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RESEARCH ARTICLE

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Inferring individual fate from aquatic acoustic telemetry data

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Abstract

1. Acoustic telemetry has become a popular means of obtaining individual behavioural data from a wide array of species in marine and freshwater systems. Fate information is crucial to understand important aspects of population dynamics such as mortality, predation or dispersal rates.
2. Here we present a method to infer individual fate from acoustic telemetry arrays of receivers with overlapping detection ranges. Our method depends exclusively on information on animal movements and the characteristics and configuration of the telemetry equipment. By answering a limited number of simple questions, our method identifies six different fates: tagging mortality, natural mortality, fishing mortality, predation, dispersal and survival.
3. Applying the method to a cod telemetry dataset, we were able to determine the fate of 97% of the individuals. We validate the results using several external sources of information, such as recaptures from fishers and control fish with known fate.
4. The method is readily applicable to a wide array of species with minimal adjustments, expanding the range of hypotheses that can be tested using telemetry data.

KEYWORDS

acoustic telemetry, dispersal, fate, fish behaviour, fishing mortality, natural mortality, predation, survival

1 | INTRODUCTION

Aquatic telemetry has revolutionized our understanding of the spatial ecology of marine and freshwater animals in the last three decades (Cooke et al., 2004; Hussey et al., 2015). Telemetry data have defined home ranges (Abecasis, Bentes, & Erzini, 2009; March, Palmer, Alós, Grau, & Cardona, 2010), delineated species distribution (Weng et al., 2005), identified breeding sites (Afonso, Fontes, Morato, Holland, & Santos, 2008; Lowerre-Barbieri et al., 2014) and characterized habitat use (Freitas, Olsen, Knutsen, Albretsen, & Moland, 2016; Topping, Lowe, & Caselle, 2005). This information has provided valuable information to estimate complex population parameters required to inform management and conservation actions (Crossin et al., 2017; Lowerre-Barbieri, Catalán, Frugård Opdal, & Jørgensen, 2019). It has also provided information on the fate of the individuals, which is particularly relevant to connect individuals to population-level processes (Heupel & Simpfendorfer, 2002; Hightower, Jackson, & Pollock, 2001; Olsen, Heupel, Simpfendorfer, & Moland, 2012).

Acoustic telemetry uses one or more hydrophone receivers (hereafter, receivers) to detect signals emitted by animal-borne transmitters. The vast majority of the studies that used acoustic telemetry to investigate fate focused on determining survival (Kraus et al., 2018; Topping & Szedlmayer, 2013), with several studies teasing apart natural and fishing mortality (Heupel & Simpfendorfer, 2002; Topping & Szedlmayer, 2013), often in combination with recaptures from fishers (Bacheler, Buckel, Hightower, Paramore, & Pollock, 2009; Faust et al., 2018; Olsen et al., 2012; Young & Isely, 2004). This is not surprising as information on the magnitude of natural mortality is essential for effective management of exploited populations (Hightower et al., 2001) and understanding population dynamics (Gulland, 1988). Accurate estimates of fishing mortality are critical to assess the efficiency of harvest regulations (Forrest, Holt, & Kronlund, 2018). Other studies also looked at emigration or dispersal patterns to understand post-release dispersal (Karam, Kesner, & Marsh, 2008; Taylor, Fairfax, & Suthers, 2013), habitat choice (Moore et al., 2017), spawning migration (Östergren, Nilsson, & Lundqvist, 2012) or gene flow (Martinez-Bakker, Sell, Swanson, Kelly, & Tallmon, 2013). Finally, telemetry data have also been used to infer predation by fish and marine mammals (Berejikian, Moore, & Jeffries, 2016; Khan, Welsh, & Bellwood, 2016) or to directly measure it using specialized predation tags (Halfyard et al., 2017).

The ability to accurately determine fate of the tagged individuals depends, however, on the configuration of the telemetry array. For instance, sparse telemetry arrays may leave 'shadows of detection', i.e. areas inside the telemetry array where individuals are not detected, making it difficult to track the movements out of the study area and therefore hindering the ability to split between dispersal and other fates (Kraus et al., 2018). Incomplete overlap of detection ranges may also prevent detecting if and when mortality happens, hindering our ability to identify survivors and dead fish. Lines of receivers are useful to track fish passage or dispersal events (Brown, Rice, Suski, & Derek Aday, 2015; Heupel, Semmens, & Hobday, 2006) but are less precise in detecting the extent and causes of mortality events. Dense receiver arrays with overlapping detection ranges have become popular to monitor the movements of sedentary individuals during extensive periods of time (Villegas-Ríos, Réale, Freitas, Moland, & Olsen, 2017), investigate habitat use (Freitas et al., 2016), monitor fish communities in small areas (Villegas-Ríos et al., 2013) and evaluate the performance of marine reserves (Da Silva et al., 2013). Such array configuration has the power to provide a continuous detection record on space and time of individuals moving inside the study area that can be used to infer the extent, timing and location of the different fates that can be experienced by aquatic animals in the wild (Heupel et al., 2006).

Previous studies estimated survival and mortality of individuals based on their continuous pattern of detections. For instance, Heupel and Simpfendorfer (2002) estimated the fate of juvenile blacktip sharks as survival, natural mortality or removals, and Olsen et al. (2012) used horizontal and vertical movement patterns, combined with recaptures from fishers to determine fate of Atlantic cod. Here we build on these previous studies to expand the fate categories that can be determined from telemetry data and formalize a method to infer fate of individuals moving inside an array of receivers with overlapping detection ranges. The method identifies a limited number of different horizontal and vertical movement patterns that correspond to six different fates (tagging mortality, harvest mortality, natural mortality, predation, survival and dispersal) after answering eight simple questions. We apply our method to a long-term telemetry dataset of cod *Gadus morhua* from Norway to illustrate the different movement patterns and fates.

2 | MATERIALS AND METHODS

2.1 | Workflow and description of fates

Our method is based on the analysis of the pattern of detections and movements of individuals moving inside a telemetry array of receivers with overlapping detection ranges. In particular, fate is inferred using the following sources of data (Figure 1): (a) a detection file for each individual, (b) movement plots, including a time series of latitude and longitude ('*XY* profile') and a time series of depth records ('depth profile'), (c) information on the duration of the battery life and (d) a map with the locations of the receivers that integrate the telemetry array. This information is used to answer eight simple questions (Figure 2) that aim to resolve whether the fish was present and moving within in the study area during the whole duration of the transmitters' battery and if its behaviour was biologically realistic:

1. Does the fish stop moving right after tagging?
2. Can a predation pattern be identified from any particular date?
3. Are there data until the end of the battery life?
4. Are last detections recorded at receivers located at the edge of the array?
5. Does the depth profile stabilize at some point?
6. Does horizontal movement stabilize simultaneously?
7. Is there a large spatial gap before and after cessation of movement?
8. Is there horizontal movement until the end of the battery life?

