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Using acoustic telemetry to estimate post-release survival of undulate ray *Raja undulata* (Rajidae) in northeast Altantic

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Abstract :

The landing obligation introduced in the reform of the European Union Common Fisheries Policy requires landing all catches of species under quota. However, exemptions may be granted for species for which "scientific evidence demonstrates high survival rates". Captivity experiments are often used to determine fish survival rates, but they are difficult to perform for large species such as rays due to the limited storage capacity of tanks. Thus, little information is available on ray survival after release despite an identified potential for high survival. We used acoustic telemetry to study rays discarded from a coastal bottom trawl fishery in their natural environment and present a new ad hoc approach to derive a minimum survival rate. After capture under commercial conditions in a semi-enclosed bay, 144 rays were tagged with a miniature acoustic transmitter. Survival was assessed based on detections from 15 acoustic receivers deployed in the area and a mobile reception antenna. Then, combining detection data with information on currents provides useful results from a management perspective, as at least 49% of the rays were found to have survived the first 14 days after released, and because the only factor identified that likely decrease survival (i.e. smaller individuals) cannot be improved easily by changing fishing practices.

Highlights

► Survival rate of Raja undulata was assessed in a coastal otter trawl fishery. ► Rays were tracked acoustically during three months after being discarded. ► An *ad hoc* approach based on currents was developed to assess survival. ► At least 52% of rays survived to discarding. ► Fishing conditions were not detected as drivers of ray's survival.

Keywords : Tagging, Discard survival, Trawl fishery, Elasmobranchs, Bay of Biscay

INTRODUCTION

Fisheries in the north-east Atlantic discard up to 50% of the catches while they are the second largest source of total removals in the world (Alverson et al., 1994; Kelleher, 2005). In this context, the European Union reformed its Common Fisheries Policy and decided on a landing obligation, which will prohibit discarding individuals of species under quota or minimum size in the Mediterranean (European Commission, 2013). However, the regulation (article 15, paragraph 4(b)) allows for exemption from the landing obligation for “species for which scientific evidence demonstrates high survival rates, taking into account the characteristics of the gear, of the fishing practices and of the ecosystem”.

Among the rays fished in European waters, the undulate ray (*Raja undulata*) is of major concern given its current high discard rate in most north-east Atlantic commercial coastal fisheries. Fishing of this species was first prohibited in December 2009 (EC 43/2009) before being assigned a zero total allowable catch (TAC) in December 2013. A small TAC (25 t) for undulate ray was introduced in ICES Division 8 in 2015 and increased to 30 t in 2018. The french catches were significantly higher (515.7 t in 2017), resulting in high discards (484 t). Consequently, strict enforcement of the landing obligation would certainly “choke” these fisheries resulting in serious financial issues (Schrope, 2010). In the territorial waters of the division 8.a, undulate rays were mostly discarded by small (<12 m) otter trawlers (29%), trammel netters (32%) and large set longliners (30%) in 2017 (source DPMA and Ifremer SIH). Among these metiers, the trawling may induce more mortality because the catch is compressed in the codend. However, evidence of the resistance potential of this species to bottom trawling and handling has already been provided (Morfin et al., 2017a). This encourages studies to estimate its survival rate after release from small bottom trawlers to assess whether this species may be subject to an exemption from the landing obligation.

To determine discard survival rates, most scientific studies follow the recommendations of the ICES Workshop on Methods for Estimating Discard Survival, keeping individuals in captivity in tanks until a survival asymptote is reached (e.g. Mérillet et al., 2018; Morfin et al., 2017a). However, for large species such as ray, captivity experiments are difficult to perform as large experimental units are required to have enough individuals to perform robust statistical analyses. Moreover, captivity experiments do not consider several parameters that are crucial for estimating long-term survival, such as predation on weakened individuals, invisible damage, or physiological stress resulting from fish exhaustion in the trawl and displacement into an unsuitable habitat, as individuals are rarely returned to the location where they were caught (Chapman et al., 2000; Raby et al., 2014; Ryer, 2002; Ryer et al., 2004; Wood et al., 1983).

Tagging and releasing individuals in their natural environment addresses most of these issues and was identified by the Expert Working Group 13-16 of the Scientific, Technical and Economic Committee for Fisheries (STECF, 2013) as a valuable method to determine discard survival. Traditional tagging studies require recapturing live individuals to estimate a survival rate, while acoustic telemetry relies on recording tagged fish passing through an acoustic detection range (Hoenig et al., 1998; Pollock et al., 1989). Thus, it requires much fewer tags as no recapture is needed to collect data. Initially used to track individuals' movements, acoustic tagging proved an interesting method to estimate survival rates of species, such as cod (Capizzano et al., 2016) and summer flounder (Yergey et al., 2012).

