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RESEARCH ARTICLE

Validating ATLAS: A regional-scale high-throughput tracking system

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Abstract

1. Fine-scale tracking of animal movement is important to understand the proximate mechanisms of animal behaviour. The reverse-GPS system—ATLAS—uses inexpensive (~€25), lightweight (<1 g) and low-power (~0.4 mJ/transmission) tags. Six systems are now operational worldwide and have successfully tracked over 50 species in various landscape types. The growing use of ATLAS to track animal movement motivates further refinement of best-practice application and an assessment of its accuracy.
2. Here, we test the accuracy and precision of the largest ATLAS system, located in the Dutch Wadden Sea, using concurrent GPS measurements as a reference. This large-scale ATLAS system consists of 26 receivers and covers 1,326 km^2 of intertidal region, with almost no physical obstacles for radio signals, providing a useful baseline for other systems. We compared ATLAS and GPS location estimates for a route (mobile test) and 16 fixed locations (stationary test) on the Griend mudflat. Precision was estimated using standard deviation during the stationary tests. We also give examples of tracked red knots *Calidris canutus islandica* to illustrate the use of the system in tracking small shorebirds (~120 g).
3. ATLAS-derived location estimates differed from GPS by a median of 4.2 m (stationary test) and 5.7 m (mobile test). Signals that were collected by more receiver stations were more accurate, although even three-receiver localisations were comparable with GPS localisations (~10 m difference). Receivers that detected 90% of the 1 Hz transmissions from our test tag were within 5 km of their furthest detection but height of both receiver and tag seemed to influence detection distance. The test tag (1 Hz) had a fix rate of >90% at 15 of 16 stationary sites. Tags on birds (1/6 Hz) on the Griend mudflat had a mean fix rate of 51%, yielding an average sampling rate of 0.085 Hz. Fix rates were higher in more central parts of the receiver array.
4. ATLAS provides accurate, regional-scale tracking with which hundreds of relatively small-bodied species can be tracked simultaneously for long periods of time. Future ATLAS users should consider the height of receivers, their

spatial arrangement, density and the movement modes of their study species (e.g. ground-dwelling or flying).

KEYWORDS
accuracy, animal tracking, ATLAS, movement ecology, positioning error, radio tags, reverse-GPS, telemetry

1 | INTRODUCTION

Tracking animal movements is important to understand the mechanisms underlying animal behaviour, with broad applications for studying key ecological and evolutionary processes (Nathan et al., 2008, 2022). Since the advent of tracking technology, insight into the often cryptic movements of animals has helped us to understand behaviours that were previously almost impossible, from the migration patterns of whales (Abrahms et al., 2019) and birds (Gill et al., 2009) to identifying differences between individuals in foraging strategies (Harris et al., 2020) or confirming the cognitive mechanisms that underlie behaviour in free-ranging individuals (Beardsworth, Whiteside, Capstick, et al., 2021; Beardsworth, Whiteside, Laker, et al., 2021; Toledo et al., 2020). In recent decades, the rapid development of global navigation satellite systems, including GPS, has led to an explosion in the number of movement ecology studies (Holyoak et al., 2008; Nathan et al., 2022). However, while GPS has become one of the primary tools of choice for monitoring movement (Cagnacci et al., 2010; Hebblewhite & Haydon, 2010; Kays et al., 2015), trade-offs between sampling frequency, battery size, tag weight, cost and life span can limit its application. Fortunately, alternative systems for tracking animal movement are continuously being developed in an attempt to address these challenges (Williams et al., 2020). These solutions form a diverse toolset for biologging, ranging from autonomous underwater videography (Hawkes et al., 2020), using biomarkers from tail hair to detect movement through landscapes (Kabalika et al., 2020) and inferring movement paths through dead-reckoning (Bidder et al., 2015). However, few technologies can attain the high-throughput movement data that are necessary for identifying decision points of individuals (Collet et al., 2017) or groups (Strandburg-Peshkin et al., 2015), or correlating movements with precise environmental covariates (Eikelboom et al., 2020). One potential alternative for regional-scale studies is ATLAS (Advanced Tracking and Localisation of Animals in real-life Systems; Toledo et al., 2020), a high-throughput system that uses an array of receivers to detect and localise low-cost and lightweight radio-transmitters to track animals within a specific study area.

Radio telemetry has a rich history for use within animal tracking (Amlaner & Macdonald, 1980; Benson, 2010) and traditionally involved using hand-held receivers to search a landscape for signals from animal-mounted, high-frequency radio-transmitters to estimate tag location through triangulation. Unlike GPS, radio tags act as transmitters rather than receivers, alleviating energy-demanding position computations and remote data communications. Miniature radio-transmitters have low-power requirements (thus requiring smaller batteries), increasing their potential for use with smaller species (as tags should not weigh more than 2%–5% of an animal's total mass; Kenward, 2001) while keeping cost minimal. However, conventional radio telemetry is labour-intensive as researchers can only track one individual at once. It is therefore not feasible to follow more than a few individuals for long periods each day, so locations are often estimated sparsely and irregularly. Attempts to automate wildlife tracking based on standard radio tags were made as early as the 1960s (Cochran et al., 1965) and more recently using a bounding array of receivers distributed within a specific region (Kays et al., 2011). Locations can be estimated from the data collected by these receivers and has the potential to be accessed almost instantaneously. However, while previous automated radio-telemetry systems have been unable to match the accuracy of GPS, ATLAS uses the same location estimation technique as GPS, time of arrival (TOA). Rather than approximating the angle of arrival of the signal (where a 1-degree error becomes an error of 17 m from 1 km away), an error in time of arrival of 10 ns remains an error of 10 ns at all distances. One difficulty of TOA systems is the need for highly accurate clocks (1–5 ppm) (MacCurdy et al., 2009), but through implementing the use of beacon tags in known locations to synchronise clocks, ATLAS relies more heavily on the stability of clocks than accuracy (Weller-Weiser et al., 2016). Through these beacons, ATLAS can synchronise clocks, characterise the accuracy of localisations and monitor the performance of the system. ATLAS therefore provides high-throughput monitoring for relatively cheap (~€25 per tag, €4,500 per receiver), lightweight (0.6 g + battery weight) and long-lasting (~8 months for tag with CR2032 battery at 1/6 Hz where each transmission costs ~0.4 mJ) tags. However, ATLAS installation requires time, resources and expertise, and its spatial coverage is limited to a regional scale where the line-of-sight from three or more receiver stations overlap. Considering these pros and cons, six ATLAS systems have recently been established in four different countries (Israel, the UK, the Netherlands and Germany), collecting rich datasets on hundreds of individuals of over 50 different species, and addressing key research questions in movement ecology (Beardsworth, Whiteside, Laker, et al., 2021; Corl et al., 2020; Nathan et al., 2022; Toledo et al., 2020). Yet detailed, strategic testing of the accuracy of ATLAS and the efficacy of receiver arrays has been limited.