Ultimately, the flowchart of questions determines the following six different fates and associated movement patterns (Figure 2):

- Tagging mortality: the fish dies shortly (e.g. a few hours or days, depending on the species) after tagging, and the dead fish with the transmitter lies on the bottom. Both *XY* and depth profiles show a horizontal flat profile with little variation due to cessation of movements, that can be preceded by unnatural behaviour.
- Natural mortality: a fish is considered to have died of natural causes when vertical and horizontal movements stabilize at the same time without any indication of harvesting (N1; see Figure 2). Then detections continue until the battery expires. We also considered natural mortality when horizontal movements stabilize later than vertical movements and detections persist until the end of the battery life (N2). In this case the fish likely died of natural cause after a pressure sensor malfunction.

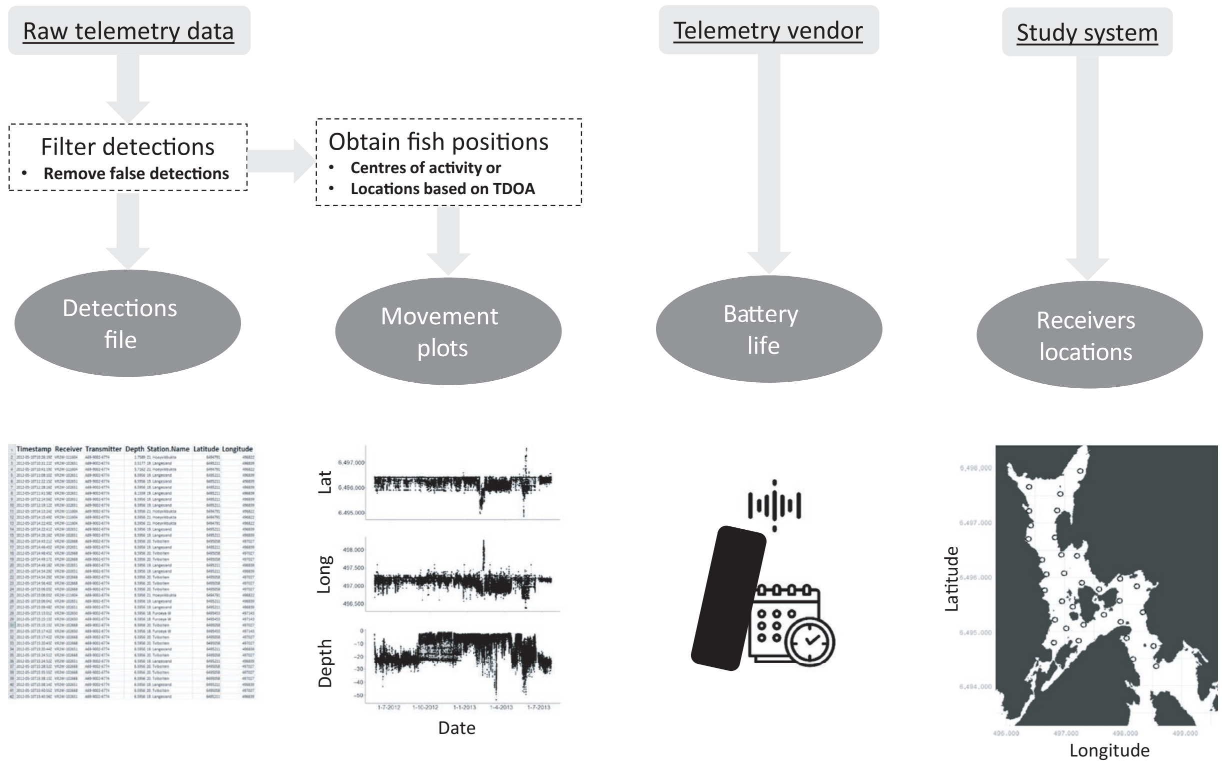

FIGURE 1 Information needed to assign fate to fish tracked with acoustic telemetry inside telemetry arrays of receivers with overlapping detection ranges. TDOA, time difference of arrival

- Predation: this fate, which is a particular case of natural mortality, is assigned when a clear change in the pattern of movements takes place and the new pattern corresponds to the behaviour of an aquatic predator of the focal species.
- Fishing mortality: we assume that two different patterns result from fishing mortality. First, we assume that a fish was harvested when detections stop before the end of the battery life of the transmitter and the last detections come from receivers not at the edge of the telemetry array (F1; Figure 2). Second, we also assume fishing mortality when vertical and horizontal movements cease, after the fish has been transported to another site inside the telemetry array, as indicated by unrealistic movements for the focal species (F2; Figure 2). This pattern is likely due to a typical fisher behaviour which consists of capturing the fish at one spot, and then discarding the guts (and the transmitter) or the specimen at a different spot.
- Dispersal: we assume that a fish has dispersed from the telemetry array when detections stop before the end of the battery life and the last detections come from receivers at the edge of the array. Often a clear directional movement towards the outermost receivers (i.e. the border of the array) can be recognized.
- Survival: this fate is assigned when a fish displays the expected vertical and horizontal movements until the end of the battery life (S1; see Figure 2), or when an anomalous depth profile is obtained (e.g. due to a sensor malfunction) from some point but there are horizontal movements until the end of the battery life (S2). Note that this fate includes fish that may temporarily disperse from the array but return afterwards.

2.2 | Application to a real dataset

We applied our method to a telemetry dataset of 291 cod in southern Norway. The different fates were assigned manually by an analyst. In 2011 an array consisting of 33 Vemco VR2W receivers was deployed in the inner part of Tvedestrand fjord (Figure 3). The array was later expanded in 2013 and 2018 to include a total of 56 receivers, but for consistency among years we only considered the original 33-receiver array in this study. Cod were tagged inside the study area between 2011 and 2017 using VEMCO transmitters V9P (power output = 146 dB) and V13P (power output = 149 dB) which are equipped with pressure sensors. The tagging procedure used in this study is described in Villegas-Ríos, Réale, et al. (2017). All fish were externally tagged with T-bar plastic tags to allow fishers to return tagged fish. Range testing conducted in May 2011 through the study area using V9P transmitters (power output = 146 dB) suggested that detection range of the transmitters was ~500 m and the spacing of receivers provided a very good coverage of the study area (Figure S1). The detection range of the V13P transmitters was assumed to be at least ~500 m too, as they emit with higher power output than V9P transmitters. Information from reference tags deployed in the study area showed no differences in the number of detections during the day and night (Figure S2). For each fish, centres of activity (COA) were calculated