Amon the many scientific studies carried out in response to the landing obligation and the potential exemption for species with "high survival rates", none have studied long-term survival of rays after release, although Ellis et al. (2017) recommended studying elasmobranchs in relation to possible future landing obligations in European waters. Previous rare initiatives studied ray survival potential by examining individual vitality on board prior to discarding (Benoît et al., 2010; Laptikhovsky, 2004) or by determining a survival rate after a few days in captivity (Depestele et al., 2014; Enever et al., 2009, 2010; Mandelman et al., 2013; Saygu and Deval, 2014a). However, no study has observed a stabilised survival rate, which generally occurs within 5-14 days for other discarded species (Mérillet et al., 2018; Morfin et al., 2017b; Uhlmann et al., 2016) and is assumed to occur after 9 days for skates (Depestele et al., 2014).

Using acoustic telemetry and recapture data, we determined the post-release survival rate of undulate ray in a coastal otter-trawl fishery in the Bay of Biscay. To infer a ray's alive status, we developed an *ad hoc* approach which combined detection data with information on currents to discriminate detections of live rays (dead rays being potentially transported by currents). The influences of fishing practices and environmental conditions were analysed to identify measures that could increase discard survival and strengthen the fishery's sustainability.

MATERIALS & METHODS

Study site

Tagging and onboard data collection were conducted between June and August 2017 in the Bay of Bourgneuf (Bay of Biscay, France, northeast Atlantic, ICES Division 8.a, Fig. 1), a 320 km² bay where the undulate ray is known to be a regular resident during summer (AGLIA, 2014; Stephan et al., 2015). This bay is shallow (from 0 to 34 m depth), the southern part being shallower and smoother while the north topography is more irregular. The substrate is composed of a variety of patchy rocky, sandy and muddy bottoms. Bottom currents are essentially driven by tides which can be very important (tidal range reaches 7 m during spring tides) and contribute to the distribution of the substrates. The climate is temperate and oceanic with meridional features (humidity, wind and low gradients in temperatures), and the mean daily air temperatures varies from 4°C in January to 23°C in August.

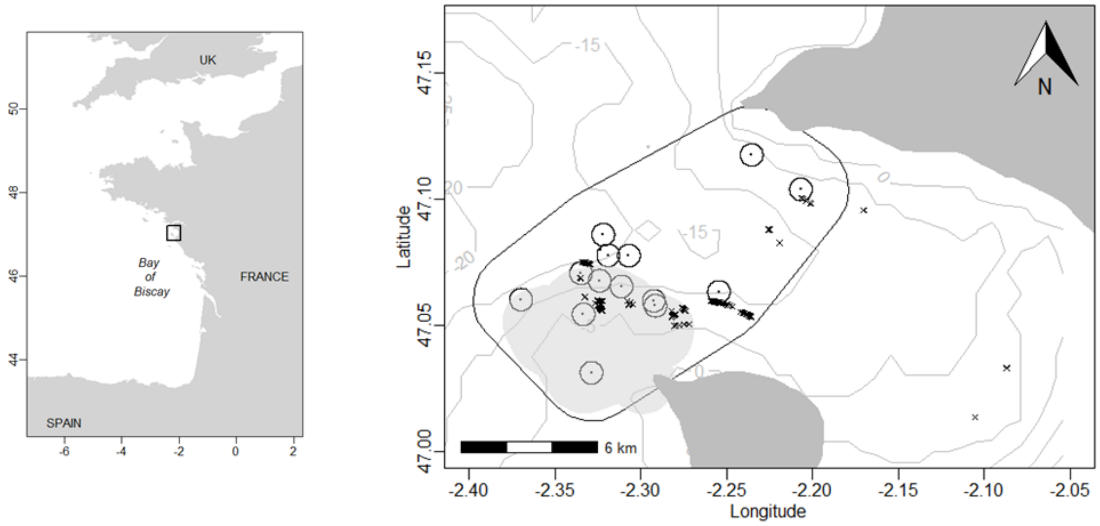

Figure 1. Location of the Bay of Bourgneuf in the Bay of Biscay (left) and map of the study area (right). Lands and isobaths are in grey. The black crosses are the release locations of the tagged rays. The black points are the locations of the receivers and the black circles their detection range. The black line defines the study area, and the light grey zone is an example of the area covered during one of the active tracking survey.

Deploying acoustic receivers

Based on fishermen's knowledge, 15 VEMCO acoustic receivers (VR2W-69kHz) were deployed in the fishing area. Receivers were located at sites for which rays had high fidelity and where trawlers or other towed fishing gear could not reach the acoustic devices (Fig. 1). Two divers deployed the receivers on the sea bottom, each with a 30 kg anchor and four SHE-3 floats of 300 buoyancy, allowing the receivers to be erected. Before deploying the receivers at sea, the number of floats and anchor weight to use were determined in a flume tank in Lorient, France (Vincent et al., 2018), by simulating the maximum current speed observed *in situ*.