Here, we characterise the accuracy and precision of the largest ATLAS system to date. The Wadden Sea ATLAS system (WATLAS, Bijleveld et al., 2021) has 26 receiver stations covering a total area of 1,326 km^2 which are most concentrated on the Griend mudflat, an important stop-over site for many shorebird species (Piersma et al., 1993). With almost no interruptions to the flat landscape of the intertidal zone, this system is particularly useful to investigate the baseline accuracy and precision of ATLAS. We assess tag reception capabilities and the influence of receiver arrangement and concentration. To define the true accuracy of ATLAS would require known locations and routes. However, on the mudflats, landmarks are scarce and roads or paths are non-existent; therefore, a comparison to a true location is challenging. Instead, we compare ATLAS localisations to the current 'gold-standard' of tracking: GPS. However, we emphasise here that GPS itself also has error (although small: <10 m) associated with its location estimates and therefore cannot be viewed as an absolutely true location. We planned a grid of locations to visit covering an area of 34 km^2 around the Griend mudflat and followed a handheld GPS to get to each location. We then compared ATLAS localisations to GPS-derived positions at 16 test sites. While stationary tests give a good overview of the accuracy and precision of a system, animals themselves are tracked in both stationary and mobile states. It is therefore useful to compare GPS and ATLAS while moving across a landscape, where variations in the array of receivers that detect the tag may occur. We therefore also calculated the difference between ATLAS and GPS en-route to each of the test sites, giving us estimates for accuracy in both stationary and moving states. In addition, since movement studies frequently filter and/or smooth movement data to reduce error in location estimates (Lewis et al., 2007), and more importantly, since GPS data are provided only after intense filtering and smoothing (Kaplan & Hegarty, 2005), we assessed the accuracy of the ATLAS system both with and without applying a simple filter-smoothing process. Finally, we provide a case study of the system's capability to track free-roaming red knots *Calidris canutus islandica* which gives the opportunity to show both the strengths and weaknesses of our current system.

2 | METHODS

2.1 | WATLAS: The Wadden Sea ATLAS system

The WATLAS system (Bijleveld et al., 2021) consists of 26 ATLAS receiver stations (Figure 1). Components include a small computer (Intel NUC i7 mini PC running dedicated ATLAS software, *v2020-04-19-stable*), a USRP N200 radio with a WBX40 daughterboard (Ettus Research) and a

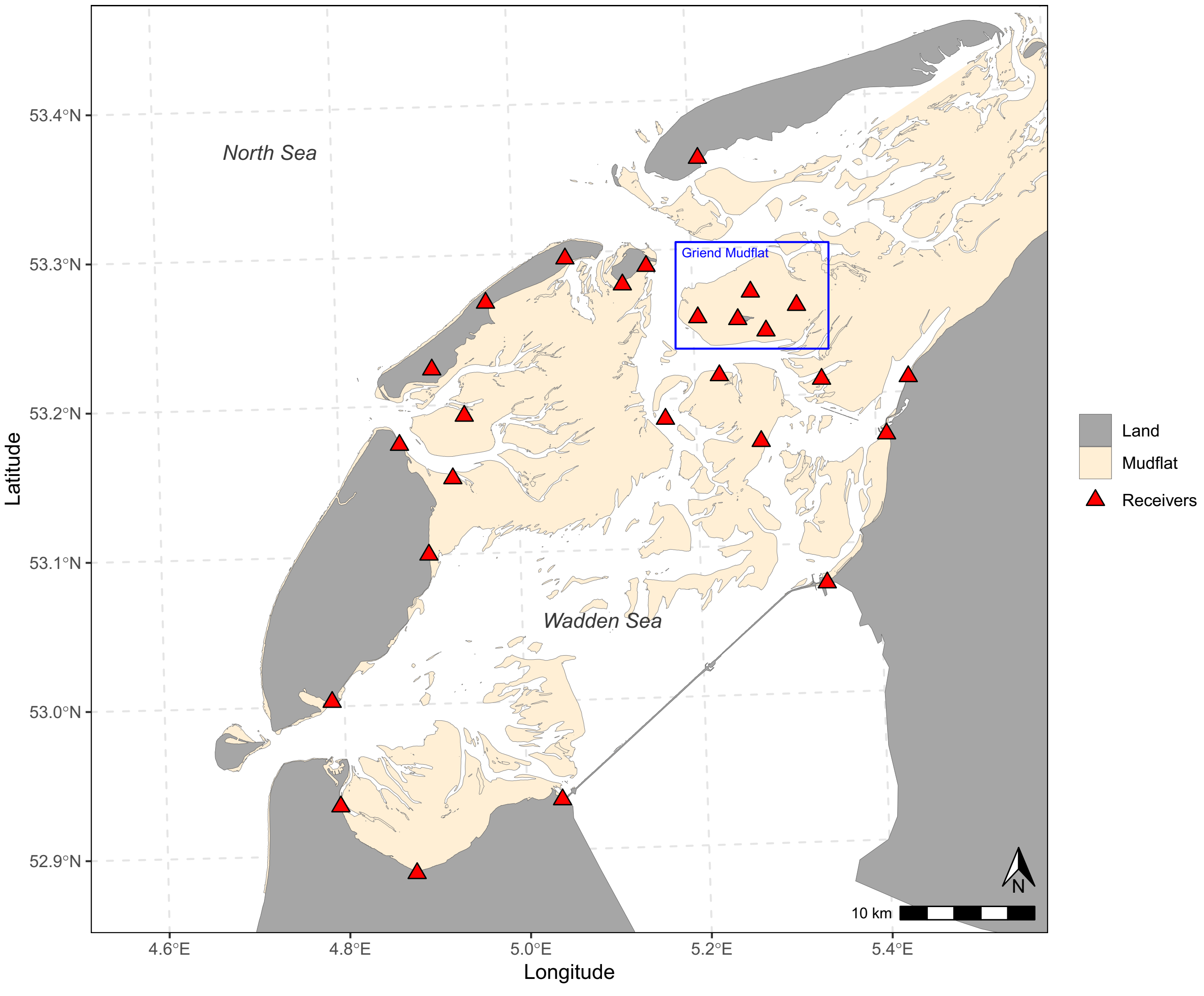

FIGURE 1 Configuration of receiver stations in 2020 around the Western Wadden Sea. The blue rectangle indicates the island of Griend, whose surrounding mudflat provides rich foraging opportunities for many shorebird species and where our receivers are most concentrated. Land is shown in grey and the exposed mudflat at −144 NAP is shown in beige. The locations of receiver stations are shown as red triangles.

GPS disciplined oscillator (GPSDO, Ettus Research), which were housed in custom-made watertight containers. The system time/GPSDO of a receiver station is synchronised using the atomic clocks from a GPS unit (which is connected to the USRP N200 radio) and calibrated using seven beacon tags, placed at known locations throughout the study area. Receiver stations were placed around the western Dutch Wadden sea to gain high coverage for tracking migrant shorebirds while they stopover in the area (Figure 1). In all, 11 receivers were built on temporary scaffolds on the mudflats and were powered with four 100W solar panels (EnjoySolar) and a 100W wind turbine (Ampair) connected to three 100Ah batteries (Beaut). The remaining 15 receivers were installed in places such as on buildings and other stable structures where power was available. Each receiver had a UHF antenna (Diamond X-50N) connected to the radio through a custom-built front-end unit (CircuitHub) and a custom-built Low-Noise Amplifier. Radio-frequency samples from tags are processed by the receiver's computer to estimate the arrival times of the signal. All receiver stations were connected to Internet using a 3G cellular model (USB dongles, Huawei E3372) to send detection reports to a central server situated at the NIOZ (Texel, Netherlands). In real time, the server calculated location estimates and stored these in a MySQL (v5.7, https://www.mysql.com/) database.

2.2 | Data collection

To test the accuracy of the WATLAS deployment and ATLAS tracking in general, we focussed our tests on the area around Griend, where we study shorebird movement and have the highest concentration of receivers (Figure 1). We tested reception and localisation accuracy at 16 sites around the mudflat, 9 of which were 1 km apart with an outer ring of 7 sites that were 2 km between each other and the 1 km sites (Figure 2). Between 21st and 27th August 2020, we travelled to these sites while carrying a handheld Garmin Dakota 10 GPS (<10 m error 95% typical)—set to record tracks on 'auto' which records at a variable rate to create an optimum representation of tracks—and an ATLAS tag. The tag we used for testing emitted a radio signal at 1 Hz. It consisted of a miniature frequency-shift-keying 434 MHz integrated radio transceiver and microcontroller (Texas Instruments CC1310) and a monopole ¼ λ gold-plated, multistranded steel wire antenna (Toledo et al., 2014). The tag was encased in plastic to protect it from mechanical stress. We attached the tag to the top of a 1.2 m wooden pole so that we could keep the height and orientation (vertical) of the tag consistent throughout the testing.

