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Animal Biotelemetry

METHODOLOGY

Open Protocols, the new standard for acoustic tracking: results from interoperability and performance tests in European waters

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Abstract

Background The lack of compatibility between acoustic telemetry equipment from different manufacturers has been a major obstacle to consolidating large collaborative tracking networks. Undisclosed encrypted signal coding protocols limit the use of acoustic telemetry to study animal movements over large spatial scales, reduce competition between manufacturers, and stifle innovation. The European Tracking Network, in collaboration with several acoustic telemetry manufacturers, has worked to develop new transparent protocols for acoustic tracking. The results are energy-efficient transmission protocols accessible to all researchers and manufacturers. Today, the Open Protocols (OP) are already available to manufacturers and developers, and the first transmitters and receivers to implement them are already in the water.

Results The main objective of this study was to confirm the compatibility between devices from different manufacturers using OP, characterise the acoustic range of each transmitter–receiver manufacturer combination, compare the detection efficiency to the standard protocols used at present (R64K and encrypted protocols), and assess its robustness against spurious detections. An international collaborative effort was made to conduct acoustic range tests in four main aquatic habitats: a river, a coastal lagoon, a coastal habitat, and the open sea. Receivers and transmitters from different manufacturers were deployed at increasing distances from each other using the same experimental design at each location. The decay of detection probability with distance was modelled for each transmitter–receiver manufacturer combination by applying logistic regression using a Bayesian approach. Furthermore, to thoroughly assess performance differences in an applied research context, we conducted a direct field comparison between groups of smolts tagged with OP and R64K tags, tracking their migration to the sea.

Conclusions Our results confirm full compatibility between the tested devices, with negligible differences in the measured acoustic ranges between OP manufacturers and when compared to encrypted protocols. The OP was also robust against spurious detections, and the field comparison between OP and R64K showed equal performance. We hope these novel insights will encourage international research groups to promote OP-based studies to ensure compatibility and maximise the benefits of acoustic telemetry networks.

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Keywords Acoustic range, Acoustic telemetry, Bio-logging, coding systems, Compatibility, European tracking network

Background

Acoustic telemetry (AT) is a well-established biologging technique that has gained significant relevance over the past decades as a tool to study the movement ecology of aquatic animals [1, 2]. Passive AT, the most widely used application of this technique, involves equipping or implanting animals with electronic transmitters that emit coded acoustic signals, which are subsequently detected by an array of receivers strategically distributed throughout the study area [3]. Recent technological advances, such as the miniaturisation of transmitters, the implementation of built-in sensors, and the development of positioning algorithms, have further enhanced AT's capabilities, allowing researchers to address complex behavioural and ecological questions. These include, for example, questions related to diel activity rhythms [4], the social structure of wild populations [5, 6], as well as the impact of human pressures on the behaviour [7]. As a result, AT has emerged as an indispensable tool in addressing pressing conservation concerns and informing targeted management strategies [8, 9].

One of the most significant trends in AT is the development of large-scale collaborative tracking networks and open databases [2, 10]. In the early days of AT research, studies primarily focused on addressing local questions, often using relatively small receiver arrays. As scientists began to explore more ambitious questions regarding large-scale movements of animals, the need for larger telemetry arrays became self-evident [11]. Due to the substantial effort and resources required to acquire and maintain extensive networks, these have usually been structured in smaller subnetworks managed by different research groups, sometimes spanning multiple countries. Examples of such networks include the Ocean Tracking Network (OTN) [12], the European Tracking Network (ETN) [10], the Great Lakes Acoustic Telemetry Observation System (GLATOS) [13], and the Animal Tracking Facility of the Integrated Marine Observing System (IMOS) [14], which have all demonstrated the feasibility and potential of large-scale AT networks. The implementation of data repositories has further supported the growth of these extensive networks. These repositories enable researchers to upload detection data, allowing cross-network validations to verify whether receivers in other AT subnetworks detected their tagged animals [15]. This collaborative approach has facilitated the expansion of AT networks to cover vast areas, expanding the scope of telemetry studies from local to continental and even cross-continental scales [16, 17].

The success of extensive collaborative networks heavily relies on the compatibility between the signals emitted by transmitters and the receivers, as it is crucial to ensure that tagged individuals are consistently detected across the entire network. Unfortunately, ensuring this compatibility has been a major challenge. Passive AT signals are typically encoded using Pulse Position Modulation (PPM), which consists of a series of pulses on a single frequency forming a train, where the information is encoded in the time intervals between the pings. The scheme that defines how the information is codified in the ping sequence is known as 'protocol'. Receivers are programmed with a 'code map' that comprises the set of protocols they can identify and decode from ping sequences. Although PPM signals can be transmitted at different frequencies (usually between 63 and 77 kHz), 69 kHz prevailed as the standard with the creation of the R64K protocol, which was in the open domain. Due to the technical characteristics of the signal structure, each protocol is limited to encoding a finite number of unique identifiers (IDs). Over time, due to this limitation and to avoid using duplicated IDs, each manufacturer ended up developing parallel proprietary protocols (e.g., Innovasea's A69-1602, A69-9007 and similar protocols, Thelma Biotel's R01M and S64K, and Lotek's MAP system), usually without considering compatibility with other brands or even with the previous protocols implemented in their own product lines [18]. The consequence is the incompatibility between tags and receivers from different manufacturers, which results in animals carrying transmitters from one vendor to pass undetected by receivers from competing vendors.

The lack of compatibility has been recognised as a primary constraint in the implementation of large telemetry arrays [10]. It hampers collaboration between institutions and competition between manufacturers, leading to missed research opportunities and overpriced equipment, respectively [18]. The high cost of these devices further entrenches compatibility issues, as researchers are often reluctant to replace existing equipment in favour of network-compatible alternatives.

The Open Protocols (OP) for AT were introduced in 2021 to address the compatibility challenges mentioned above [18]. This solution was developed through a collaborative effort between the ETN and several AT equipment manufacturers, who agreed to create a compatible coding system. OP are based on the PPM system and include two distinct coding schemes: OPi for signals transmitting ID numbers and OPs for signals transmitting ID and sensor values. The responsibility of assigning the ID codes was delegated to a third party, the Flanders Marine Institute (VLIZ, Belgium), to avoid duplicated IDs being used at the same time. The OP have already been implemented and are accessible to any device developer or manufacturer that agrees to a memorandum of understanding and signs a licence agreement. The first devices that incorporate OP are already available on the market and are being deployed in multiple research projects. According to the European Tracking Network database, 2291 OP transmitters have been implanted in fish, and 1565 OP-enabled receivers have been deployed (https://europeantrackingnetwork.org/, accessed on November 2024), although the actual numbers are known to be (much) higher as the metadata exchange between manufacturers and ETN is in the process of implementation.

Being at their incipient stage, it is crucial to rigorously test the performance of the OP in different environments and compare them with already existing protocols. AT protocols differ in signal structure and length, potentially making specific protocols more susceptible to noise interferences, thereby affecting the acoustic range, or facilitating the production of false detections (i.e., detections assigned to IDs that do not exist or are not present in the study area). Therefore, evaluating new equipment is a critical step in AT research to ensure a proper understanding of the devices' capabilities and an accurate interpretation of the data [19, 20]. More specifically, range tests are crucial to assess how the detection probability decreases as a function of the transmitter–receiver distance, as well as the effect of environmental (e.g., ambient noise) and technical (e.g., transmitter power output) conditions [21, 22]. Tests should span a sufficiently long duration to capture most environmental variations. Common testing procedures involve deploying receivers and transmitters with different distances between them and modelling how the detection probability declines with distance. Moreover, signals emitted by two transmitters in a short interval of time may collide, leading to a loss of both detections or to the generation of false detections. False detections are a particular concern in environments with high noise levels that might interfere with acoustic signals [23]. The probability of obtaining false detections depends on the signal structure implemented in the protocol, which may increase the random emergence of valid IDs from interferences between signals and environmental noise, and on the sensitivity of receivers to identify valid pings, which depends on signal-to-noise ratios. By thoroughly testing new devices, researchers can optimise their performance and ensure the reliability of the data collected in their studies.

