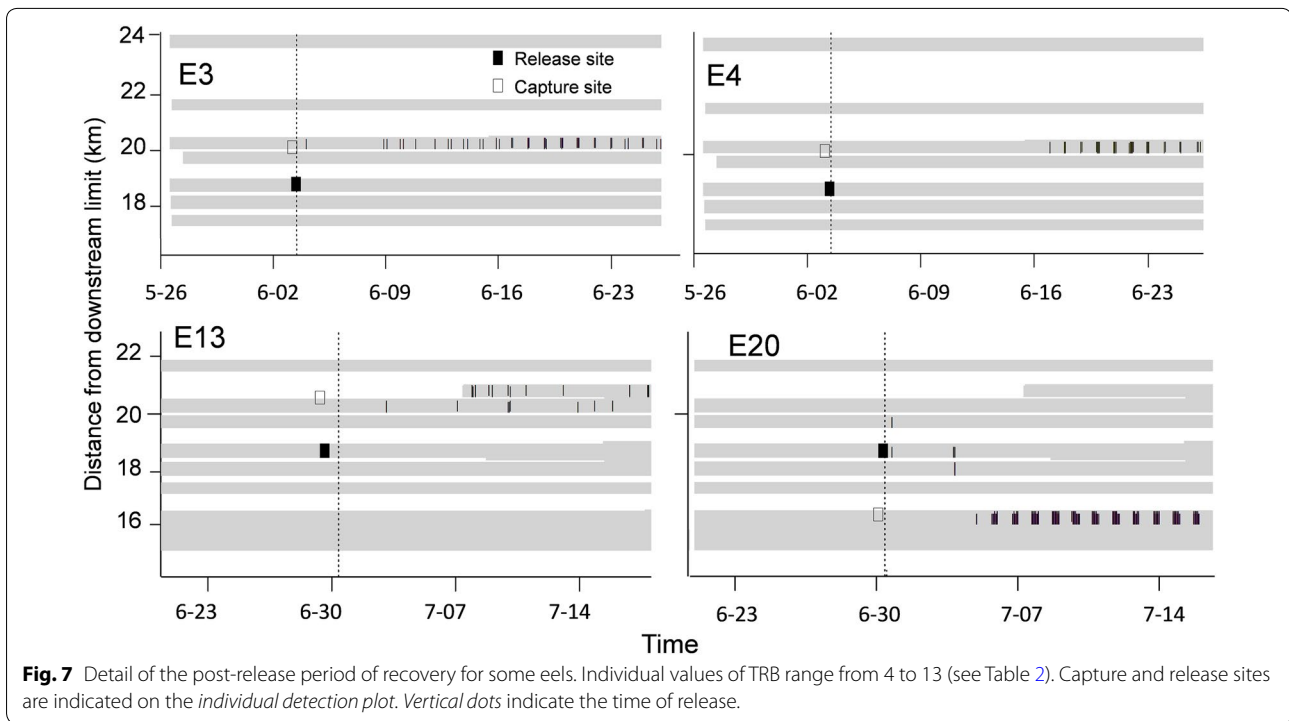


Fig. 7 Detail of the post-release period of recovery for some eels. Individual values of TRB range from 4 to 13 (see Table 2). Capture and release sites are indicated on the *individual detection plot*. Vertical dots indicate the time of release.

handling and transmitter insertion, as well as providing information on general stress responses exhibited by certain species. In this study, we identified major differences in time taken to return to normal behaviour from one species to another. Once the recovery time for a given individual has been quantified, it is easier to interpret post-release movements. Another clear advantage of this approach is that fewer data are discarded. As behavioural analysis requires a large dataset, it is important to keep data for as long a period as possible. While this approach does not require any additional experimentation, it could benefit from additional relevant information, such as observations on return to shoal.