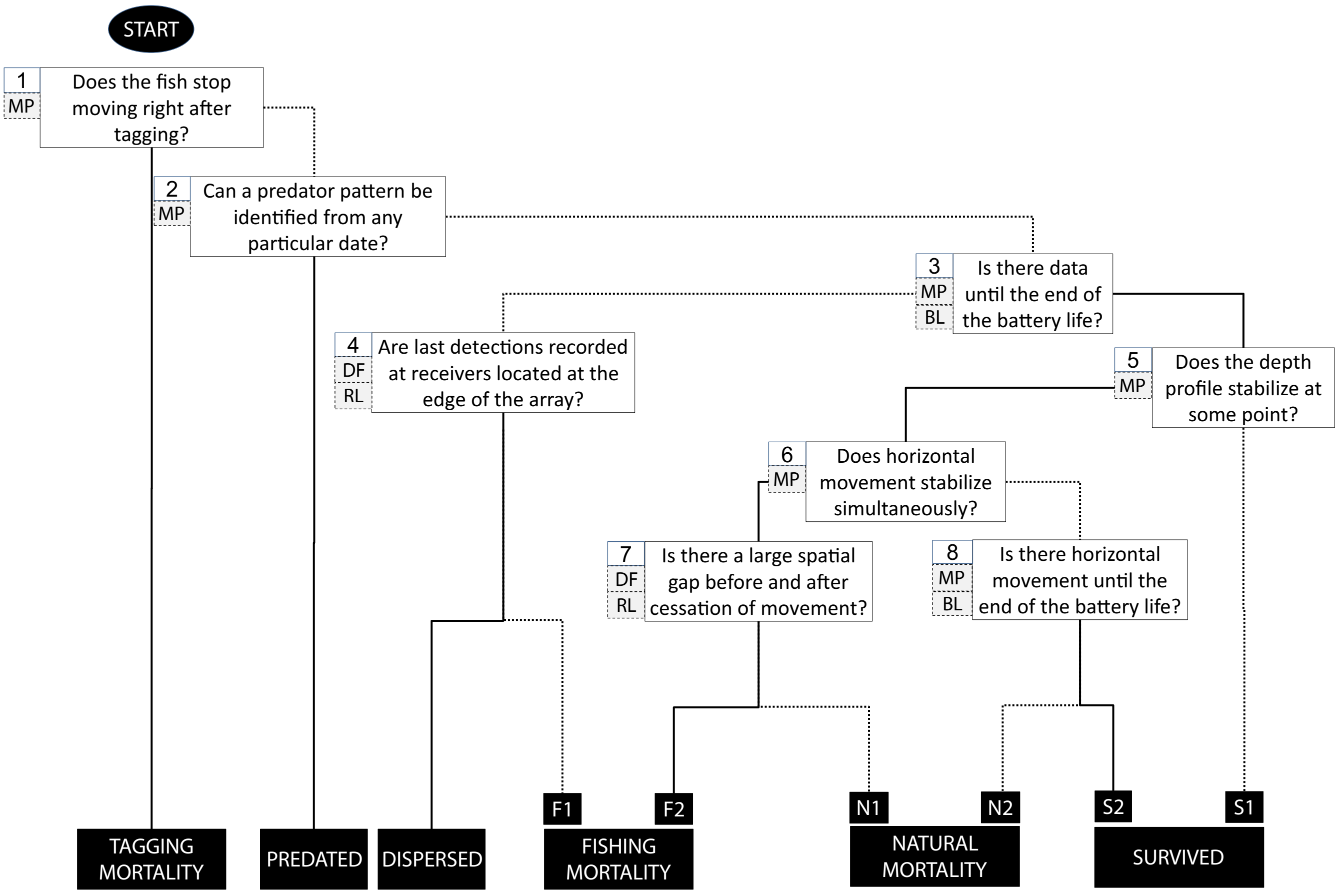

FIGURE 2 Flowchart showing the eight questions needed to determine fish fate in a telemetry array of receivers with overlapping detection ranges. Solid lines indicate a positive answer whereas the dashed line indicates a negative answer. Initials inside grey squares indicate the information needed to answer each question (BL, battery life; DF, detections file; MP, movement plots; RL, receiver locations) as described in Figure 1

every 30 min (Simpfendorfer, Heupel, & Hueter, 2002) from the tagging date until the end of the battery life or until cessation of transmissions. Then, *XY* profiles were constructed by plotting the latitude and longitude of the COAs over time. Depth values were extracted directly from the receivers and filtered to avoid redundant data when a single transmission was picked-up by more than one receiver (Freitas, Olsen, Moland, Ciannelli, & Knutsen, 2015). We considered that the battery had expired when detections stopped on the expected date (based on the tagging date and the duration of the battery supplied by the telemetry equipment manufacturer) ±2 days.

2.3 | Validation of fates

We used different strategies to validate whether the fates that we assigned with our method corresponded to the real fate of the individuals in our cod telemetry dataset. Patterns of natural and tagging mortality were compared to patterns of a cod that was tagged after being found dead inside a fyke net during the annual fish survey in the study area, as well as to detections from a reference tag deployed at a fixed position. Seal predation patterns were not directly validated in our study system but were compared to the typical harbour seal behaviour from other studies in the Norwegian and Danish coast (Bjørge et al., 1995; Chudzinska, 2009). These studies report that individuals display repeated visits to the same foraging sites that can be several km away from the haul-out sites, swimming speeds of 1.1–1.6 m/s and average dive duration of 3.3 min reaching depths of up to 200 m to forage near the seabed. Such movement behaviour contrasts with typical cod spatial behaviour in the study area characterized by limited horizontal displacements (median home range 0.08 km^2) and diel vertical migrations, typically occupying deeper waters during the day (Freitas et al., 2016; Villegas-Ríos, Réale, et al., 2017). Fishing mortality was validated from the movement patterns of 29 fish returned by fishers and comparing the fate assigned by our method to the real fate (i.e. fishing mortality). Dispersal patterns were validated by looking at patterns of fish that temporarily abandoned the fjord (n = 5), and patterns of fish that dispersed and where later fished outside the study area (n = 3). Movement patterns of potential survivors were validated by comparing them to the pattern observed in real survivors, i.e. fish that were recaptured by us during the annual fish