In this study, our primary objectives were to confirm the interoperability of the new OP between devices of different manufacturers, evaluate their performance in various environments, and compare the performance of the OP against a commonly used protocol (R64K) in a direct test with wild animals. To achieve this, we carried out standardised range tests in different habitats across Europe. By deploying telemetry devices from multiple manufacturers and different coding protocols, our study design ensured a comprehensive evaluation of interoperability and compatibility. The results obtained from these tests will contribute to a deeper understanding of the performance and limitations of different protocols and help researchers optimise the use of telemetry devices for future studies, ultimately advancing the field of aquatic animal movement ecology.

Methods

Study areas

We conducted the acoustic range and interoperability tests at four locations across four European countries: Belgium, Spain, Portugal, and Denmark (Fig. 1, Table 1). We chose these locations to cover the main aquatic habitats where AT studies are usually carried out: the open sea, nearshore coastal habitats, coastal lagoons, and rivers. We carried out the open sea tests at the C-Power Wind Farm, ~ 30 km offshore the coast of Belgium. The wind farm is situated on a natural sandbank of medium to coarse sand. The turbines are 500 to 800 m apart and the depth varies from 18 to 24 m [24]. The coastal habitat tests were carried out within the marine protected area of the Bay of Palma (Mallorca, Balearic Islands, Spain), at 400 m from the coast in shallow waters (from 15 to 20 m) characterised by sandy bottoms and *Posidonia oceanica* seagrass meadows. The coastal lagoon tests were conducted in Ria Formosa (Portugal), a mesotidal lagoon composed of a complex network of channels interconnected with six sea inlets, allowing water recirculation within the system and permanent exchange with the adjacent Atlantic Ocean. This coastal lagoon includes extensive areas of mudflats and seagrass beds with an average depth of 2 m. River tests were carried out in the Yser River (Belgium), a small (78 km) lowland river originating in France and discharging in the North Sea in Belgium. At this site, the tests were conducted at ~ 35 km from the river mouth, where the river is ~ 2 m deep and 20 m wide. The river is characterised by silty to muddy bottoms and banks covered with trees. During the study period, discharge ranged between 0.09 and 0.55 m^3/s.

In addition to the acoustic range tests, we evaluated whether OP produce comparable results when applied

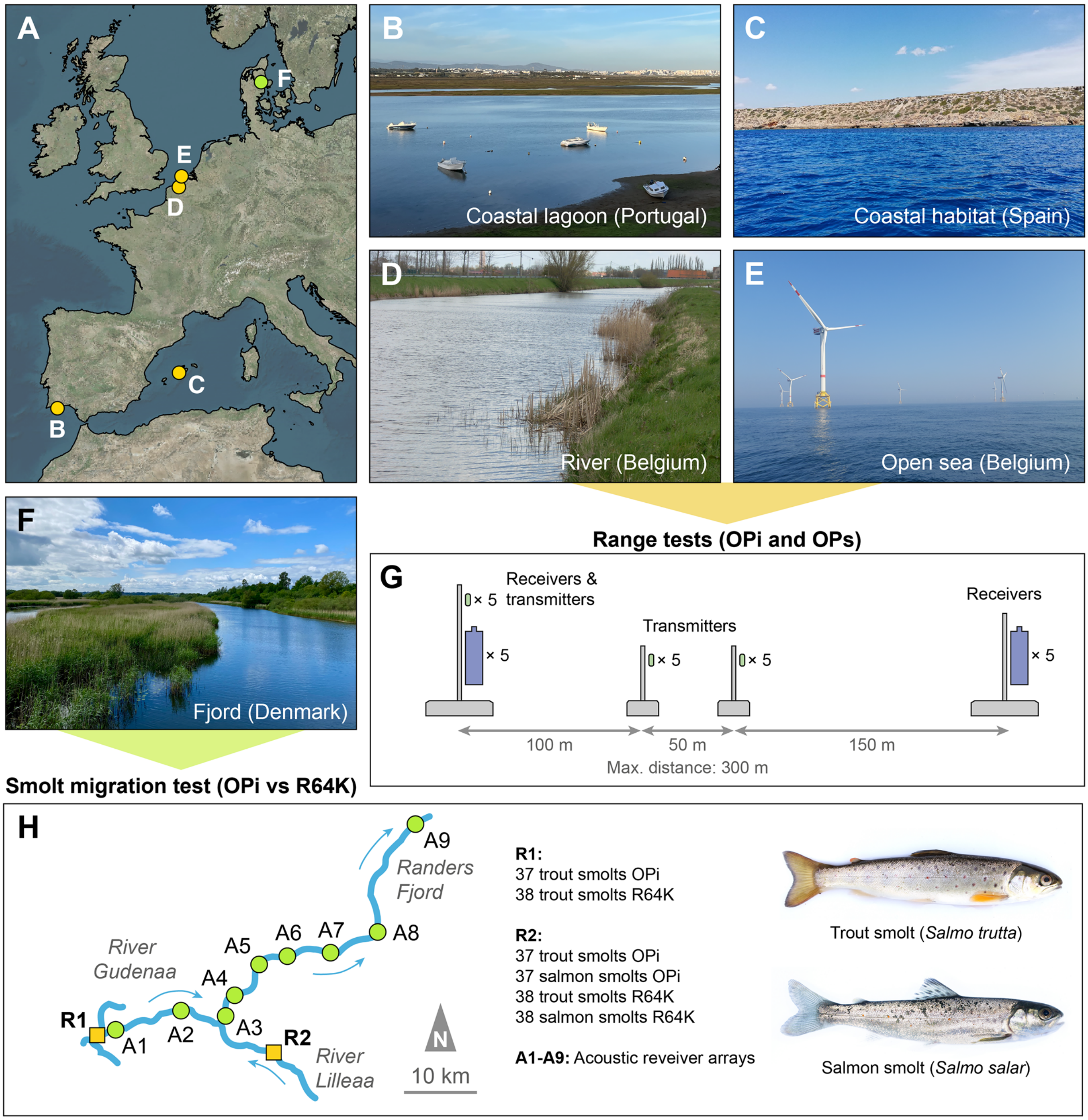

Fig. 1 Map and pictures of study locations and study designs. **A** General map of the locations of the range tests (orange dots) and the smolt migration test (green dot). **B**–**F** Pictures of the study locations. **G** Representation of the deployment design used in the range tests in the open sea and the river (number of transmitters and receiver changed in the other tests). **H** Representation of the setup used with trout and salmon smolts, where A1–A9 (green dots) represent the acoustic receiver arrays (sets of two receivers), R1 and R2 (yellow squares) the release location of tagged smolts, and the blue arrows indicate the water flow direction. Photo credits: D. Abecasis (**B**), E. Aspillaga (**C**); P. Verhelst (**D**); J. Reubens (**E**); K. Birnie-Gauvin (**F**, **H**-trout smolt), M. H. Larsen (**H**-salmon smolt)

in a practical research context. To do this, we compared the performance of OP and R64K transmitters in measuring the migration success of Atlantic salmon (*Salmo salar*) and brown trout (*Salmo trutta*) smolts during their migration from the River Gudenaam through the Randers Fjord to the Kattegat Sea in Denmark. The River Gudenaa (mean annual water discharge of 32 m^3/s) is the major freshwater source of the narrow Randers Fjord. The 30 km long Randers Fjord is divided into two parts: a narrow inner section and a wider outer section that exits into the Kattegat Sea. Salinity varies with water discharge in the River Gudenaa, but the fjord can be generally

Table 1 Summary of the OP tests conducted in different habitats

Country	Habitat	Location	Target protocol	Duration (days)	Depth (m)	Max. tested distance (m)
Range tests (OPi and OPs)						
Belgium	Open sea (OS)	C-Power Wind Farm	OPi	12	25	300
			OPs	21	25	300
	River (R)	Yser River	OPi	30	2	300
			OPs	20	2	300
Spain	Coastal habitat (CH)	Palma Bay Marine Reserve	OPi	14	15	450
Portugal	Coastal lagoon (CL)	Ria Formosa	OPi	11	5	300
			OPs	12	5	300
Smolt migration test (OPi vs R64K)						
Denmark	Trout and salmon smolt migration	River Gudenaa and Randers Fjord	OPi, R64K	90	–	–

characterised as brackish with increasing salinity, depth and distance from the river mouth.