We walked to 13 of the sites during the day at low tide on the 21st, 23rd and 27th August (Figure 2). Between sites, the pole holding the tag was kept upright meaning that the tag was consistently ~1.2 m from the ground. On arrival at each of these sites, we pushed the pole into the sand so that the tag was 1 m above the mudflat and attached the GPS to the pole. We collected ATLAS and GPS data at each site for 5 min. Due to weather and time constraints, we were unable to travel to each site on foot. On the 24th August, we sailed a rubber boat to the some of the furthest sites in the western and northern mudflat (Figure 2) and conducted the stationary test for sites 1, 4 and 12 while at anchor. The pole with the ATLAS tag

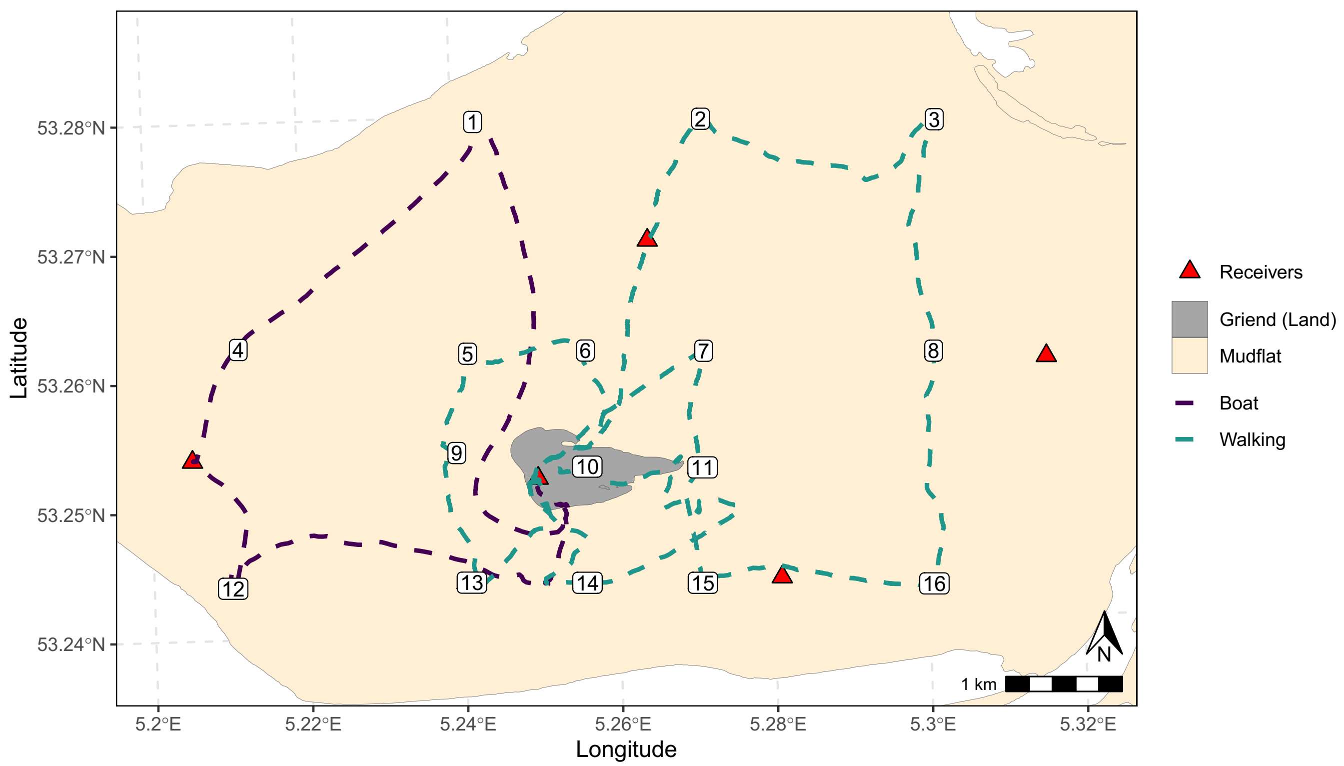

FIGURE 2 Stationary test sites (numbered) on the Griend mudflat and routes between them which are mapped using GPS data. Due to time and weather constraints, we used a boat to test the western side of the mudflat (purple) but the rest was walked (green).

and GPS tag attached was held upright in the middle of the boat; therefore, the tag was ~1.3 m above the water level. Despite being at anchor with a taut rope, there were waves and therefore the boat was not completely stationary during the test; therefore, we expect slight overestimates in the location error and larger standard deviations for these positions.

2.3 | Filter-smoothing

Filtering and/or smoothing location data before use is common to reduce errors in positioning estimates (Bjørneraas et al., 2010; Gupte et al., 2022). As GPS data are regularly smoothed without a practical option to retrieve the raw data (Kaplan & Hegarty, 2005), we used a simple filter-smoothing process on the raw data. ATLAS provides some error estimates automatically, namely variance in the Easting and Northing (VARX and VARY). We removed localisations that had high VARX and VARY (>2000) and then smoothed the data by computing a three-point median smooth across the localisations (Appendix S1).

2.4 | Accuracy analysis and tag reception

We split the analysis into two parts, analysing data at test sites (stationary test) and between test sites (mobile test) separately.

2.4.1 | Stationary test

For the stationary test, we calculated the mean GPS-derived location estimate at each of the 16 test sites and compared it to the ATLAS-derived location estimate; hence, our measure of accuracy (which we henceforth call 'error') refers to the difference in metres between the two estimated locations. For each site, we calculated the mean error (m), standard deviation, the median error (m) and the 95th upper and lower percentiles. We investigated the tag reception at each location by calculating the fix rate (number of localisations/300 [max possible localisations in 5-min period at 1 Hz]) and the mean and standard deviation of the number of receivers that contributed to each location estimate.

2.4.2 | Mobile test

When the tag was mobile, we paired each ATLAS-derived location estimate to the nearest (in time) GPS-derived location estimate. Pairings that were >2 s apart were removed from the analysis. The average walking speed was 1.01 m/s ± 0.33 and boating speed was 2.90 m/s ± 2.33. For pairings 2 s apart, we therefore expect the error to be approximately 2 m for walking and approximately 5.8 m for boating. We calculated the distance (m) between the ATLAS location estimate and GPS location estimate to determine 'error'. As in the stationary test, we calculated the mean error (m), standard deviation, the median error (m) and the 95th upper and lower percentiles to assess accuracy. We aggregated these summary statistics by the number of receivers that contributed to each location estimate to assess the influence of the number receiver stations on accuracy and investigate the overall coverage of our system. To assess tag reception around the mudflat for specific receivers, we plotted each receiver station and the location estimates that they contributed to on separate maps and calculated the furthest detection distance for each receiver station.