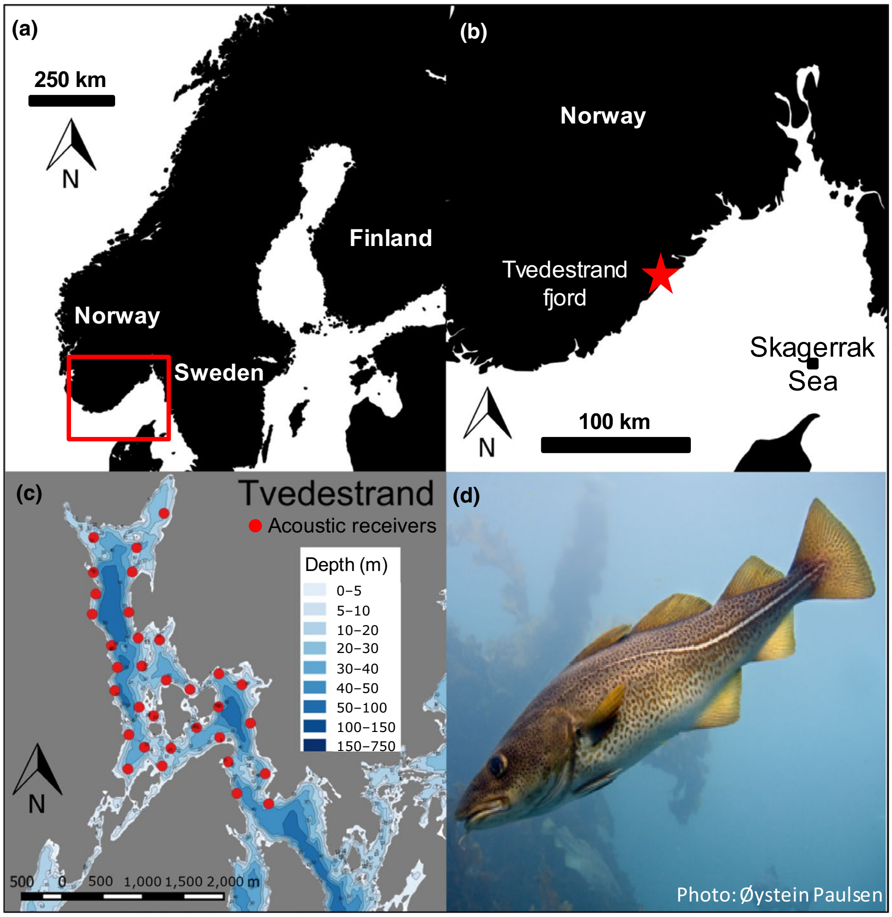

FIGURE 3 Map of the study area (a and b) showing the location of the 33 Vemco VR2W receivers in Tvedestrand fjord (c), and the study species, the Atlantic cod *Gadus morhua* (d)

survey mentioned above, confirming that the tag was still inside the original fish ($n = 39$).

3 | RESULTS

A total of 22 hr (~4.5 min per individual) were needed to assign fate to 291 cod in our study. Fate was assigned to 97% ($n = 282$) of the individuals, but could not be assigned to 3% ($n = 9$) of the individuals due to either transmitter malfunction or too few or sparse detection data (e.g. fish moving at the edge of the array and being detected intermittently). Overall, we identified all possible fates and eight out of the nine possible patterns described above (pattern N2 in Figure 2 was not detected).

Three individuals were classified as tagging mortality based on horizontal *XY* and depth profiles with little variation after 1–3 days from tagging (Figure 4a). Natural mortality was assigned to a total of 49 individuals based on a simultaneous cessation of horizontal and vertical movements (Figure 4b), with no records of cases in which the depth sensor failed and the horizontal movements stabilized afterwards (N2 in Figure 2). The flat part of the *XY* and depth profiles in both cases (tagging and natural mortality) was comparable to the profiles resulting from the tagged dead fish (Figure 4c) and a reference tag placed at a fixed location (Figure 4d).

Nineteen individuals were classified as predated. In all cases, the predation event was characterized by a clear change in the horizontal and vertical movement patterns. Before the predation event, movement behaviour was characterized by short displacements in the fjord and limited short-term movement in the water column (Figure 5a,b). The detection pattern after the predation event, that we call the ‘seal pattern’, was characterized by intermittent presence within the study area alternated with long periods of absence of 1–3 days (Figure 5a,b). During those visits, large and rapid displacements over the whole study area were observed (typically several kilometres per hour) and water column use alternated short visits to deep areas (probably to hunt close to the seabed) with other periods on shallow and surface waters (probably to breath). This observation coincides with the typical seal behaviour as reported from published studies (Bjørge et al., 1995; Chudzinska, 2009).

A total of 114 individuals were assigned a fishing mortality fate. The vast majority, 111 individuals, showed cessation of movement inside the telemetry array (Figure 6a), while only in one occasion we identified a pattern that could be explained by a fisher having discarded the guts or the fish far away from the capture location (Figure 6b). A total of 29 tagged cod from our dataset were reported as recaptured by fishers. Our method assigned fishing mortality to 24 of them (Table 1), and the remaining five cod were captured after the battery expired and our method assigned a dispersal ($n = 3$) or survival fate ($n = 2$).