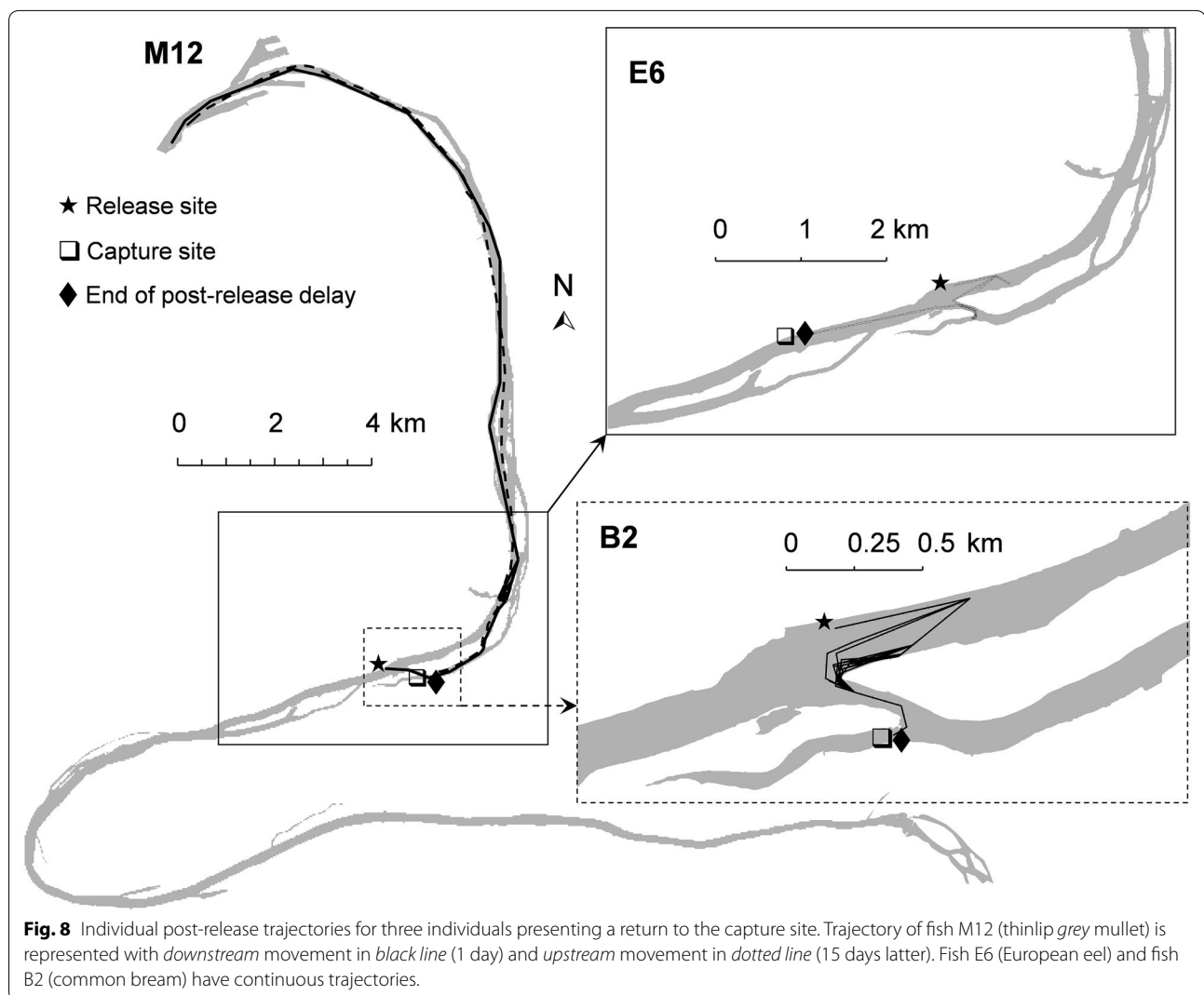
The approach is compatible with all types of tracking data that can generate detection plots and trajectories. The main receivers identified in this study can be considered equivalent to main locations in manual tracking. Main locations are those that detected a given individual with the greatest frequency (locations could be organised as in Fig. 6).

We did not pre-define a value for TRB, as this depends on a variety of external factors. When analysing the TRB and associated behaviour, it is necessary to differentiate what would be analysed in this period. Individuals are either captured in their natural environment before tagging or stocked with hatchery-reared fish. Wild fish can be in the process of migrating (anadromous or catadromous). In that case, the return to migration behaviour can be assessed through the first upstream (adults salmon,

shad or sturgeon) or downstream detection (e.g., salmon smolts, silver eel) [32]. For wild fish, the level of stress when released depends on capture method, handling, anaesthesia, and transmitter attachment procedures [33]. In case of translocation, there is an additional lag when fish return to their capture site or settle in another suitable habitat. With the multi-criteria approach, this lag is taken into account when estimating TRB. Because other factors (temperature, flow conditions, status of the fish, etc.) can affect post-release behaviour, it is crucial to identify the individual TRB for each experiment. Because some fish use intertidal habitats, the potential effects of tide on our study site also had to be considered.

For stocked hatchery-reared fish, individuals recover after surgery in a tank for several days before release. In this case, the TRB corresponds to the time needed to learn to adapt to the new environment and establish a core area of activity (TRA) or adopt migratory behaviour (TRM). Acolas et al. [34] observed four downstream migration patterns of one-year-old hatchery-reared European sturgeon (*Acipenser sturio*) after release in the Gironde Estuary. Kawabata et al. [15] identified a TRB of 3 months before hatchery-reared black-spot tuskfish established a stable home range.