Tested equipment

To assess the compatibility and interoperability among existing coding protocols, we employed AT devices (receivers and transmitters) from four manufacturers (Thelma Biotel, Norway; Lotek Wireless, Canada; Sonotronics, USA; and Innovasea Systems, USA) that implemented different transmission protocols: OPi, OPs, R64K, and Innovasea's A69-1602 and A69-9007. This combination of devices facilitated a comparative assessment of the detection performance of the open-access OP and R64K protocols while also testing for potential differences with respect to two commonly used proprietary protocols (A69-1602 and A69-9007). The devices operating with the OPi and OPs were provided by the three manufacturers that had signed the 'Memorandum of Understanding for the organisations involved in the Open Protocols' in support of the scientific community's effort to make open and transparent AT systems: Thelma Biotel, Lotek Wireless, and Sonotronics (Table S1). The receivers from these manufacturers were programmed to detect and record 69 kHz acoustic signals coded in the two OP versions (OPi and OPs) and were also compatible with the R64K protocol. Innovasea later adhered to the memorandum of understanding, but the tests had already been performed by that time, so only non-OP receivers and transmitters from this manufacturer were tested. The Innovasea receivers, based on proprietary code maps (MAP-114 and MAP-115), were used in all but the coastal habitat tests. Despite the four manufacturers produce R64K transmitters, only Thelma Biotel's R64K transmitters were tested due to equipment availability. All the transmitters had similar power outputs, ranging between 144 and 158 dB (Table S1).

Design and deployment of range tests

To ensure comparability, we replicated the same deployment design across the range tests conducted in the four environments. In each location, we deployed sets of receivers and transmitters at different distances among them to characterise the relationship between distance and detection probability [20, 25]. Four moorings were installed at each test site, aligned along the bottom (Fig. 1G). The moorings were constructed using a rope and a submerged buoy (tests in coastal habitat and coastal lagoon tests) or metal structures (open sea and river tests). A receiver of each manufacturer was installed on the two outermost moorings (between 3 and 5 receivers per mooring, depending on the habitat, Table S1), while a set of transmitters of each manufacturer was attached to the two middle moorings and to one of the outermost moorings (between 3 and 5 receivers per mooring, depending on the habitat, Table S1). We chose the distance between the two outermost moorings to be within the maximum detection range at median environmental conditions in each habitat based on prior knowledge of the local research teams (maximum distances ranging from 300 to 450 m, Table 1). The combination of the two moorings with receivers and three moorings with transmitters allowed us to quantify the detection probability at five distances in each test (distances in the open sea, coastal lagoon, and river environments: 0, 100, 150, 200, and 300 m; distances in the coastal habitat: 0, 150, 225, 300, and 450 m; Fig. 1G).

The duration of the tests ranged from 11 to 30 days. In three habitats (open sea, river, and coastal lagoon), we tested the OPi and OPs protocols separately by repeating the same experimental design in two consecutive deployments, each using transmitters with one of the protocols (Table 1). In the coastal habitat, only the OPi protocol was evaluated. At the end of each test, moorings were retrieved from the sea or riverbed and data from receivers was uploaded to the ETN database (https://www.lifewatch.be/etn/). Finally, the data were imported to the R computing environment [26] for statistical analysis.

Detection range analysis

The detection record was first pooled into 2-h intervals to ensure a sufficient number of detections for calculating robust detection efficiency estimates, regardless the time interval between signals. This approach resulted in an average of 20 expected detections per interval for transmitters emitting every 300–420 s and 60 expected detections for those emitting every 90–150 s. We then calculated the detection efficiency of each receiver–transmitter pair and distance combination as the ratio between the detected signals and the expected emitted signals, estimated based on the average emission period of the transmitter. The acoustic range was calculated for each deployment by fitting the following logistic model using a Bayesian approach:

$$P(x) = \frac{L}{1 + e^{-b(x-\mathrm{inf})}}$$

where $P(x)$ represents the detection probability at distance x, b is the steepness of the sigmoid, L stands for the maximum detection probability of the sigmoid, and inf represents the value of the midpoint (inflection point). At the observation level, the detection efficiency was assumed to follow a binomial distribution with a probability modelled by the mentioned logistic model. Two additional levels were added to the model: receiver–transmitter manufacturer combinations were included as a fixed factor (method level), and separate days were included as a random factor (trial level). Therefore, the model drew trial-level specific parameters from method-specific normal distributions. The Bayesian inference, applied using the 'R2jags' package for R [27], was chosen over other statistical methods due to its ability to handle complex data sets, explicitly state the model structure, and quantify uncertainty in parameter estimates. All details on the implementation of the model and the selected prior distributions, as well as the code and the data used in all the analyses, can be found in the following GitHub repository: https://github.com/aspillaga/ETN-OP-TEST.

We extracted the posterior values (distributions of the three model parameters given the observed data and the Bayesian priors) from 1000 Bayesian iterations and used them to calculate two more easily interpretable parameters: the maximum detection probability (P_0) and the acoustic range (x_r). P_0 corresponds to the detection probability at a distance of 0 m. It should be equal to one when only one transmitter is present in the array but becomes lower due to signal collisions when several transmitters co-occur or to physical phenomena such as close proximity detection interference (CPDI) [28]. x_r is the distance at which the detection probability was equal to 50% of P_0. Therefore, the posterior distributions of P_0 and x_r for each deployment and receiver–transmitter manufacturer combination were used to compare acoustic performances, providing a more realistic representation of the detection performance under the specific environmental conditions of each test.

Analysis of false detections

To characterise the number and nature of false detections in the data set, we adapted the methodology of Simpfendorfer et al. [23], which distinguished two types of false detections: those with an ID of non-existing tags (type A) and those with the ID of transmitters used in the study (type B). To assess type A false detections, detections corresponding to transmitters used in the range tests or other transmitters known to be either implanted in fish or installed as control tags were removed from the database. The remaining detections, considered type A false detections, were then pooled into daily bins, habitat type, and protocol type to compare daily occurrence rates between the receiver manufacturer models. To assess type B false detections, the time difference between subsequent detections of each receiver–transmitter pair was calculated. As the random delay between transmissions varied between the used transmitter models (300–400, 300–420, 90–150, and 30–120 s, Table S1), we considered a time buffer of 10% of the minimum interval as the time difference threshold to account for any temporal drift in the receiver and transmitter clocks (time thresholds of 270, 270, 81, and 27 s, respectively). Consecutive signals with the same ID detected at intervals below the time threshold were then considered a type B false detection. However, this approach did not reveal false positives of type B; therefore, only type A false detections were considered for this work.