2.4.3 | Case study: Monitoring red knot movement

To illustrate the performance of the system for tracking wild animals, we present and discuss examples of red knots tracked around the island of Griend and the wider area of the Dutch Wadden sea. Knots were caught using mist-nets during new moon periods between July and October 2020 on the Griend mudflat. ATLAS tags with a CR2032 battery (total 4.4 g – 3.2% [*SD* = 0.2] of body mass) were attached to the birds' rumps with cyanoacrylate glue and transmitted at a rate of 1/6 Hz. Tags are expected to fall off on feather regrowth. To gain an idea of how effective tags were for a small species (tags were ~10 cm from ground level, Appendix S2), we filter-smoothed the data and then categorised movements into transit or residence (Appendix S3, Gupte et al., 2022). While transitory movements could be at a variety of different heights during flight, we assume that the bird is on the ground within residence patches. We filtered out residence patches of under 2 min to ensure that the movement had not been misclassified, then calculated the fix rates of residence patches that were in our core sampling area (Griend). Ethical approval and permits to catch, handle and tag red knots was granted to the NIOZ under protocol number NIOAVD8020020171505.

3 | RESULTS

3.1 | Stationary test

For the stationary test, we calculated a median error [2.5%–97.5%] of 4.2 m [0.6–110.1] over all sites, which reduced to a median error of 3.1 m [0.5–27.5] after filter-smoothing the data (Figure 3). When analysed individually, we found that the least accurate sites were the three most Northern sites (1–3). These sites were outside of the core array of receivers present on the Griend mudflat and each had a mean of <4 receiver stations detecting the tag (Figure 3, Table 1). In 15 out of 16 sites, the fix rate was >90%. One site (site 2) had a fix rate of 73% and the lowest accuracy (median error = 110.5 m [5.5–1,059.4]) and mean number of receivers detecting the tag there (mean error ± *SD* = 3.4 ± 0.8). This low accuracy was able to be mitigated by applying the filter-smooth, which increased accuracy so that the median error was 28.2 m [7.6–67.5]. It should be noted however that for this particular site the number of location estimates

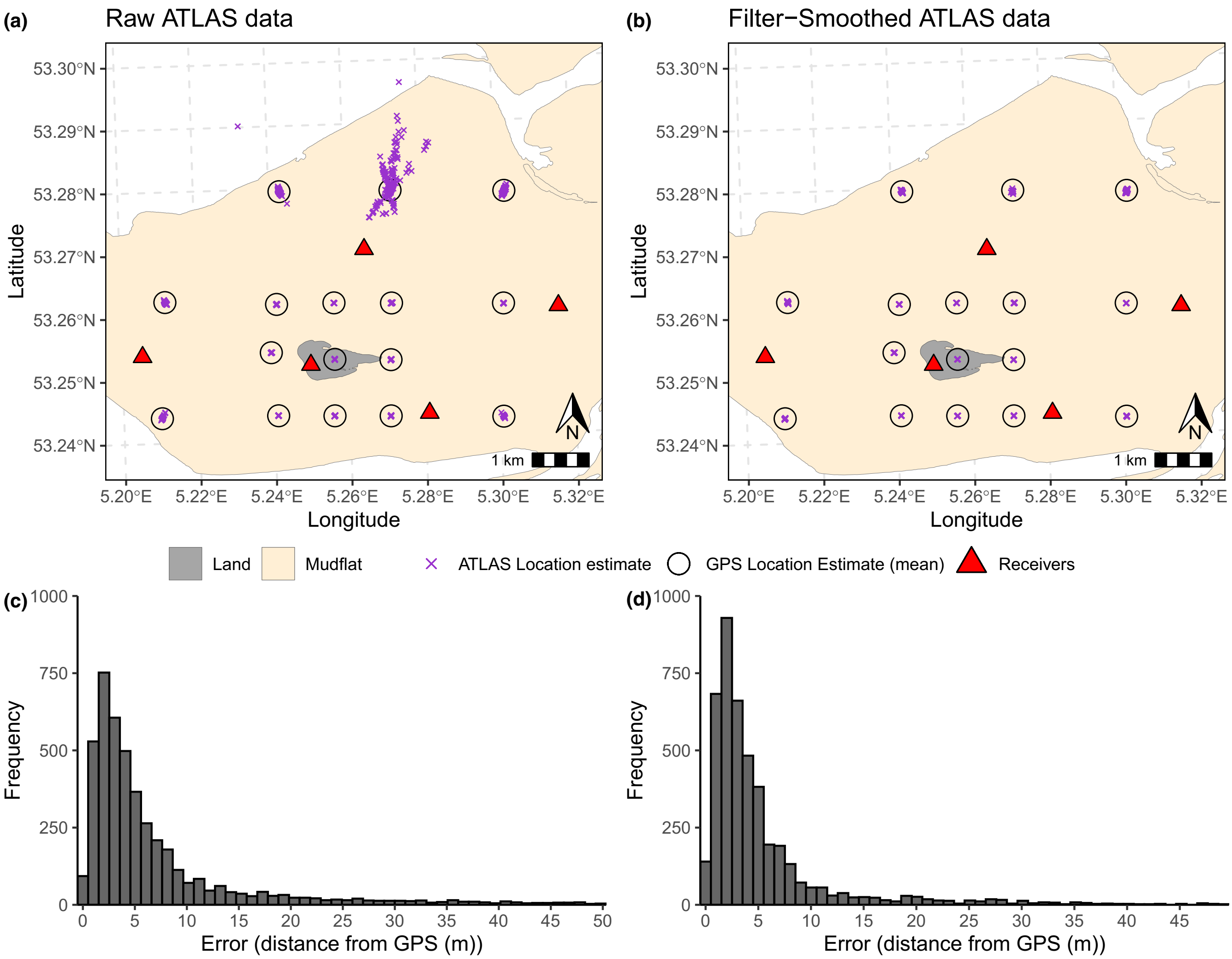

FIGURE 3 Comparison between ATLAS- and GPS-derived localisations for raw (a and c) and filter-smoothed (b and d) data. Purple crosses denote positions calculated by ATLAS over a 5-min period and larger, the centre of black circles indicate the GPS-derived location estimate. The histograms (c and d) show the error in positions at all stationary sites combined, indicating with a peak in accuracy <5 m for both raw and filter-smoothed data

that remained after smoothing was only 9.7% of the expected number of points.

3.2 | Mobile test

ATLAS location estimates had an overall median [2.5%–97.5%] of 5.7 m [0.9–63.3] away from the GPS estimates. In general, localisations where only three receiver stations detected the tag were the least accurate and accuracy increased with receiver number (Table 2). Larger errors were more likely to occur on the edges and outside of the core receiver array (Figure 4a). The filter-smoothing that we implemented decreased overall error to a median of 4.4 m [0.7–27.4] (Table 2, Figure 4b). A total of 10 receiver stations received tag signals during the mobile test and ranged from detecting 0.58% of signals to 97.87% (Figure 5). The furthest distance at which a receiver detected a signal was 14,764 m, but this was the highest of the receivers (44.4 m) and only contributed to 1.17% of localisations. The receivers that detected >90% of signals were within 5 km of their furthest detection.

3.3 | Red knot case study

We show red knot tracks throughout the Wadden sea, with realistic tracks within and outside the core area of Griend (Figure 6a,b). Figure 6b shows the flights from birds across the centre of the Wadden sea and on the edges of the North Sea. Since it is unlikely that these shorebirds would be in the water, we assume that the birds are flying and therefore higher than sea level, although we do not know how high. For these tracks, the closest base stations are ~15 km away. Some of the tracks outside the array also seem realistic flight paths. Between 28th August 2020 and 11th November 2020, grounded red knots on Griend had a mean fix rate (±SD) of 51.29%±32.49 (n = 32,178 residence patches; 151 unique tides; 165 unique birds, Figure 6c,d).