One potential limitation of the multi-criteria approach would be if there was insufficient prior knowledge of normal behaviour criteria. In this case, a graphical representation of detections, trajectory analysis, and core areas of activity could be used in the first instance to study

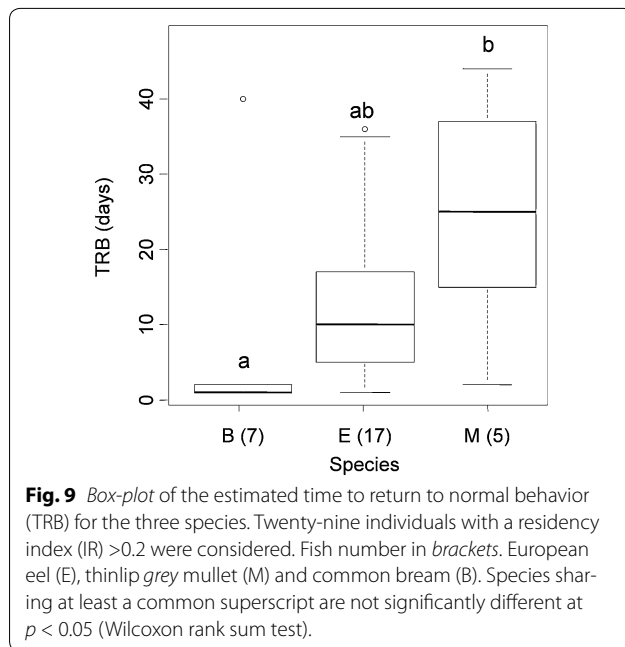


post-release behaviour. Because TRA is designed for a frequency of at least one detection per day, it requires an application of at least 3 days to be effective. The design of the monitoring array and the deployment of receivers could also limit the detection of some individuals. In such cases, only a superior threshold of time was determined (Table 2). In addition, a TRB value of 1 day does not imply that there is no stress—the approach does not consider all dimensions of stress (e.g. physiological parameters).

Post-release movements

All mullet exhibited rapid and straight downstream trajectories a few days after release, with a downstream outlet of the study site. Five individuals returned to the study site in July, 2–6 weeks after tagging (2 tagging period, see Table 2). Therefore, the TRB for these individuals is the

time between tagging and return to the study site. However, given the outputs of the study area systematically observed for this species, it can be assumed that the TRB is actually shorter and that this species has used other habitats downstream of Rouen. This can be seen from the round trips observed for fish M12. As this rapid and straight downstream movement is also observable later in the monitoring period, it can be hypothesised that the quickness of this reaction is specific. However, the long delay before their return to the study site turns out to be not only an effect of post-release stress, but also the result of normal use of the tidal estuary by large shoals of mullet, which often change their feeding habitats. Almeida [35] has observed that the upper reaches of the Mira estuary (Portugal) were the area most commonly used by this species. Oliveira and Ferreira [36] have studied this species in a freshwater stretch of the River Tagus



and found that the major upstream migration occurred until the summer months (high food availability and high observed growth).

Eels showed a low activity during the post-release period. Over this period, there were a low number of detections, which could be interpreted in two ways: a resting phase, buried in the sediment or under blocks that prevent the detection of the signal by receivers, or small movements, before moving to an area where eels were picked up by a receiver. The recovery of movements was also observed, mostly at night, with a return to the capture site or to a new refuge site. McGovern and McCarthy [37] observed only 1–5.5% of movements in the trajectories of eels and mainly twilight activity at dusk. These authors also mentioned a post-release downstream movement of 4,300 m for an individual that returned 12 h later to establish a refuge 640 m downstream of the release site. This rhythmic pattern of activity was recently confirmed for the American eel *Anguilla rostrata* [38].

The TRB for breams was very short or even non-existent. Individuals exhibited behaviour that was fairly similar to that shown over the study period. For this species, previous studies using biotelemetry did not attribute a TRB for externally attached tags [11, 39]. In one such study, after a 5 km translocation in an Irish canal, individuals returned to their capture site within 5 days [11]. For intraperitoneally implanted tags, Lyons and Lucas [13] excluded a nine-day post-tagging period, while Horvath et al. [40] did not mention any TRB. These authors also

observed a fairly similar activity pattern to that in the Seine estuary. In our study, two peaks of detections were observed during the post-release period, one at night (10 pm to 3 am) and one during daytime (11 am to 5 pm). The daytime activity peak may be related to the daytime feeding pattern (with afternoon peaks at 1 pm and 5 pm) that was observed for large bream by Vasek and Kubecka [41] with distinct night-time declines in gut fullness. This author assumed that large bream (total length >200 mm) used vision to locate patches with higher zooplankton densities and therefore fed only when there was enough light. In our study, most breams fed in intertidal backwaters, in which case, their activity pattern may be partly tied to the tidal cycle. Combining acoustic tracking and echo sounding, Lyons and Lucas [13] observed that bream began moving near dusk and tended to move throughout the night, while they were relatively inactive during daylight hours. These fairly contradictory results for bream demonstrate that depending on context (reservoir, freshwater river, and tidal estuary), patterns of activity (and detections) could be modified. Therefore, there is no reason to consider a pre-defined TRB or even a non-existent TRB.

The multi-criteria approach proposed in this paper allows researchers to objectively estimate individual time to recover for any biotelemetry study focusing on behaviour and habitat use. It takes into account the ways in which different species of fish respond to tagging and other kinds of human intervention.

Authors' contributions

CLP, JC and ER designed this study and worked on the data acquisition in the field. JC performed the post-processing and the validation of the database. CLP and ER led the data analysis and wrote the manuscript. All authors read and approved the final manuscript.

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Compliance with ethical guidelines

Competing interests

The authors declare that they have no competing interests.

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