Field tests with smolts

To test the OPi under realistic study conditions, we took advantage of an ongoing study exploring the behaviour of migrating brown trout (*Salmo trutta*) and Atlantic salmon (*Salmo salar*) smolts in the River Gudenaa, Denmark (see Sortland et al. [29], for full details). A total of 18 Thelma Biotel receivers (OP and R64K compatible) were installed in 9 arrays (two receivers per array), situated along a stretch of the River Gudenaa and Randers

Fjord, covering a total distance of 65 km (Fig. 1H). A total of 150 brown trout and 75 Atlantic salmon were internally tagged with Thelma Biotel ID-LP7 tags (7.3 mm diameter, 17 mm length, 1.8 g in air), half programmed to emit OPi codes and half R64K codes. Brown trout smolts were captured by electrofishing three tributaries to River Gudenaa (River Lilleaa, Møbæk Mill Stream, and Skibelund Stream), whereas Atlantic salmon were obtained from a hatchery. The fish were tagged alternately with OPi and R64K transmitters on the river bank following a brief period of anaesthesia and released shortly thereafter. Salmon were released exclusively in River Lilleaa (release location R2), whereas trout were released at their capture site (release locations R1 and R2, Fig. 1H). Fish were subsequently tracked as they migrated downstream, through River Gudenaa and Randers Fjord until they exited into the Kattegat Sea for the duration of the smolt run in Denmark (from tagging in mid-March until the beginning of June).

To test the possible effect of the tag protocol in estimating migration success, we applied a survival analysis approach. From the detection data, we first calculated the number of smolts detected in each array separately for each species, release site, and tag protocol. To adjust the survival analysis, we identified migration failures when fish stopped being detected when moving downstream. A migration failure event (equivalent to 'dead' in survival analysis) was attributed to each fish at the first array immediately after the one in which it was furthest detected downstream. Fish detected in the last array (A9) were identified as 'alive' at the end of the experiment. For fish not detected by any receiver, migration failure events were assigned in the first array downstream of their release site (array A1 for fish released at location R1 and A3 for fish released at location R2). We then used the 'survival' package for R [30] on this data to estimate Kaplan–Meier survival curves and to compare the migration successes of fish tagged with different protocols using a log-rank test.

Results

Compatibility of devices

All receivers that incorporated the OPi and OPs protocols in their code map detected the transmitters using the same protocols, as well as the transmitters using the R64K protocol (Table 2). Only receivers using Innovasea's

Table 2 General compatibility table between tested receivers (columns) and transmitters (rows) from different manufacturers using different protocols

Transmitters / Protocols		Receivers: Thelma Biotel	Receivers: Lotek	Receivers: Sonotronics	Receivers: InnovaSea MAP-114	Receivers: InnovaSea MAP-115
Thelma Biotel	OPi	+	+	+	–	–
	OPs	+	+	+	–	–
	R64K	+	+	+	+	–
Lotek	OPi	+	+	+	–	–
	OPs	+	+	+	–	–
Sonotronics	OPi	+	+	+	–	–
	OPs	+	+	+	–	–
InnovaSea	A69-1602	–	–	–	+	+
	A69-9007	–	–	–	+	+

Positive signs (+) indicate compatibility, while negative signs (–) denote incompatibility or absence of detections

MAP-114 and MAP-115 proprietary code maps detected the A69-1602 and A69-9007 encrypted protocols. These receivers did not detect any OPi and OPs signals, and only MAP-114 was compatible with R64K signals. Receivers with the MAP-115 coding scheme only detected the signals encoded in Innovasea's A69-1602 and A69-9007 protocols.

Device and habitat-specific variations of acoustic range parameters

A significant decrease in detection probability with distance was observed in all deployments and receiver/transmitter combinations (Fig. 2 and Figs. S1–S3). The parameters of the fitted logistic regression model revealed notable differences between environments and, to a lesser extent, between manufacturers (Figs. S4–S6).

The estimated acoustic ranges (x_r) were highly consistent within environments (Fig. 3). Overall, we observed similar x_r distances in the open sea (214 m [159–341 m], median and 95% range of estimated parameters for all receiver–manufacturer combinations), the river (261 m [148–319 m]) and the coastal habitat (293 m [198–384 m]), while the deployments in the coastal lagoon presented lower values (98 m [40–174 m]). Differences between manufacturer combinations were relatively small and mainly non-significant, as shown by the high overlap of the 95% posterior distribution values obtained for each combination (Fig. 3). However, we observed a high dispersion of x_r estimates for specific transmitter–receiver manufacturer combinations in some environments (e.g., Sonotronics receivers–Thelma Biotel R64K and Lotek OPi tags in the open sea, Fig. 3A) and Lotek receivers–Lotek and Sonotronics OPi tags in the coastal habitat, Fig. 3D), indicating higher uncertainty in model convergence across Bayesian iterations (e.g., Sonotronics receivers in the open sea and Lotek receivers in the coastal habitat). These dispersed convergences were not consistent across all the transmitters and manufacturers used in the same deployment and were related to low detection probabilities at small distances, which hampered the fit of the sigmoidal model due to the small difference in detection probability between short and long distances (Figs. 2 and S3). In the river test, a higher variability of the acoustic range estimations was observed for OPs deployments compared to OPi deployments (Fig. 3B).

In contrast, the maximum detection probability (P_0) showed higher variability than the acoustic range within environments (Fig. 4). Overall, higher P_0 values were estimated in the open sea (0.81 [0.21–0.93], median and 95% range of estimated parameters all the receiver–manufacturer combination) and the river (0.82 [0.66–0.94]) than in the coastal habitat (0.49 [0.19–0.59]) and the coastal lagoon (0.48 [0.37–0.87]). Sonotronics receivers consistently presented lower P_0 values than other receivers for all the compatible protocols at the open sea test (Fig. 4A), and for some protocols at the river (Fig. 4B), the coastal lagoon (Fig. 4C) and the coastal habitat (Fig. 4D). Similar to the acoustic range, higher variabilities of P_0 values were observed in the OPs deployments at the river compared to OPi deployments.

False detections

Out of all the detections in the data set, 0.18% ($n=2240$) were identified as type A false positives (hereafter 'false detections') as they could not be attributed to any known tag and did not match the expected detection pattern of a tagged fish (e.g., multiple detections per day and across different receivers). OPi and OPs protocols presented the lowest false detection occurrences compared to other protocols included in the receiver's code maps, especially R64K and S256 (equivalent to the R64K shared protocol, but for transmitters with sensors). Among all deployments (99 days in total), only 0.02% of the detections were attributed to false OP codes, corresponding to 13.8% of false detections (OPi: $n=136$, 0.01% of detections, 6.07% of false detections; OPs: $n=174$, 0.01% of detections, 7.77% of false detections). In contrast, 0.11% of the detections were attributed to false R64K signals ($n=1350$), corresponding to 60.3% of all false detections. The remaining false detections were attributed to the protocols S256 ($n=327$, 0.03% of the detections, 14.6% of the false detections) and A69-1602 ($n=175$, 0.01% of the detections, 7.81% of the false detections). Other protocols (e.g., shared: R04K; Thelma Biotel: R01M, S64K; Innovasea: A69-1601, A69-1604, A69-9006) were also eventually recorded, but only accounted for 0.01% of total detections ($n=78$, 3.48% of false detections).

False detections usually accounted for less than 1% of the daily detections in each receiver (0.21% [0–1.35%], mean and 95% value range, Fig. 5). Thelma Biotel receivers presented the lowest maximum proportions of false detections in all environments compared to other manufacturers, reaching maximum values of 0.16% of daily detections in the river, 0.38% in the coastal habitat, 0.64% in the open Sea, and 3.75% in the coastal lagoon. In contrast, Lotek receivers consistently presented higher rates of false detections across protocols, especially R64K, reaching maximum daily false detection rates of 1.85% in the coastal habitat, 1.60% in the open sea, and 1.06% at the river. Sonotronics receivers also presented relatively high maximum proportions of false detections in some environments, such as the coastal lagoon (6.52%) and the open sea (2.04%), while lower rates were observed at the river (0.30%) and the coastal habitat (0.59%).