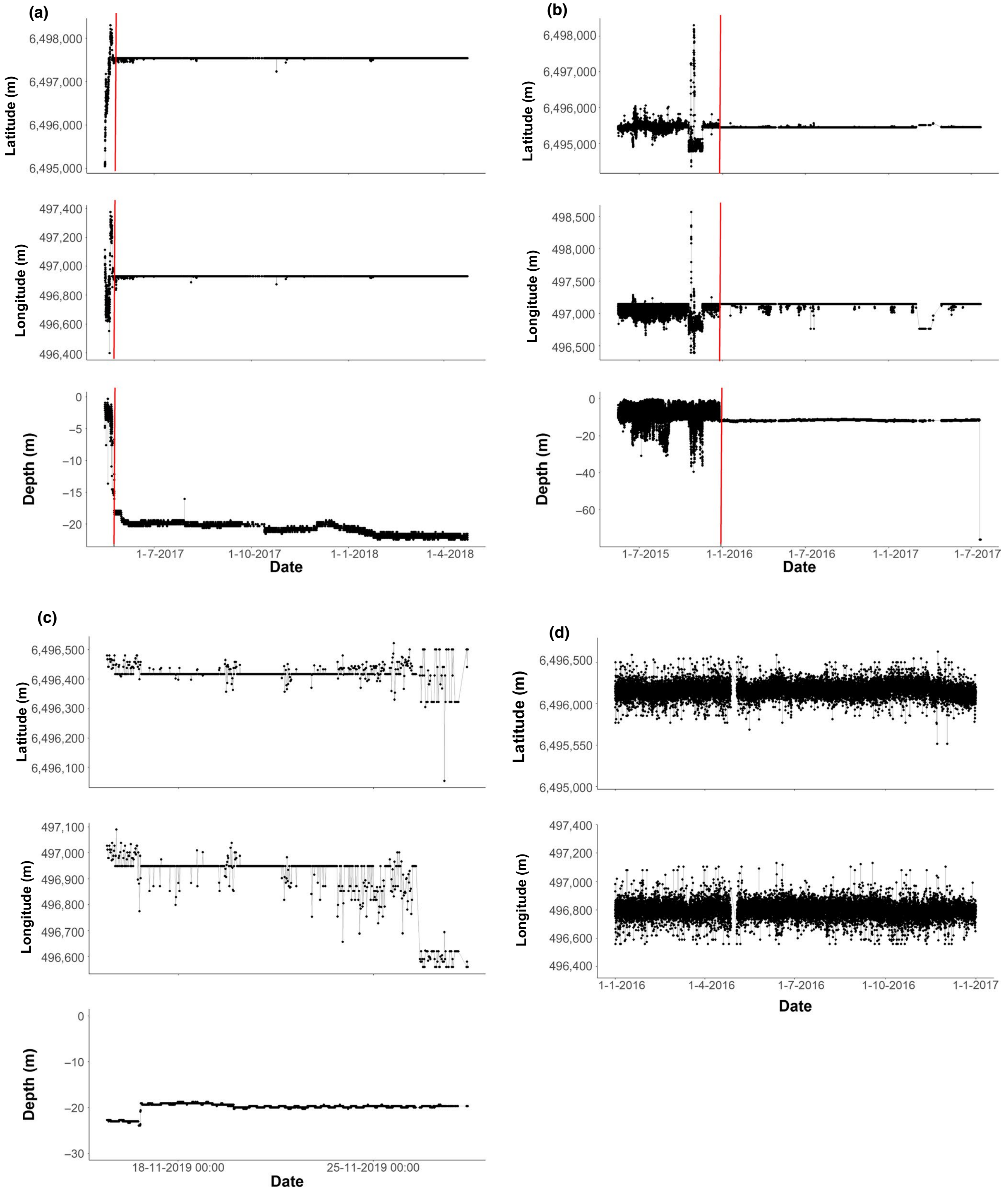

FIGURE 4 Tagging and natural mortality. Both tagging (a) and natural (b) mortality of tagged fish are characterized by simultaneous cessation of movements followed by stable *XY* and depth profiles, which coincides with the profiles resulting from a tagged dead fish (c). Note that as a result of the technology and calculation methods used, *XY* profiles coming from a transmitter placed at a fixed position (d) tyically show a small amount of apparent movement, which is also recognized in the dead fish patterns. The scale of the *Y*-axis differs among plots. The vertical red lines in panels (a) and (b) indicate the date of the putative mortality event

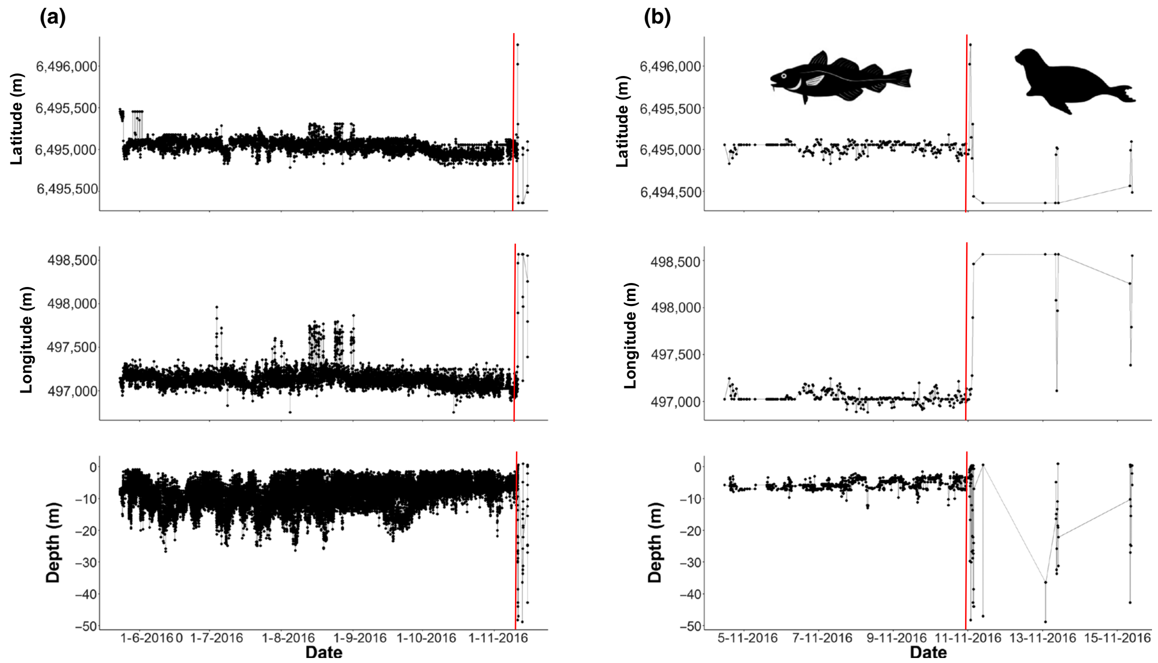

FIGURE 5 Predation. Horizontal and vertical movement patterns of a cod likely eaten by a seal (a), showing a detailed view of the movement patterns some days before and after the predation event (b). Note the dramatic change in the movement patterns after predation characterized by large displacements and regular visits to the surface, alternated with periods of absence from the telemetry array. The vertical red lines indicate the date of the putative predation event