TABLE 1 Accuracy (error = distance (m) to GPS-derived location estimate) and fix rate (% localisations at 1 Hz, max 300) of ATLAS tags (both raw data and filter-smoothed data) that were stationary over 5 min. IDs relate to locations on Figure 2. ID1, ID4 and ID12 (boxed) were taken on an anchored boat; therefore, we may expect higher standard deviations on these results.

	Raw					Filter-Smoothed				
ID	N	Fix Rate (%)	Mean N Receivers (SD)	Mean Error (m) (SD)	Median Error (m) [95%]	N	Fix Rate (%)	Mean N Receivers (SD)	Mean Error (m) (SD)	Median Error (m) [95%]
1	276	92	3.8 (0.8)	23.8 (83.8)	13.9 [1.5-59.5]	265	88.3	3.8 (0.8)	11.7 (8.3)	9.1 [1.2-30.1]
2	219	73	3.4 (0.6)	248.2 (299.6)	110.5 [5.5-1059.4]	29	9.7	3.6 (0.8)	28.8 (15.1)	28.2 [7.6-67.5]
3	299	99.7	3.8 (0.4)	29.5 (19.9)	26.3 [4.1-77.6]	282	94	3.8 (0.4)	21 (12.0)	19.4 [4.3-47.8]
4	298	99.3	3.4 (0.6)	12.5 (9.9)	9.4 [1.6-40.6]	298	99.3	3.4 (0.6)	8.2 (6.1)	7 [1.3-28.5]
5	300	100	4.6 (0.7)	3.2 (2.4)	2.9 [0.3-8.5]	300	100	4.6 (0.7)	2.3 (1.5)	2 [0.3-6.2]
6	300	100	5.3 (0.7)	3.1 (1.7)	2.8 [0.7-7.4]	300	100	5.3 (0.7)	2.7 (1.4)	2.5 [0.8-5.9]
7	299	99.7	3.8 (0.4)	5.3 (3.8)	4.1 [0.7-14.3]	299	99.7	3.8 (0.4)	3.4 (2.4)	2.9 [0.4-8.8]
8	300	100	4 (0.1)	4.7 (2.3)	4.4 [1-9.7]	300	100	4 (0.1)	4.2(1.6)	4.2 [1.6-7.5]
9	300	100	5.7 (0.5)	3.9 (2.5)	3.4 [0.7-9.7]	300	100	5.7 (0.5)	3.2 (1.9)	2.8 [0.7-7.9]
10	295	98.3	3.9 (0.4)	2.4 (1.7)	2.2 [0.5-6]	295	98.3	3.9 (0.4)	2.1 (1.1)	2 [0.5-4.5]
11	279	93	4.8 (1.0)	3 (2.4)	2.3 [0.5-9.6]	279	93	4.8 (0.4)	2.1 (1.4)	1.8 [0.4-5.4]
12	281	93.7	4 (0.9)	8.1 (11.6)	5.4 [0.8-24.3]	274	91.3	4 (1.0)	4.6 (3.6)	3.9 [0.5-16]
13	282	94	5.8 (0.8)	2.2 (1.3)	2 [0.3-4.8]	282	94	5.8 (0.8)	1.7 (0.9)	1.6 [0.2-4]
14	300	100	5.2 (0.4)	4.8 (3.1)	4.4 [0.4-12.5	300	100	5.2 (0.4)	4.3 (2.5)	4.1 [0.6-9.7]
15	300	100	5.8 (0.4)	3.6 (2.6)	3.1 [0.5-9.2]	300	100	5.8 (0.4)	2.7 (1.8)	2.2 [0.2-7.0]
16	299	99.7	5.2 (0.8)	7.3 (6.9)	5.7 [0.9-20.5]	299	99.7	5.2 (0.8)	4.8 (2.8)	4.6 [0.6-11.3]

TABLE 2 Accuracy of tag when moving according to the number of receiver stations (NRS) that detected the tag. Error is calculated by measuring the distance between the ATLAS localisation and the (temporally) closest GPS localisation (if <2 s difference).

	Raw			Filter-smoothed		
NRS	*N*	Mean error (m) (*SD*)	Median error [95%]	*N* (*N* removed by filters)	Mean error (m) (*SD*)	Median error [95%]
3	4,285	24.1 (44.8)	10.7 [1.3–150.1]	3,850 (−435)	11.1 (19.0)	6.3 [1–47.6]
4	8,712	9.9 (15.4)	5.6 [0.9–50.3]	8,464 (−248)	6.5 (7.5)	4.3 [0.7–25.9]
5	4,379	5.9 (6.4)	4.4 [0.7–18.9]	4,378 (−1)	4.9 (4.2)	3.8 [0.6–15.3]
6	1,358	5.3 (3.9)	4.2 [0.7–15.8]	1,358 (0)	4.6 (3.4)	3.6 [0.6–14.2]
7	53	4.4 (3.5)	3.4 [1.1–13.1]	53 (0)	3.4 (3.0)	2.3 [0.8–10.5]

4 | DISCUSSION

ATLAS location estimates were comparable to GPS. The median difference between raw ATLAS-derived location estimates and GPS-derived location estimates was 4.2 m [0.6–110.1] for stationary tags and 5.7 m [0.9–63.3] for moving tags. Accuracy was higher if more receivers detected the tag. However, the tag's location in respect to the receiver array configuration also had a large effect, with less accurate estimates occurring when the tag was on the outskirts or outside the array of receivers. More accurate ATLAS localisations can therefore be achieved through strategic placing of receiver stations. Transmissions from our test tags were received over 5 km away. In contrast, in the case study of tagged red knots, we found that flying birds could be localised with receiver stations more than 15 km away, although tag height is unknown. Finally, we show that errors can be mitigated through a simple filter-smoothing process, as is routinely and intensively applied to raw GPS location estimates (Kaplan & Hegarty, 2005). Thus, ATLAS provides a viable and accurate alternative to GPS for regional-scale systems.

In TOA systems, error scales as a function of array geometry and location estimates are generally less reliable outside the array (MacCurdy et al., 2019). We found the most extreme errors occurred when the test tag was outside the receiver array, matching the results seen in another ATLAS system (Beardsworth, 2020). Specifically, for the sections of the study that occurred in the most northern part of the mudflat, all detecting receiver stations were located to the south of the tag, and therefore the tag was outside the array of receiving stations. While one receiver station was situated to the north of Griend, on Terschelling, 10 km away, this seems to be outside the range of reception for tags at 1 m above ground, despite another receiver to the West, on Vlieland, detecting the tag 14.8 km away. However, we received realistic location estimates of two red knots flying between Griend and Terschelling (Figure 6c: dark blue and light green) suggesting that flight may increase detection probability. During our case study, we also tracked one bird flying through an area with four receivers and then to the Northern side of Texel (Figure 6c: dark blue), outside of the array of receivers. While we cannot confirm if the bird was there or not, the track looks like a realistic flight path. Nonetheless, tracks outside of the tracking area should be interpreted with caution and users should ensure that the receiver array encompasses the entire area of interest. We show actual error (as well as the error estimates from the ATLAS software, Figure S4) is lower within the array. However, as shown in the test, filtering localisations on given error estimates (such as VARX and VARY) and smoothing can remove or mitigate the most erroneous location estimates (see Figures 3 and 4; Figure S4). Graphical assessment of tracks post-filtering can also help to identify the realism of a track and therefore identify potential outliers.