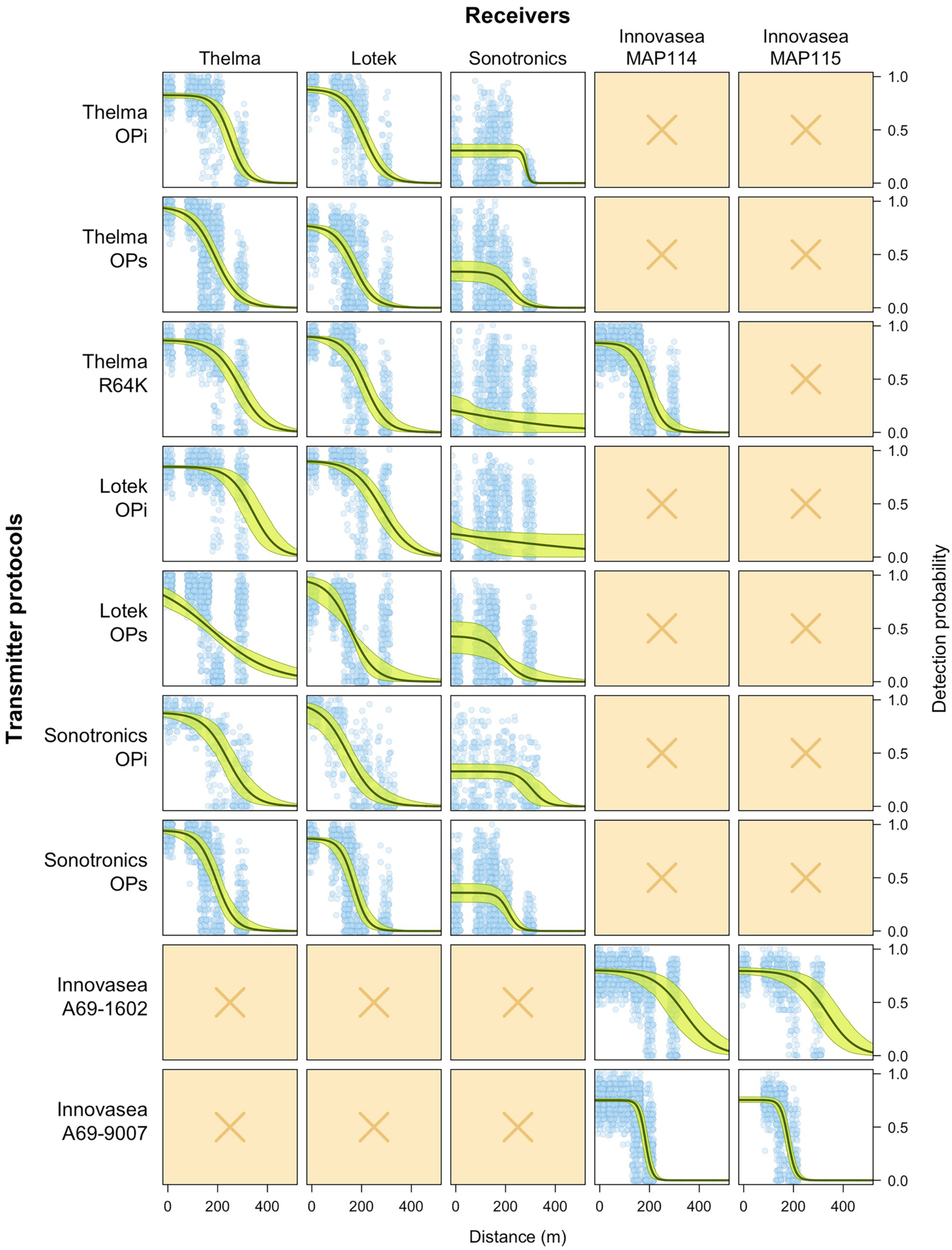

Fig. 2 Example of the results of the acoustic range test conducted in the open sea (C-Power wind farm, Belgium) using OPi and OPs transmitters. Data points represent detection efficiencies (percentage of detected signals in 2 h intervals) at different distances for each receiver (panels in columns) and transmitter (panels in rows) combination. The green line and the green area represent the median logistic model and the 95% interval of posterior values, respectively, of 1000 Bayesian iterations. Empty panels with a cross indicate receiver–transmitter combinations that did not result in any detection due to device incompatibility. The results and fitted models from the other tests are provided as online supporting information in Figs. S1–S3

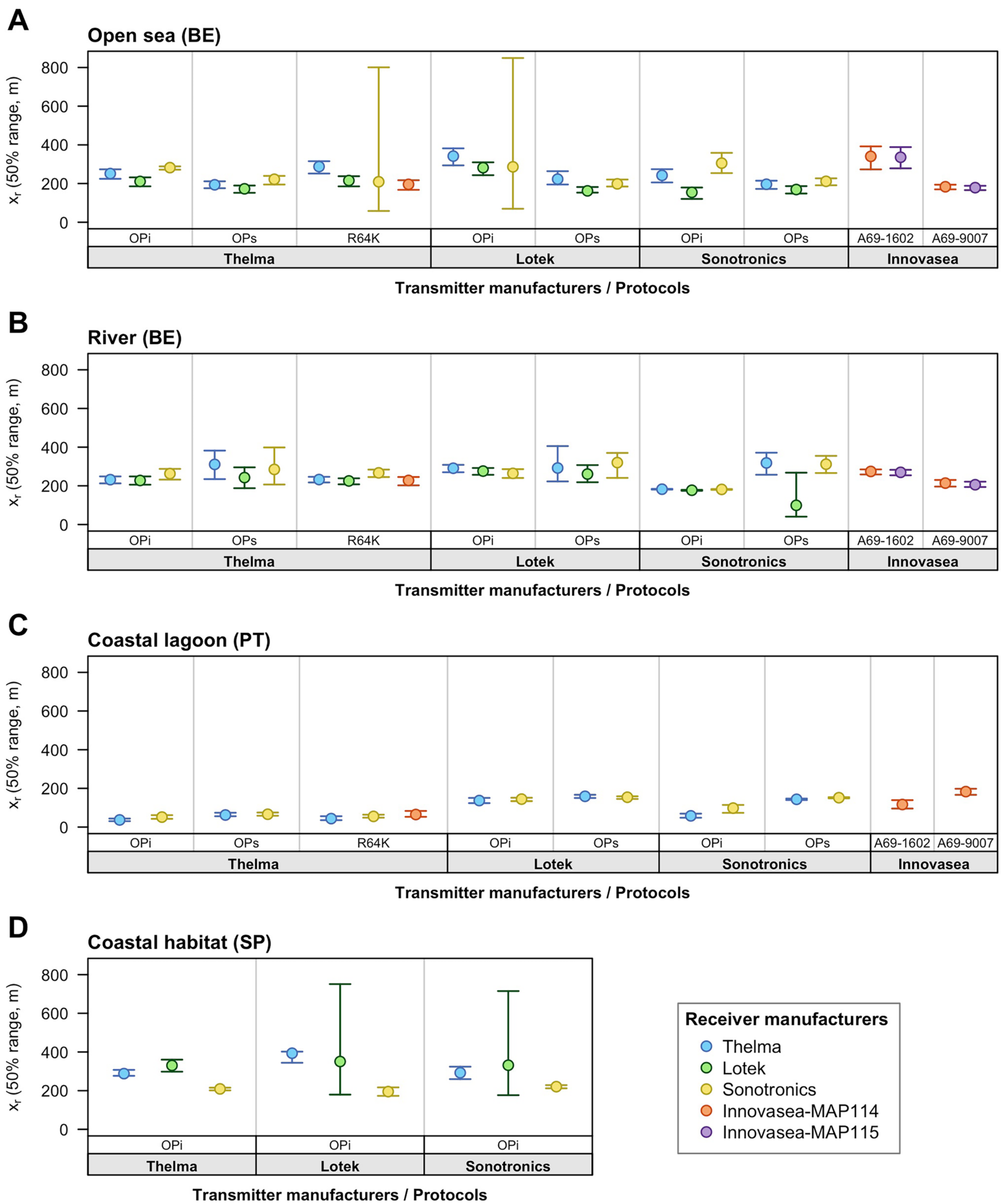

Fig. 3 Posterior distributions of the acoustic range values (x_r, distance at which 50% of the maximum detection probability was achieved) for each transmitter–manufacturer combination. Values were calculated by applying the logistic function to the coefficients estimated in each iteration. Each panel (**A**–**D**) represents the results for the different environments tested. Points and whiskers represent the median value and 95% range of 1000 Bayesian iterations