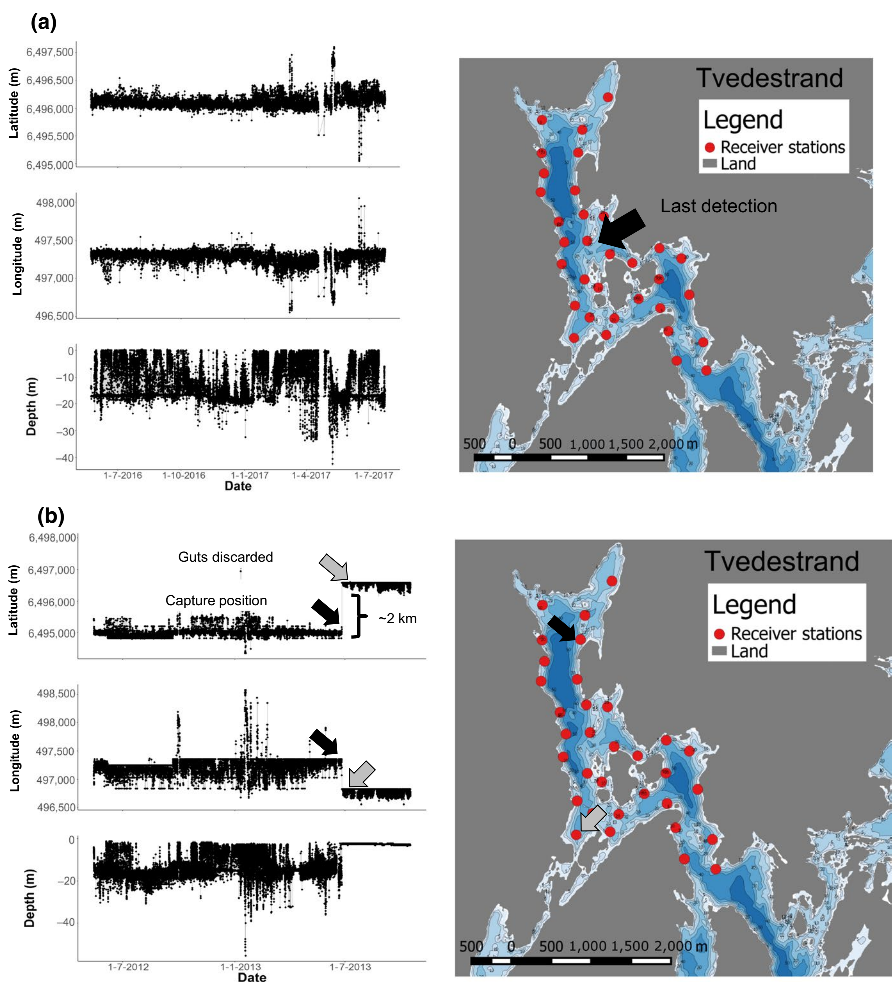

FIGURE 6 Fishing mortality. When a fish is captured inside the telemetry array it shows a normal horizontal and vertical movement pattern until it disappears, and the last detections come from receivers not at the edge of the telemetry array (a). Sometimes fishers discard the guts or the whole specimen far away from the original capture position (b)

TABLE 1 Validation of the fishing mortality patterns. Tagged cod ID's returned by fishers with reported date of capture and inferred fate and date of fate using the method described in this study. F, fishing mortality; S, survival; D, dispersal. Reported dates by fishers are not always accurate

Cod ID	Reported date of capture	Inferred fate	Estimated date of fate
A9854	30.6.2011	F	30.6.2011
A9858	5.8.2011	F	28.7.2011
A9950	17.8.2011	F	17.8.2011
A9903	30.8.2011	F	5.8.2011
A9930	26.9.2011	F	26.9.2011
A9856	15.10.2011	F	1.10.2011
A9948	22.1.2012	F	24.1.2012
A9927	28.2.2012	D	29.5.2011
A9943	4.3.2012	F	4.3.2012
A9937	7.4.2012	D	8.9.2011
A9924	20.4.2012	S	12.10.2012
E0026	26.5.2012	F	3.8.2012
E0034	27.5.2012	F	27.5.2012
E0113	6.6.2012	F	6.6.2012
E0025	4.7.2012	F	4.7.2012
E0024	4.7.2012	F	4.7.2012
E0015	4.7.2012	F	4.7.2012
E0109	14.8.2012	F	9.8.2012
E0016	15.8.2012	F	28.5.2012
A9926	31.3.2013	F	30.3.2013
E0101	1.5.2013	F	1.5.2013
E0014	15.6.2014	S	10.10.2013
A9942	9.9.2014	F	23.8.2011
E0493	4.4.2015	D	3.3.2015
E0481	7.4.2015	F	7.4.2015
XH0414	13.7.2015	F	13.7.2015
XH0485	1.9.2015	F	23.8.2015
XH0222	27.2.2016	F	27.2.2016
E0618	24.6.2017	F	24.6.2017

Twenty-six individuals were classified as dispersed from the telemetry array (Figure 7a), all of them detected last by the southernmost receiver that connects the study area with the outer part of the fjord. Two different sources of evidence provided certainty to the assignment of this fate. First, we found three temporary dispersal events from our telemetry array that resulted in a typical dispersal pattern. Those temporary dispersers returned to the study area later confirming that our assumed dispersal pattern indeed corresponds to dispersal and not anything else (Figure 7b). Second, three of the dispersed fish were later recaptured by fishers outside the telemetry array confirming that those fish were alive for some time after leaving the fjord (Figure 7c).

Seventy-one individuals were classified as survivors. Most of them ($n = 68$) displayed typical cod movements until the end of the battery life (Figure 8a), but in three cases the depth sensor failed so survivorship was assigned based on the horizontal movements alone (Figure 8b). Patterns of inferred survivors were similar to those of real survivors as obtained from our own recaptures (Figure 8c,d).

4 | DISCUSSION

This study describes a simple method to infer fate of aquatic animals tagged with transmitters equipped with pressure sensors and moving within a telemetry array of receivers with overlapping detection ranges. Validation data suggest that the patterns used to determine each fate are highly indicative of the real fate. Applying the method to a dataset on Atlantic cod, we were able to assign fate to 97% of the individuals suggesting that our method accommodates the large majority of the variability in detection and movement patterns in a wild population. We argue that our method can be readily applied to a wide array of situations and species providing valuable information to expand the width of hypotheses that can be tested with telemetry data. Our method is based on the manual assignment of fate. Manual assignment is advantageous in that it can easily accommodate the particularities and knowledge of the study system by the analyst. The potential subjectivity resulting from manual analysis could be buffered by the application of the method by more than one analyst.

Our method expands and formalizes previous attempts to infer fate of aquatic animals moving in telemetry arrays composed of overlapping receivers. Heupel and Simpfendorfer (2002) used data from acoustic transmitters to infer survival, natural mortality and ‘removals’ (which included fishing mortality). However, their approach neither attempted to split the different sources of natural mortality (e.g. predation), nor explicitly considered dispersal and tagging mortality as potential fates. Olsen et al. (2012) and Olsen and Moland (2011) used information on horizontal and vertical movements to develop a similar approach to ours and inferred fate of tagged cod in southern Norway. However, in those studies fishing mortality was inferred in a conservative way using only tags recovered and reported from fishers, and predation was not explicitly considered. Building on those previous studies, our method explicitly considers six different fates and it is independent from external sources of data such recoveries from fishers. This is a major advantage as the percent of recaptured fish is usually low (Fairchild, Siceloff, Howell, Hoffman, & Armstrong, 2013) and even when a fish is recaptured, fishers are sometimes reluctant to report it to scientists (Winter, Jansen, & Bruijs, 2006). This is particularly important in cases when the fishers capture fish below the legal size or at protected places such as marine reserves or individuals of protected species (Abecasis et al., 2009). In this regard our method is particularly important to detect poaching which would otherwise remain unrevealed.