Signal detection requires a clear 'line of sight' between the receiver and the tag, and the range at which receivers can detect transmissions can differ markedly between habitat types and topography (MacCurdy et al., 2009). For instance, detections of radio tags have been previously shown to be blocked by hills, buildings or dense vegetation (Beardsworth, 2020; Kays et al., 2011). However, the WATLAS system has very few topographical obstacles that limit reception of transmissions by receivers, making it an ideal 'baseline' scenario. It is likely that the height of the tag and/or the receiver are the most important factors influencing reception here. In other habitats, reception range is likely to reduce with more obstacles than the mudflats. Because of the effects of reflections from ground and sea, higher receiver stations can typically continue detecting tags at larger distances than receivers that are closer to the earth's surface (Xia et al., 1993). This may also explain why the highest receiver station (44.4 m high on Vlieland) was able to detect the test tag almost 15 km away, but the Terschelling receiver station (35.1 m high) was unable to detect the tag 10 km away.

While receiver height is important, tag height also affects the reception of a signal. This effect was particularly evident in our case study, which showed realistic tracks of red knots flying across areas of the Wadden and North sea that were in some cases at least ~15 km away from the nearest receiver stations. Tags attached to animals in flight have previously been found to have much larger detection ranges than animals on the ground (Xia et al., 1993); for instance, localisations of Egyptian fruit bats *Rousettus aegyptiacus* during flight were based on receiver detections from up to 40 km away in the Hula ATLAS system (Toledo et al., 2020). If flight locations (as opposed to ground locations) are sufficient for a particular study, a sparser array of receivers, as we have in the South of the Wadden sea, can be appropriate to maximise coverage of an area. Ground locations can instead be inferred from take-off and landing

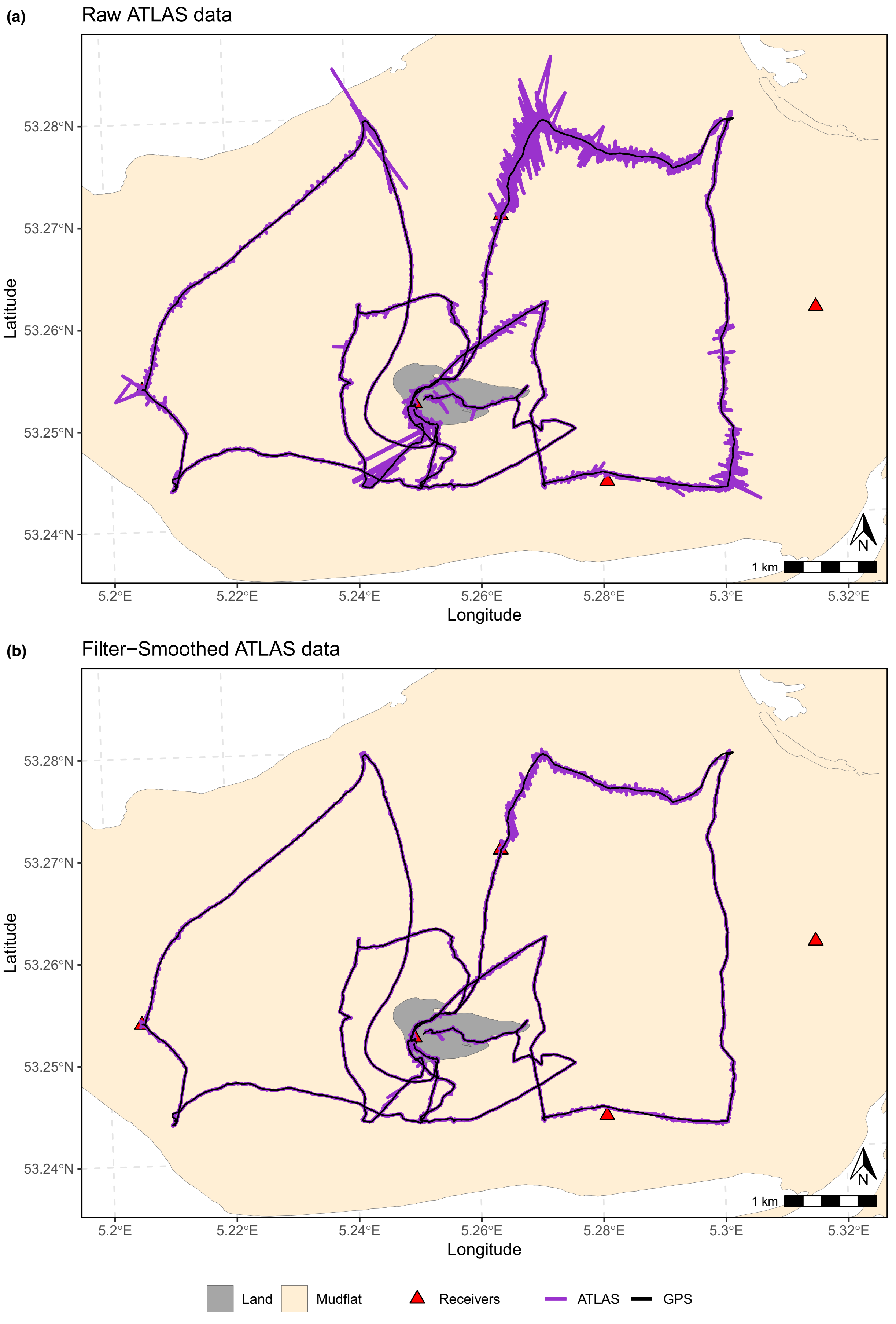

FIGURE 4 Comparison between ATLAS- (purple line) and GPS- (black line) derived localisations for raw (a) and filter-smoothed (b) data from the mobile test.