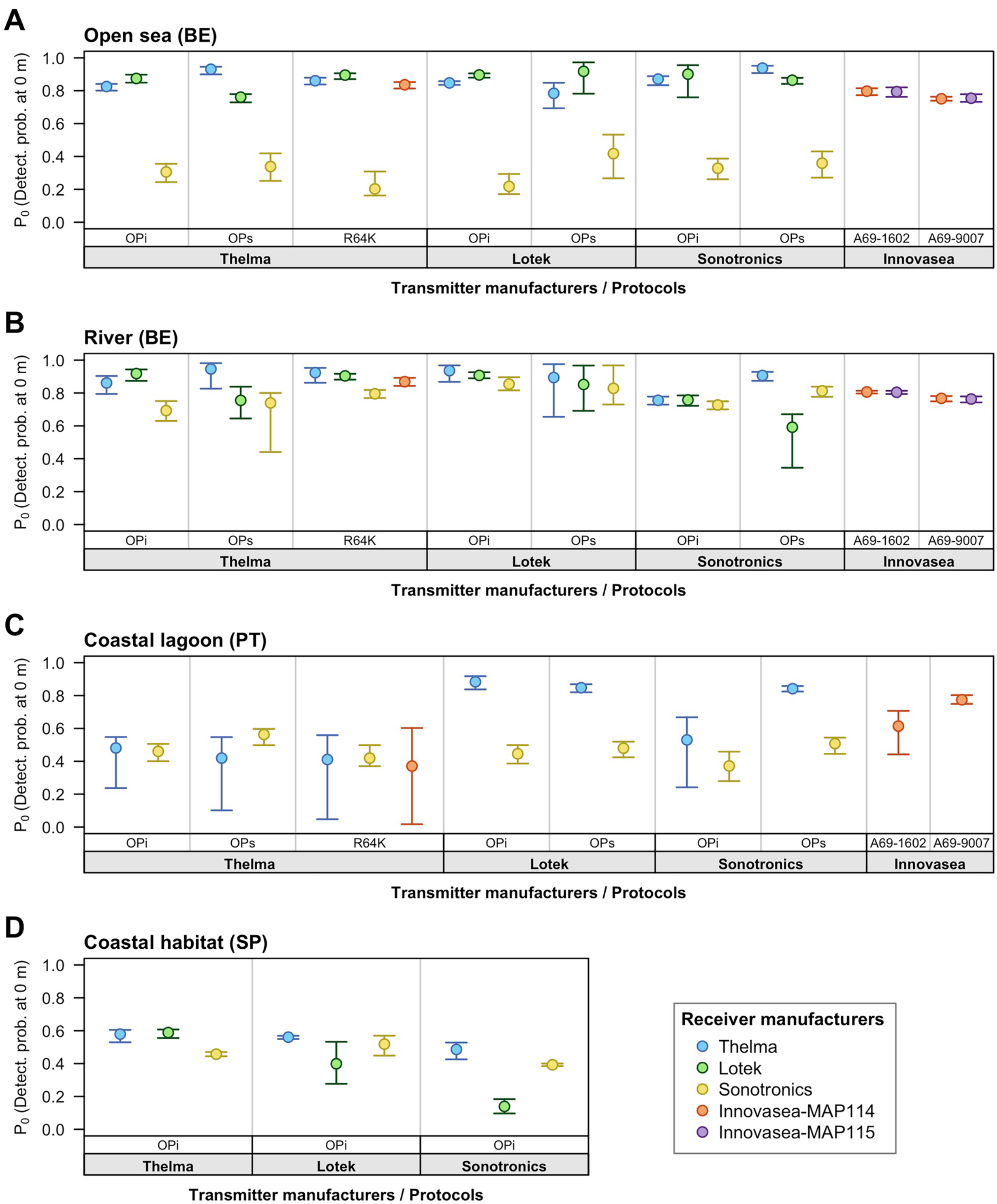

Fig. 4 Posterior distributions of detection probability values at a distance of 0 m (P_0) for each receiver–transmitter manufacturer combination in each test. Values were calculated by applying the logistic function to the coefficients estimated in each iteration. Each panel (**a**–**d**) represents the results for the different environments tested. Points and whiskers represent the median and 95% range, respectively, of 1000 Bayesian iterations

A total of 911 false IDs were detected across all the deployments. Of these codes, 97.6% (889 unique IDs) were detected less than 10 times in the entire data set, accounting for 61.2% of the false detections ($n = 1371$). Therefore, the remaining 38.8% of false detections ($n = 869$) corresponded to a limited set of codes (22

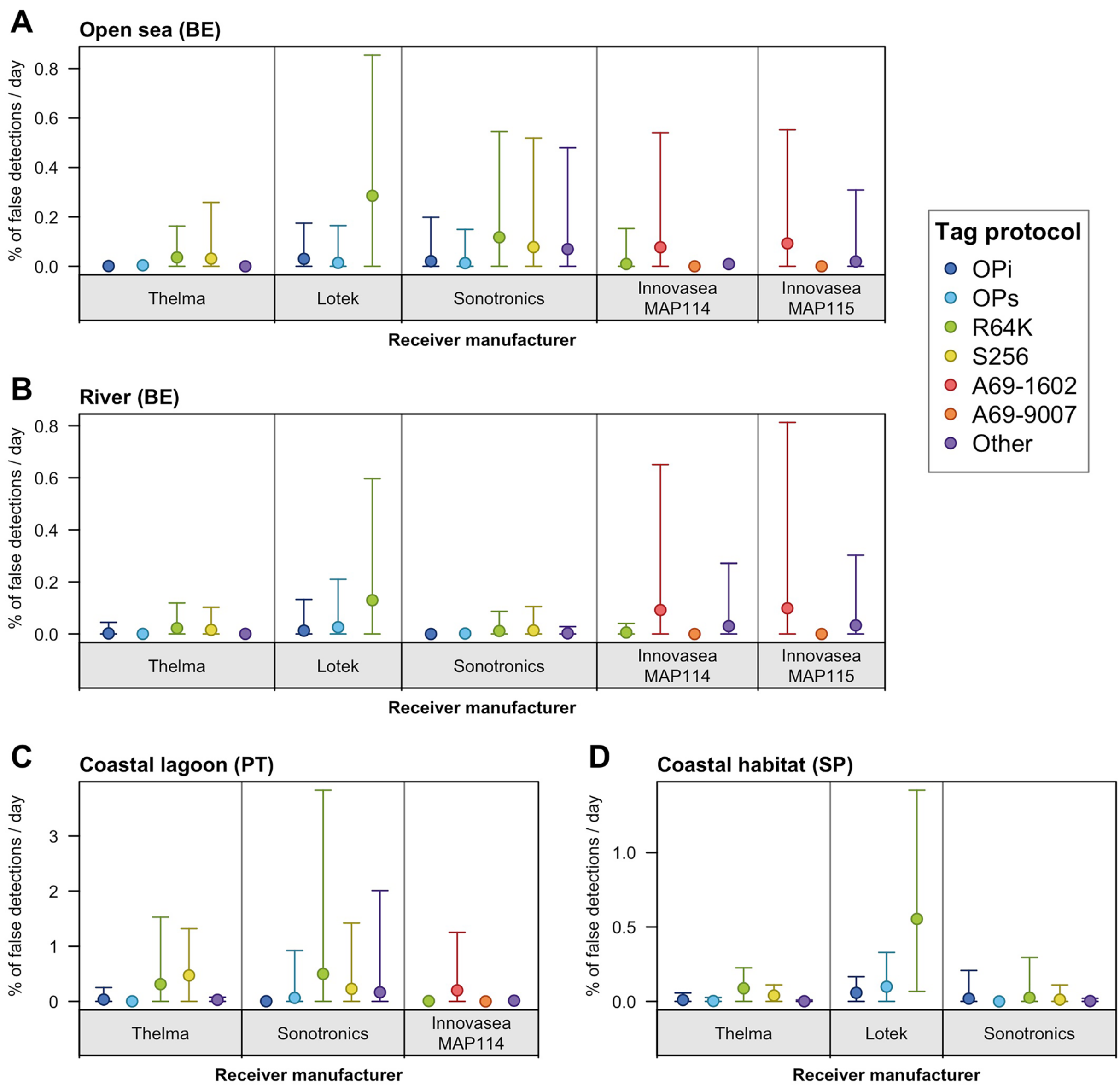

Fig. 5 Daily proportions of type A false detections (% detections per day and receiver) for different transmitter protocols (colours) and receiver manufacturers (divisions within each plot). Points and whiskers represent mean values and 95% ranges, respectively. Each panel (**a**–**d**) shows the results for the different tested environments