The input data for our method includes information on the telemetry array and the characteristics of the transmitters. We have illustrated our method using one of the most popular telemetry

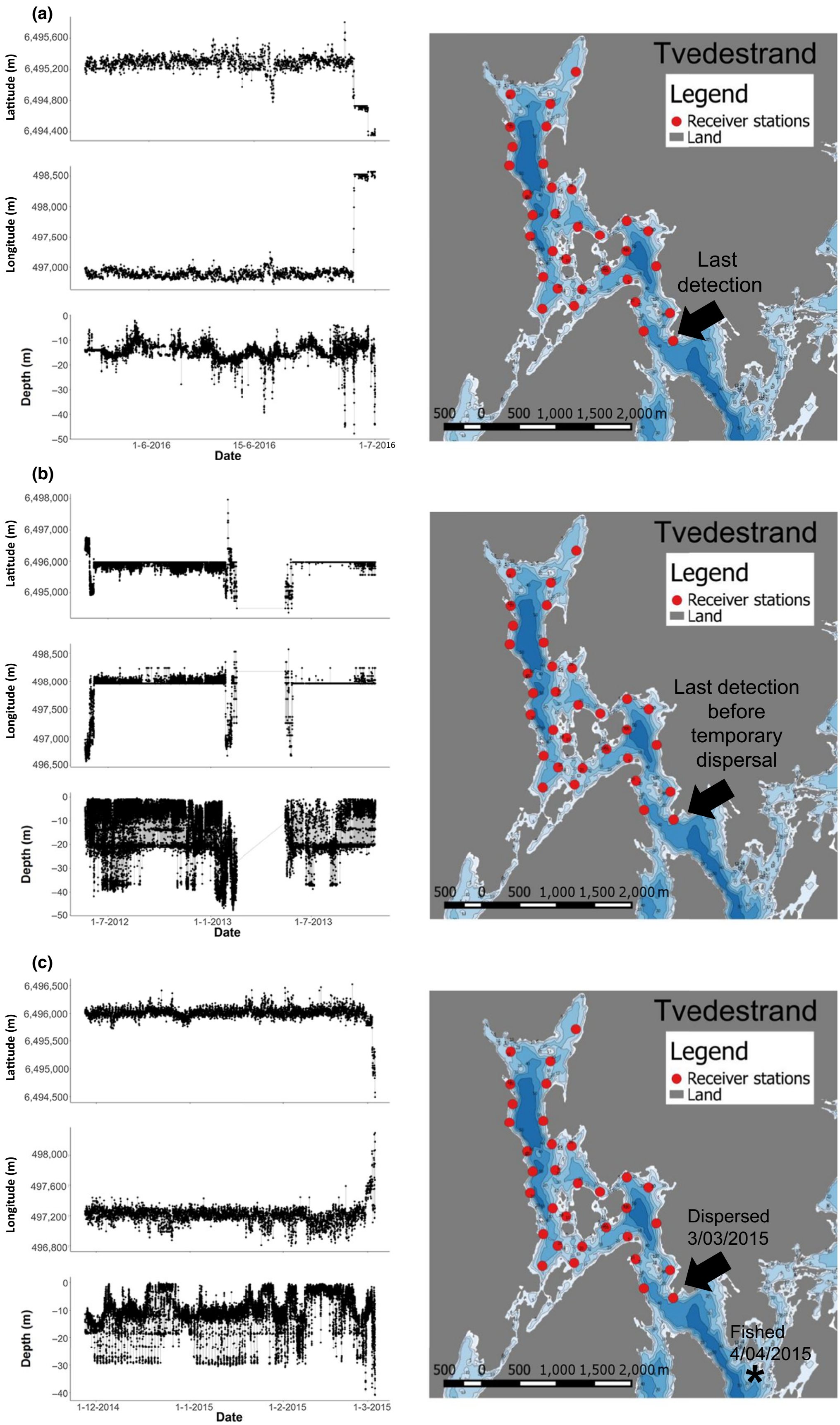

FIGURE 7 Dispersal. Horizontal and vertical movement patterns of a cod dispersing from the Tvedestrand telemetry array and map indicating the last receiver that picked a signal from this individual (a). Certain movement patterns of real dispersers can be obtained from fish that temporarily strayed outside the array (b) or fish that dispersed beyond the array and was later recaptured by fishers (c)