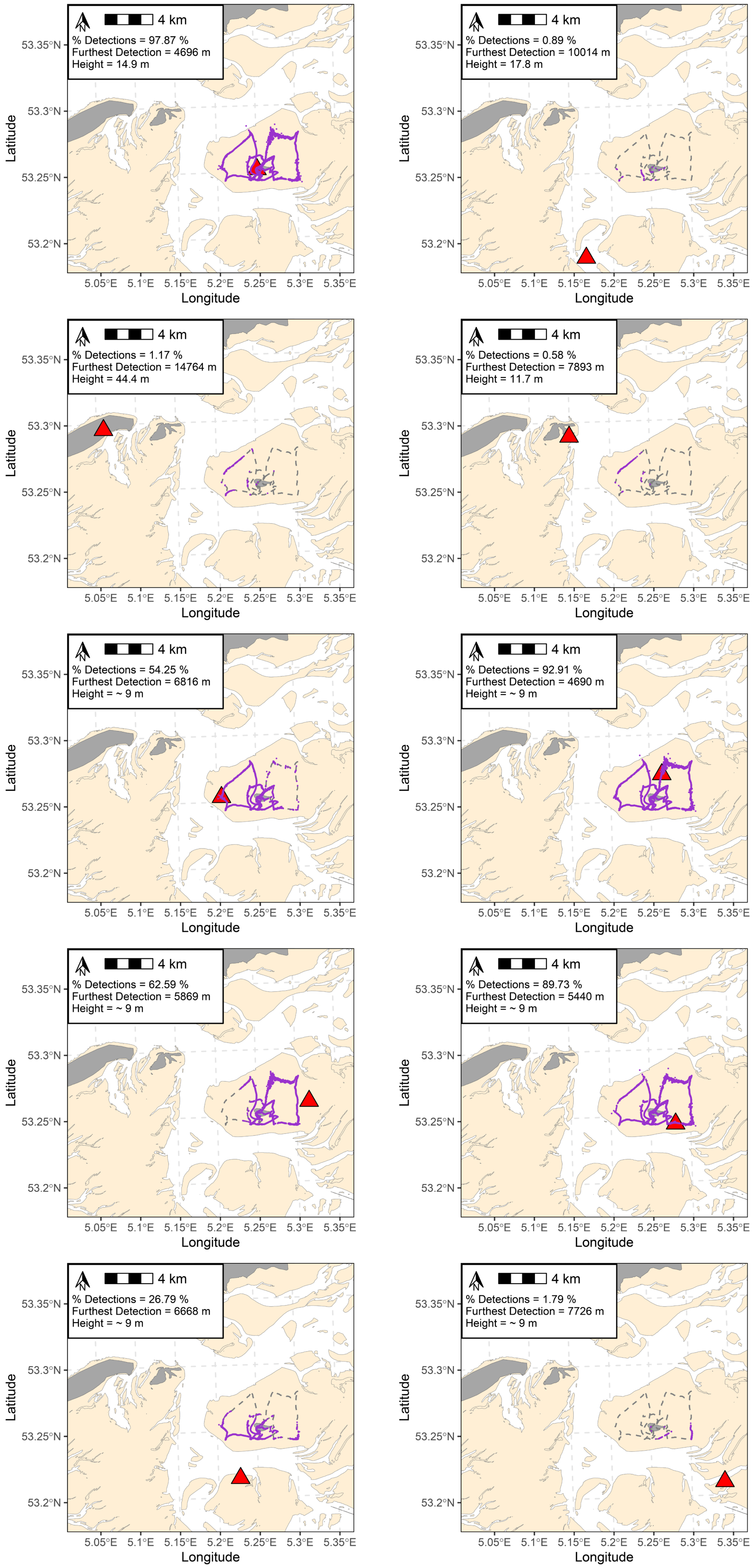

FIGURE 5 Detections for each of the contributing receiver stations and information on the percentage of total localisations that the receiver detected, the furthest detection from the receiver and the height of the receiver. Purple crosses denote location estimates that each receiver (red triangle) contributed to. The grey dashed line shows the path (tracked by GPS) of the researcher during the tests

locations. Similar inferences are made in marine systems, where diving behaviour prevents satellite tracking, thus movement tracks are reconstructed between surfacing events (Hussey et al., 2015). For systems that track ground-dwelling animals, receivers should be positioned <5 km away from the study area as we (with the tag 1.2 m above the ground) found the most successful receivers (>90% of signals detected) were within 5 km from the test locations. Depending on the animal tracked and its habitat type, smaller distances between receivers might be beneficial. However, since each system is unique, each should have tests independently to calculate the expected error within their system.

We found a high fix rate within our stationary test (>90%), but our tagged red knots had a mean fix rate of 51% while on the ground on the Griend mudflat (Figure 6a,c,d). The fix rate of the tagged birds had high spatial bias with very high fix rates central to the array and lower fix rates on the outskirts of the array (Figure 6d). Since we cleaned the data to remove the most erroneous points before classifying the residence patches, the fix rates in these areas may also be subject to bias because high error estimates are more likely to occur at the outskirts of the array. However, for small-scale movements analyses on subjects such as habitat selection, these potentially erroneous locations should be removed to minimise false-positive localisations. For accurate movement assessments of small animals, the entire area should therefore be encircled by receiver stations so that areas of interest do not occur near the edge of the array. Outside our core study area, we expect lower fix rates since we have a sparser array of receivers. However, for large-scale movements, accuracy may be less important and therefore higher thresholds for error removal could be used. It is important to note that despite a lower fix rate on small, grounded birds, the data yielded from the ATLAS system were still collected at a high sampling rate (0.085 Hz) and because of the low-power requirements of ATLAS tags will last for a longer period than many other tracking technologies of a similar weight (see Nathan et al., 2022: Figure 1b). For example, a GPS/satellite tag of similar weight (Lotek PinPoint GPS ARGOS tag, 3.5 g without harness) yields 60 location estimates during the entire tracking duration (if the fix rate is 100%), whereas the tested 4.4 g animal-mounted ATLAS tag yields on average ~7,300 localisations *per day* (with a fix rate of 51%). These high sampling rates can enable the detection of animals almost as soon as they are in range of receivers, even if this is brief. In Figure 6b, we show large-scale movements of birds with varying fix rates and where clear gaps in the data can be seen. However, the birds are localised again once they are back in range of receivers; therefore, some of the patterns of transit could be inferred.

While we did not specifically assess signal strength in this study, this can also have a strong influence on the accuracy of a location estimate. Signal strength can be affected by multiple causes. For instance, the height, orientation and distance between both the receiver's and tag's antennas influence the strength of the signal received. Another factor that affects the signal strength is the transmitter power. While the transmitters in ATLAS tags have a power of 10 mW, the relatively short tag antenna (which is necessary for use with animal-borne tags) reduces efficiency. Ping duration (8 ms) and bandwidth (1 MHz) also influence accuracy (Weller-Weiser et al., 2016). However, these values are typical for ATLAS and are optimised for miniature tags. Finally, interference from other transmitters, such as radio remote controls, can degrade the performance of the system. Due to the remoteness of the Wadden sea, there is little interference in the 434 MHz band. This is evident from the fact that the gain, moderated by automatic gain control (AGC) at each receiver, is often very high, unlike in heavily populated areas. Nevertheless, this level of interference is site dependent and should be considered when establishing an ATLAS system.

The number of receivers detecting a tag also influenced accuracy. Test tag signals detected by ≥4 receivers had a median error of ≤5.6 m while signals detected by three receiver stations had a median of 10.7 m error. This result may tempt users of ATLAS systems to use the number of receivers that contribute to a location estimate to filter movement data, removing three-receiver localisations. Indeed, this has previously been suggested (Weller-Weiser et al., 2016). However, despite 10 (out of a potential 26) receiver stations detecting the test tag at various positions on the mudflat, 22.8% of signals were detected by only three receivers. Implementing such a broad filter may be detrimental to the amount of data retained about the animal's movement. Furthermore, while an error of 10.7 m is acceptable in many cases, our simple filter-smoothing process reduced the error of three-receiver location estimates to 6.3 m. We refer the reader to Gupte et al. (2022) for an in-depth assessment of filtering and smoothing techniques for ATLAS data.

It is important to note again that throughout this study, we based measures of accuracy on GPS location estimates yet GPS itself is susceptible to errors (Hofman et al., 2019). According to its specification, our particular GPS unit gives location estimates of <10 m error; therefore, it is possible that ATLAS could be more or less accurate than we report. For studies with no true location with which to measure accuracy, standard deviation in fixed locations gives an indication of the precision of a system. The standard deviation for 10 of the 16 stationary test sites was <5 m and thus, apparently similar to GPS (Forin-Wiart et al., 2015; Tomkiewicz et al., 2010). After filter-smoothing, 12 of the 16 sites had a standard deviation of <5 m. In these locations, the mean number of receivers detecting the tag signal ranged from 3.8 to 5.8 but all locations were within the core array, indicating that arrangement of receivers may be more important than concentration of receivers. Even the least accurate test location (site 2: which was outside the receiver array and detected by only a mean of 3.4 receiver stations) had a standard deviation of 15.1 m after filter-smoothing. Since most environmental covariates are measured at larger scales than this, ATLAS gives an appropriate level of accuracy and precision for many studies.