unique IDs) that were detected more than 10 times during the deployments. Of these false codes, those that produced the highest number of false detections were 'R64K-4097' (334 detections, 14.9% of false detections), 'S256-51' (102 detections, 4.5% of false detections), 'R64K-10753' (80 detections, 3.6% of false detections). The most common false code ('R64K-4097') appeared in all habitats and all receiver manufacturers, despite most detections ($n = 310$) occurring in one of the Lotek receivers deployed in the coastal habitat. None of the false ID codes with more than 10 occurrences throughout the data set were OP. The OP false IDs that were detected most frequently were 'OPs-0' (8 detections, 0.36% of false detections), 'OPi-1000005' (7 detections, 0.31% of false detections), 'OPi-18' (5 detections, 0.22% of false detections), and 'OPi-4096' (5 detections, 0.22% of false detections). All other false OP codes (252 unique IDs) were detected less than 4 times during the experiments, accounting for 12.7% of false detections.

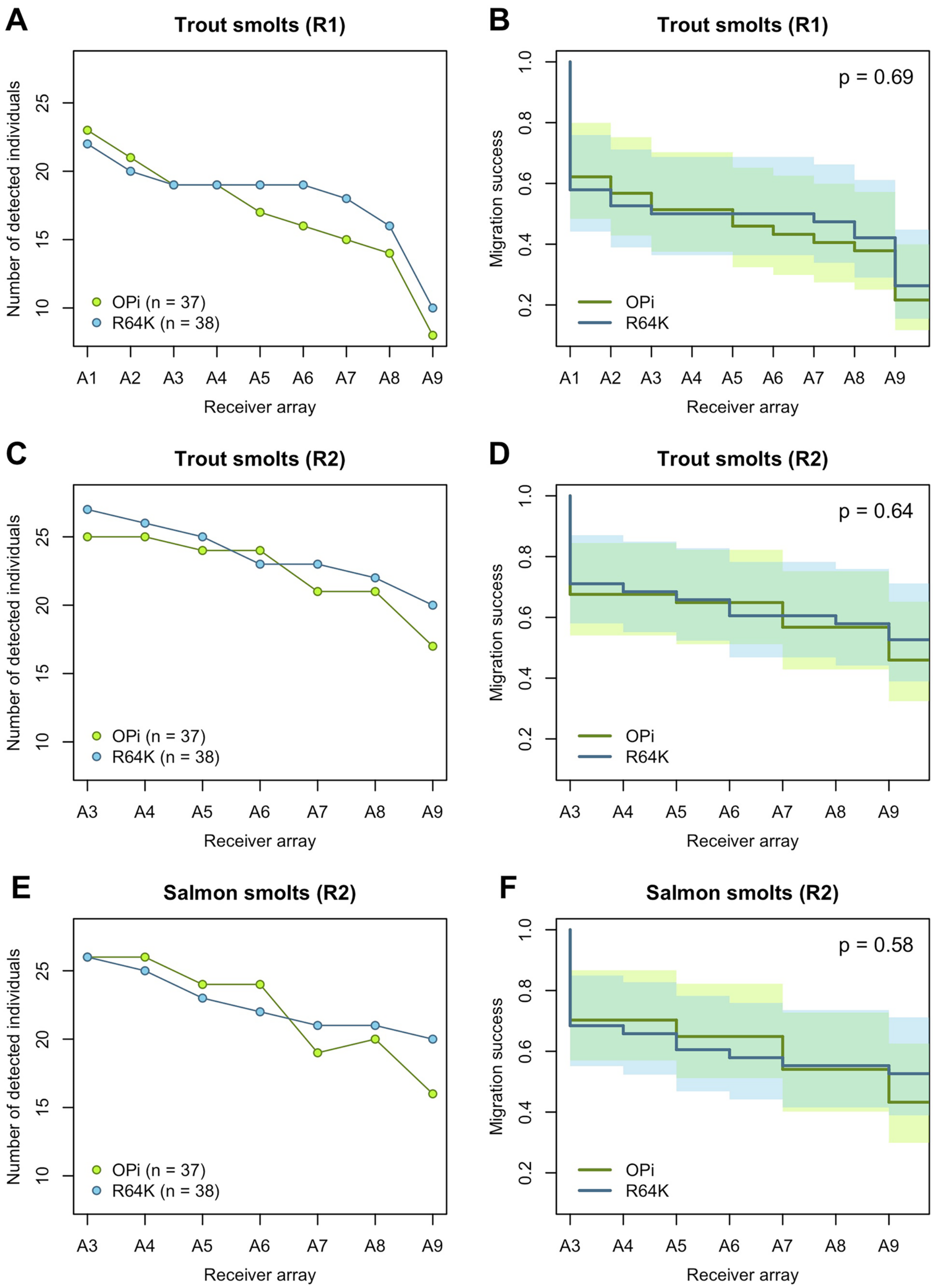

Fig. 6 Comparison between OP (green) and R64K (blue) to study the survival and migration of trout smolts released at locations R1 (**A**, **B**) and R2 (**C**, **D**) and salmon smolts released at location R2 (**E**, **F**). Panels on the left represent the total number of smolts detected at each array, panels on the right represent the Kaplan–Meier survival curves for each group, and *p* values represent the significance of log-rank tests comparing both curves

Smolt migration test

Of the 225 tagged smolts, 149 were detected in the receiver arrays throughout the fjord and river (97 out of 150 trout smolts and 52 out of 75 salmon smolts). The total number of detected smolts decreased throughout their migration (Fig. 6). The lowest numbers (55 trout smolts and 36 salmon smolts) occurred in the lower array (A9).

No significant differences were observed between the migration success estimated for smolts tagged with the OPi and R64K protocols (log-rank tests; trout smolts released at R1: $\chi^2 = 0.16$, $df = 1$, $p = 0.69$; trout smolts released at R2: $\chi^2 = 0.21$, $df = 1$, $p = 0.64$; salmon smolts released at R2: $\chi^2 = 0.31$, $df = 1$, $p = 0.58$). In some arrays, the number of detected OPi-tagged smolts was slightly lower compared to R64K-tagged smolts, but those differences were not significant and were, therefore, attributable to sample size. In the lower array (A9), migration successes of 0.22 [0.12–0.40] and 0.26 [0.15–0.45] (mean and 95% confidence interval) were estimated for trout smolts tagged with OPi and R64K transmitters, respectively, and released at location R1. For the trout smolts released at location R2, the estimated migration successes were higher than those released at R1 but similar between the tag protocols, with 0.46 [0.32–0.65] and 0.53 [0.39–0.71] for OPi and R64K tags, respectively. The migration success of salmons released in R2 was similar to trouts, 0.43 [0.30–0.63] and 0.53[0.39–0.71] for OPi and R64K transmitters, respectively.