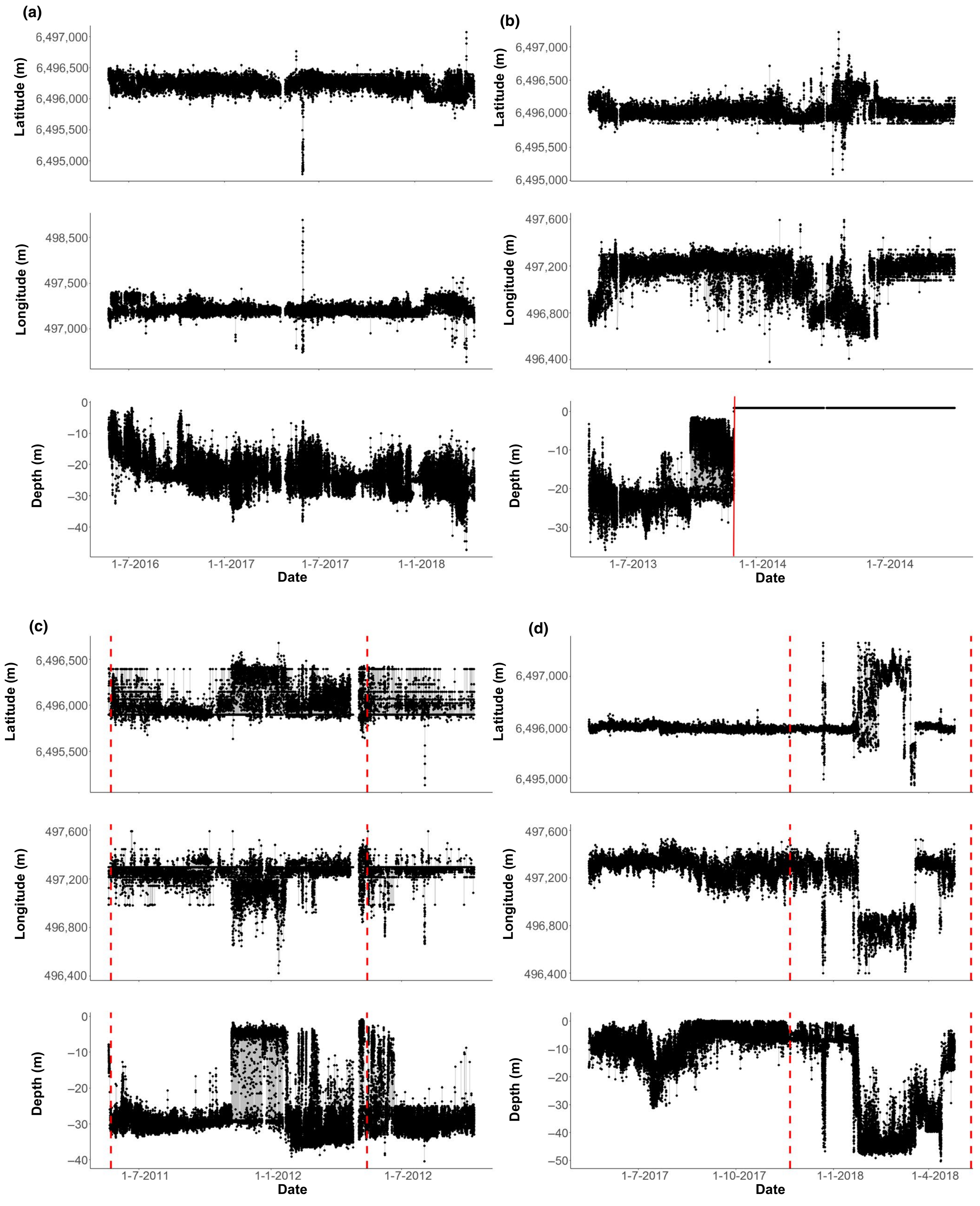

FIGURE 8 Survival. Horizontal and vertical movement pattern of cod that survived throughout the tag's battery life showing regular horizontal and vertical movement (a) and another cod that also survived but displayed a flat depth profile from a particular date (vertical red line) and onwards as a result of a pressure sensor malfunction. Patterns of those fish can be assumed to correspond to normal cod behaviour based on the profiles from cod recaptured and released (c, d). The vertical red dashed lines in panels c and d represent recapture events and confirm that the patterns observed before such events indeed correspond to the focal individuals originally tagged

equipment among the research community, but we acknowledge that it could be adapted to equipment from other vendors and alternative data processing techniques. For instance, our *XY* profiles are based on COA (Simpfendorfer et al., 2002), which in turn are based on weighted averages of detections across multiple receivers during specific time bins. The use of COAs may result in apparent horizontal movement when a transmitter is in fact lying in the bottom (e.g. after a natural mortality event), as we have observed in the *XY* profile of reference tags at fixed positions. This can be due to variations over time in sound transmission capacity in the fjord as a result of changing conditions, which ultimately may affect how many receivers detect each signal and the resulting COAs. To buffer this effect, our method incorporates depth information, which is measured directly by sensors integrated in the transmitters. By looking at both the *XY* and depth profiles it is possible to get a more realistic picture of the movement of the fish, which is critical to assign fate. More accurate positioning techniques such as methods that use passive time difference of arrival (TDOA) will provide more accurate estimates of fish locations further increasing the precision of fate assignments (Baktoft, Gjelland, Økland, & Thygesen, 2017). Similarly, our method could be complemented with the use of other sensors (e.g. predation, physiological) that would increase the certainty in the fates assigned. For instance, stabilized *XY* and depth profiles accompanied by cessation of heart beats or tail beats could be a clear indication of mortality (Whitney et al., 2016). In telemetry arrays where individuals are equipped with transmitters that are emitting a signal at shorter time intervals, there could be potential for detecting fishing events directly, as a series of detections along decreasing depths followed by a sudden cessation of detections.

In spite of the clear advantages offered by this method, there are also some challenges that may make fate assignment difficult under some circumstances. For instance, a fish may be harvested and the guts are discarded at the same place during the period of time between consecutive transmissions. In this case, a typical 'natural mortality' pattern would be obtained, while the fish was actually fished. Another ambiguous situation would take place if the fish is harvested or predated right at the edge of the telemetry array, so the tag disappears with a typical dispersal pattern. It should also be noted that in some systems it may be difficult to separate the pattern of the focal species from that of the predator. This was not the case in our cod telemetry dataset because harbour seals and Atlantic cod behave very differently yielding very distinct and characteristic movement patterns. When this is not the case, predation events may not be caught by our method, but as long as the tag is expulsed by the predator, a conservative natural mortality pattern would be assigned. Information on retention times by different predators may be important when retention times are longer than digestion-egestion rates (Klinard, Matley, Fisk, & Johnson, 2019). A particular predation situation that would be difficult to detect by our method are instances of aerial predation by birds, which would result in a pattern very similar to fishing mortality, i.e. the focal fish disappearing suddenly. Our method, as previous methods (Kraus et al., 2018), cannot allocate instances of tag shedding (that would result in typical natural mortality pattern; Hightower et al., 2001) or complete tag malfunction. Similarly, our method can only estimate fate during the duration of the battery life of the transmitter. However, battery lives of commonly used acoustic transmitters can now exceed 10 years of duration, opening up an opportunity to track individuals' fate during a great part of their lives. Finally, our method relies on being able to identify when a fish is dead by its movement patterns. Although we assumed that dead cod in our study system would yield almost flat depth and *XY* profiles, tagging a dead individual provided confirmation to our assumption. Tagging dead animals may also prove useful to investigate movement of dead fish in more hydrodynamic systems (Havn et al., 2017), such as coastal areas subject to strong current or tides, setting a baseline against which movement patterns from other fish can be compared.

Being able to accurately determine fate for a large number of individuals in nature can dramatically expand the range of hypotheses that can be tested in aquatic wild populations. Knowledge of tagging mortality rates is essential to evaluate the performance of telemetry methods and to calibrate the parameters estimated from telemetry studies (Bennett, 2006). Natural mortality and survival are normally difficult to assess given that natural mortality events are typically unobservable in nature (Quinn & Deriso, 1999). However, direct estimations of natural mortality and survival in the wild have clear applications to fishery management and evaluation of regulations. For instance they can greatly improve stock assessment models, assess the performance of introduced species (Lennox, Blouin-Demers, Rous, & Cooke, 2016) or evaluate post-release mortality (Raby et al., 2015). Being able to tease apart fishing and natural mortality can help understand patterns of natural versus fishing selection, which in turn are relevant to understand eco-evolutionary processes of aquatic animals including studies of local adaptation. Estimation of dispersal rates can be useful for studies of effectiveness of marine protected areas (Villegas-Ríos, Moland, & Olsen, 2017), and combined with genomics it can bring significant insights on the migratory ecology of non-model organisms in the wild with potential to understand processes of gene flow and local adaptation (Barth et al., 2019; Moore et al., 2017). Predation rates are usually difficult to estimate directly in the wild. Provided that the predator and the prey have clearly distinct behaviour and that this is reflected in the detections and movement patterns, our methods represent a strong, minimally invasive technique to investigate trophic interactions and trophic dynamics, that can replace or complement the use of costlier predation tags.

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AUTHORS' CONTRIBUTIONS

All authors collected the data, conceived the ideas, designed the methodology and interpreted the data; D.V.-R. and C.F. analysed the data; D.V.-R. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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DATA AVAILABILITY STATEMENT

Data used in this manuscript can be accessed at Dryad https://datadryad.org/stash/share/Gtqz442s5I481j6aMi7TTnnwSphGFZuKyiBdULBXuTU.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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