In summary, we provide evidence for the high accuracy and precision of a novel localising system: ATLAS. In the design of an ATLAS system, we suggest that receiver stations are placed as high as possible and surround the study site with a direct line of sight. The density of receivers is important but depending on the number of receivers available for a study, trade-offs may have to be made between coverage and density of receivers. Considerations should

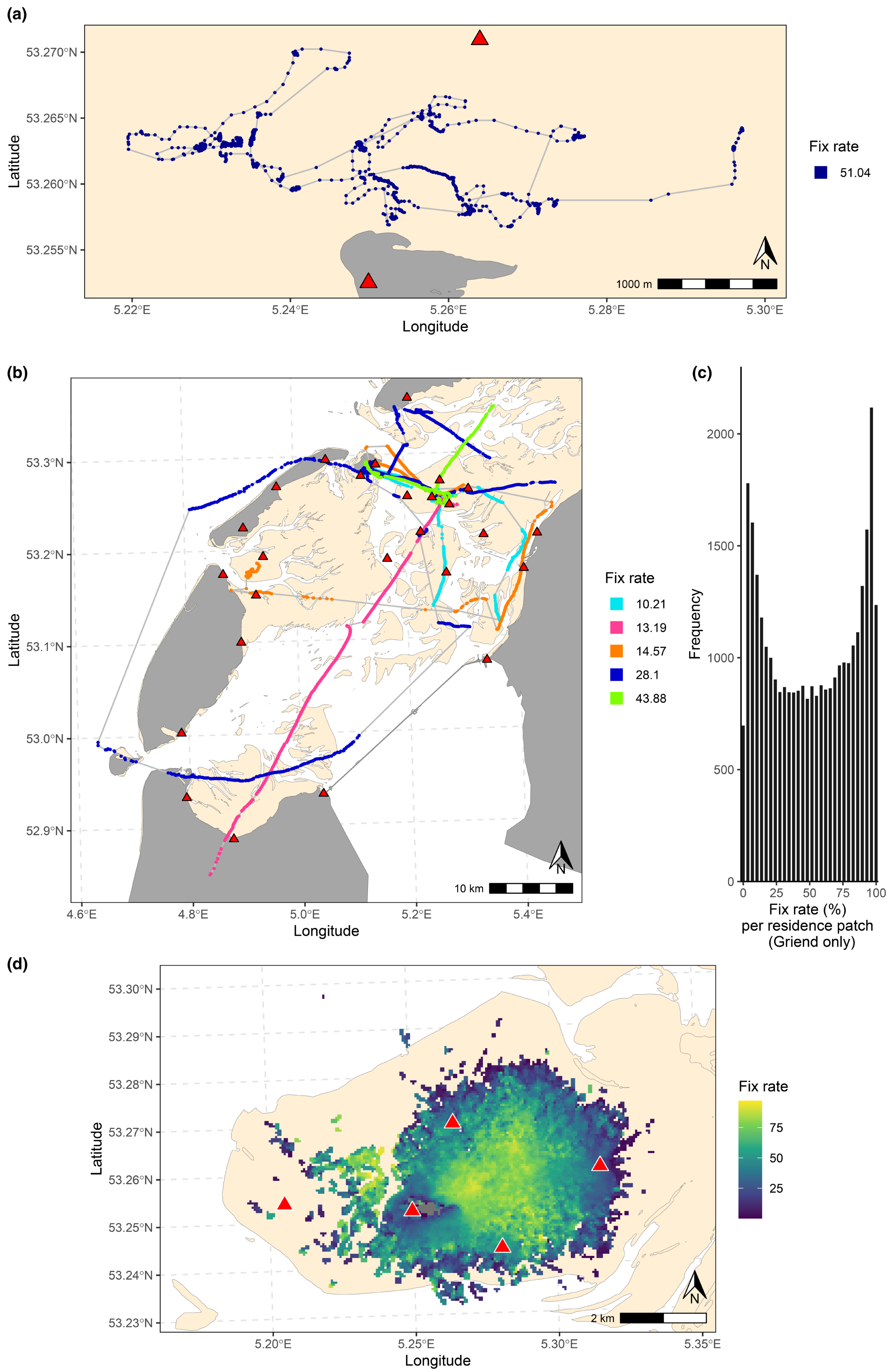
(a)
Latitude
53.270°N
53.265°N
53.260°N
53.255°N
5.22°E
5.24°E
5.26°E
5.28°E
5.30°E
Longitude
Fix rate
51.04
N
1000 m
(b)
Latitude
53.3°N
53.2°N
53.1°N
53.0°N
52.9°N
4.6°E
4.8°E
5.0°E
5.2°E
5.4°E
Longitude
Fix rate
10.21
13.19
14.57
28.1
43.88
N
10 km
(c)
Frequency
2000
1500
1000
500
0
0
25
50
75
100
Fix rate (%)
per residence patch
(Griend only)
(d)
Latitude
53.30°N
53.29°N
53.28°N
53.27°N
53.26°N
53.25°N
53.24°N
53.23°N
5.20°E
5.25°E
5.30°E
5.35°E
Longitude
Fix rate
75
50
25
N
2 km

FIGURE 6 Example tracking data from ATLAS-tagged red knots around the Griend mudflat (a) and the wider Dutch Wadden Sea (b). Each example track is of one bird for a single tidal period but not necessarily the same tide. The fix rate is shown for each individual. Fix rates were also calculated for within residence patches on Griend, when the bird was most likely on the ground. The fix rates within patches are shown in a histogram (c) and spatially where the mean fix rate of residence patches that overlapped 50 m raster cells was calculated (d). Receivers are shown as red triangles, mudflat as beige polygons and land as grey polygons.

also be made according to the height of the tag, with small, ground-dwelling species requiring a denser receiver array than species that may fly between places of interest. However, a sparser array can be used for flying species as demonstrated by our case study, where red knots were localised flying more than 15 km away from the closest receivers. ATLAS provides an opportunity to track animals remotely at high spatial and temporal resolution that rivals GPS technology at regional scales and can be effective even with only three receiver stations. While we focus our study on a flat, intertidal region, ATLAS is not limited to flat landscapes. Several ATLAS systems have been operating successfully in hilly landscapes and complex agricultural systems (all other ATLAS systems), as well as wetlands (Israel) and woodlands (UK). These systems have successfully tracked >50 species of birds, mammals and reptiles, including small (8–15 g) insectivorous bats and passerine birds for which GPS tracking at high temporal resolution is practically infeasible. In the focal ATLAS system, two smaller-bodied bird species, sanderling, *Calidris alba* (~50 g) and red knot (~120 g) have been successfully tracked. Approximately ~200 individuals per year are tagged, enabling the monitoring of complex biotic and abiotic interactions. However, it must be noted that ATLAS is limited to much smaller scales than GPS and therefore is unsuitable for certain studies. Furthermore, unlike military and commercially motivated multipurpose development of GPS, the ATLAS system was developed and is being applied by multidisciplinary teams of scientists for movement ecology research (Toledo et al., 2016). Each ATLAS system has been installed and is maintained by scientists, and often requires collaborations with landowners and organisations for establishing receiver locations. This is in stark contrast to (often) plug-and-go GPS tags. However, the advantages of ATLAS are large and we encourage further use of this high-throughput wildlife tracking system which is suitable for use with a broad range of study systems that require accurate, high-throughput tracking to answer biological questions.

AUTHORS' CONTRIBUTIONS

C.E.B. and A.I.B. conceived the idea for the manuscript; C.E.B., E.G. and A.I.B. collected the data; C.E.B. and E.G. analysed the data; C.E.B. led the writing of the manuscript; R.N. and S.T. developed the ATLAS system and provided support throughout data collection; A.I.B., B.D., A.D. and F.v.M. built and maintained the WATLAS system and tags, and provided local support throughout data collection; all authors contributed critically to the drafts and gave final approval for publication.

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CONFLICT OF INTEREST

The authors declare no conflict of interests.

PEER REVIEW

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DATA AVAILABILITY STATEMENT

Data and relevant code for this research are stored in GitHub: https://github.com/CBeardsworth/watlas_validation and have been archived within the Zenodo repository: https://doi.org/10.5281/zenodo.4527613 (Beardsworth et al., 2022).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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