Discussion

This study provides a robust confirmation of the interoperability of the new Open Protocols (OP) for acoustic telemetry (AT). We showed that all the OP-enabled receivers (Thelma Biotel, Lotek, and Sonotronics) were able to detect OP transmitters, including both OPi and OPs signals. As expected, proprietary coding protocols were only detected by receivers of the same manufacturer (Table 2). On the contrary, we found that the R64K protocol is a versatile option, as it is compatible with receivers operating with either OP or Innovasea's MAP-114 code maps. Therefore, R64K could serve as a suitable transition protocol for research groups moving towards interoperability as long as receivers are programmed to support this protocol (i.e., Innovasea's MAP-114 or the more recent Generation 2 code map). Several Innovasea code maps suppress this compatibility, such as MAP-115, which cannot detect tags programmed with OP, R64K, and other shared protocols. The most recent Innovasea's code map, Generation 2, which incorporates MAP-114 and MAP-115, supports the OP, but a fee is charged to activate this compatibility. We strongly support the integration of OP into Innovasea's code maps, but the current application of an activation fee is contrary to the usual free-of-charge software updates in every manufacturer's equipment and discourages OP compatibility. Therefore, it is crucial that users are aware of the code map programmed in their receivers and informed about the implications of any future updates.

We have demonstrated that the acoustic range performance of OP is comparable to previously existing protocols, providing evidence that transitioning to OP does not affect the performance of tracking experiments. We conducted standardised range tests in different habitats and tested different protocols (OPi and R64K) in live fish without finding substantial differences between devices or protocols. The only exceptions were Sonotronic devices, which consistently presented lower maximum detection probabilities (P_0) than other manufacturers in the open sea test. These low efficiencies at short distances, which did not affect the overall detection range (x_r), might indicate that the receivers of this brand were more susceptible to environmental noise or to close proximity detection interferences (CPDI). The CPDI phenomenon has been described as a reduction of the detection probability at short distances due to strong signal echoes caused by nearby reflective surfaces, such as the surface of calm water and hard substrates [28]. We also found lower P_0 values in the coastal habitat tests, but since they were consistent across all combinations of manufacturers, we attribute them to the shorter emission period of the employed transmitters (between 30 and 150 s, compared to 300–420 s used in the other tests, Table S1), which in turn increased the collision rate between the acoustic signals. It is important to note that this study was conducted with the devices available in 2021, and that manufacturers might have released updated versions of their devices with improved hydrophone sensitivity or new signal processing algorithms, which might outperform those tested here. Therefore, conducting prior range and performance tests is highly recommended to characterise and fully understand the acoustic performance of new devices in each study.

By testing the devices in different environments, we observed a notable effect of habitat type on the acoustic range, emphasising the relevance of habitat-specific challenges when designing and implementing AT arrays. Several previous studies have already identified the physical characteristics of a study area, such as depth, substrate type, and environmental noise, as factors influencing the probability of signal detection [20, 31]. Tag power output is also known to affect acoustic range [20, 32]. In this study, all the transmitters operated within a similar power output range (144–158 dB), and no notable differences were observed in detection performance across transmitter models. The acoustic ranges we estimated in the open sea and coastal habitat (average $x_r = 225$ and 304 m, respectively) were consistent with the general detection ranges usually reported in marine environments (e.g., [25]). Low detection ranges were observed in the coastal lagoon (average $x_r = 110$ m), together with lower P_0 values, indicating the influence of environmental factors that substantially reduce acoustic performance. Recent studies conducted in similar estuarine environments also reported low detection ranges (~ 100 m) [33, 34] and attributed them to environmental noise and shallow depths, which increase the signal reflections at the surface and bottom. The variability observed in this study underscores the importance of considering habitat-specific factors as the main effect when designing AT experiments.

Although they are a small proportion of the telemetry data set, false detections might be a notable concern, as they can lead to inaccurate conclusions on fish residency and movement behaviour [23]. Our tests demonstrated that the OP were more robust against false detections than the R64K protocol and performed similarly to Innovasea's encrypted protocols. However, there were evident differences between OP manufacturers in the occurrence rate of false IDs, with the tested Lotek receivers being more prone to produce them. This indicates that there are differences between manufacturers in the sensitivity of receivers or in the noise filtering algorithms that distinguish valid signal pings from environmental noise. Therefore, more sensitive receivers will be more likely to register false detections due to erroneous decoding of the ping sequence.

Most false detections were easy to filter out due to their low occurrence (i.e., less than 10 detections of each ID in non-consecutive days). However, some R64K false IDs were identified to be more likely generated than others. These 'weak' IDs typically had simple binary translations, which we assume are easier to arise from interference with environmental noise. For example, the most repeated false ID corresponded to 'R64K-4097', internally coded as '4096' and translated to 10^{12} in binary. The OP partially solves this problem due to its more robust coding system, as proved by the lower abundance of OP false IDs. However, 'weak' codes can become a major concern if they coincide with the IDs of transmitters implanted in fish, as their random emergence in active receivers may generate a misconception of their movements. Consequently, it would be helpful to take into account the code 'weakness' (i.e., the probability of the random emergence of a given ID) when validating spurious detections, especially when attributable to fish tagged by other research groups or in distant locations. A few codes generated the majority of false detections, so we suggest that excluding these codes when producing tags may also reduce the number of potential false detections in future studies.

The smolt migration study specifically demonstrated that OP and R64K protocols were equally effective for detecting smolts, yielding identical results when estimating migration success. These results confirm the reliability of OP for applied studies in natural environments, emphasising that adopting OP does not compromise the integrity or outcomes of such research. Consequently, our results provide further support for transitioning to OP, as it enhances interoperability across telemetry networks while preserving scientific quality.

Conclusions

In this study, we carried out an international collaborative effort to reveal the performance and compatibility of the new OP for AT, with the aim of encouraging researchers to implement OP in their telemetry research. Ensuring compatibility between devices is a solution to a major obstacle when implementing large-scale collaborative AT networks. Thus, the OP can mark a new era in the field of aquatic biotelemetry, offering unique collaborative opportunities between researchers, manufacturers, and telemetry networks to track aquatic animals moving through receiver networks and administrative boundaries, and promote the creation of innovative solutions (e.g., new sensors) to enhance the relevance of telemetry studies. Neglecting the compatibility of AT devices, even in short-term studies, will seriously compromise long-term research opportunities. For this reason, we advocate for urgently abandoning the traditional closed protocol approach and strengthening our commitment as researchers to open science. Moving towards interoperability will enhance long-lasting collaborative efforts to improve our understanding of aquatic ecosystems, inform conservation and management strategies, and work towards the long-term preservation of the world's aquatic resources.

Supplementary Information

The online version contains supplementary material available at https://doi.org/10.1186/s40317-024-00396-9.

Supplementary Material 1.

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Author contributions
EA, JR, KA, PV, DA and PA conceived the idea and designed the methodology; EA, SB, JA, PV, DA, KA, KBG and JR collected the data. EA, SB and MP analysed the data. EA led the writing of the manuscript. All authors made critical contributions to the drafts and gave final approval for publication.

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Availability of data and materials
The data generated and the R scripts needed to reproduce the analyses of this study are available in Zenodo (https://doi.org/10.5281/zenodo.14333087) and GitHub (https://github.com/aspillaga/ETN-OP-TEST). Data from range tests is also accessible on the European Tracking Network data platform (www.lifewatch.be/etn) under the "OP-Test" project name (https://marineinfo.org/id/dataset/7857).

Declarations

Ethics approval and consent to participate
All experimental procedures involving the handling and tagging of fish were conducted in strict compliance with ethical guidelines for animal welfare. The protocol was reviewed and approved by the Danish Experimental Animal Inspectorate (permit number 2017-15-0201-01164).

Consent for publication
Not applicable.

Competing interests
The authors declare no competing interests.

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