Each receiver recorded each successfully decoded ping as a single detection, which was then stored in its memory as a unique transmitter number, date and time of detection.

As the configuration of the study area did not allow to carry out a range test in good conditions, we relied on the study realised by Huveneers et al. (2016) who studied the range detection probability in many environmental conditions with the same receiver type. The maximal distance beyond which no detection are possible whatever the conditions appeared to be lower than 850 m. Furthermore the detection range in our study is expected to be lower as the power of the transmitter was lower (144 dB versus 147 db) and the depth of both tags and receivers were in shallower water, where the sound propagation is expected to be the most affected (Medwin and Clay, 1998). Therefore, the maximum range from which no detection could be recorded was set at 850 m. The receivers remained under water for three months to ensure that fish mortality or recovery was monitored over a sufficiently long period and data were uploaded at the end of this period. At the end of the experiment, almost no fouling organisms were found on the receivers. We could thus be confident that the detection capability of the receivers was not alterated during the study.

Fishing conditions

The experiment was carried out on board a 10.95 m long commercial trawler equipped with a 150 kW engine power and rigged with a single bottom trawl (5 m vertical opening, 18 m headline, 70 mm diamond mesh codend), commonly used to target multispecies fish assemblages in the area. During five one-day trips, 22 hauls (each lasting 51-127 min) were performed, and the crew was asked to maintain standard fishing and on-board handling commercial practices. For each haul, parameters likely to influence ray survival were recorded, including biological parameters (i.e. total fish length), environmental parameters (i.e. thermal shock, which equals the difference between sea-bottom and air temperatures) and fishing operation parameters (i.e. tow duration, mean tow depth, catch volume, presence of stones or potentially injuring elements in the trawl and duration of air exposure) (Table 1). Towing speed was maintained at 3±0.5 knots. The net retrieving speed was also maintained constant and not considered in further analyses. These conditions were similar to the bottom trawling activities of vessels <12 m in the same area (ICES 8a, territorial waters, source Ifremer - SIH). The vessel length and power were among the highest values of the fleet. Fishing depths were slightly smaller (~10 m less in average) as the experiment was constraint to the semi-enclosed bay, but the tow duration, catch volume and fish length were in the same ranges. Consequently, the air exposure was certainly representative as it is most of the time proportional to the catch volume. Only the thermal shock was in the upper range of the expected values, as the experiment was conducted in summer when exposure to high light intensity and high air and sea temperatures are expected to be more stressful for individuals (Davis, 2002). Thus, the post-release survival rate estimated would be considered a minimum value compared to other seasons.

Tagging

Rays were collected during catch sorting by the crew, at the time at which they would normally be discarded at sea. All rays were tagged, except those dead or those for which the wing was considered too thin to carry the tag (corresponding to individuals <32 cm in total length). Rays were tagged externally to avoid surgery and potential confounding effects. A VEMCO ultrasonic transmitter (model V8-4L, 69 kHz, 144 dB, 30 - 90 seconds delay, 145 days expected battery lifetime) was attached to a 3/4" laminated disk tag (Floy Tag & Manufacturing) with epoxy glue and a Colson-type plastic hose clamp. A second disk was placed between the hose clamp and the wing to minimise skin abrasion. The tag was attached to the ray with a stainless steel pin that was pushed through the wing and secured on the ventral side using a third disk. In a previous study, the influence of these tags on the survival of 32 rays in good condition was tested in captivity; 94% of the rays were still alive after one month (Hennache, 2013). An ID number and the institute's phone number were printed on the top laminated disk so that fishermen could report the capture of a tagged individual.

Active tracking via a mobile reception antenna

To enhance the spatial coverage of the experiment, a GPS-equipped VEMCO VR100 mobile receiver with an omni-directional hydrophone was used from a skiff four times during the lifetime of the transmitter batteries (June-August 2017) to locate tagged individuals. The skiff ranged the study area during 4 hours and travelled 25 km in average to track actively the individuals in the zones out of the fixed receivers' ranges. The receiver's builder estimated its maximal range at 1,329 m, corresponding to a mean covered area of 39 km² *per* survey (an example of one track area is shown in Fig. 1). At each detection, the individuals were located within the maximal range around the position of the hydrophone.

Determining survival

Using acoustic detection to determine a ray's alive status was challenging because (1) a tag from a dead ray could have drifted in the current, (2) ray movements could not be recorded continuously as the receivers covered the study area only partially (Fig. 1), (3) the rays were expected to migrate from the Bay at the end of summer. Owing to these features, we adopted a conservative approach using *ad hoc* criteria to provide only indisputable proof of survival (Fig. 2). In other words, rays that were demonstrated alive according to criteria detailed below were assumed alive until the last date one of the criterion was fulfilled, and all the rays that were never demonstrated alive (detected or not) were assumed dead throughout the study period. Therefore, only a minimum survival rate was estimated.

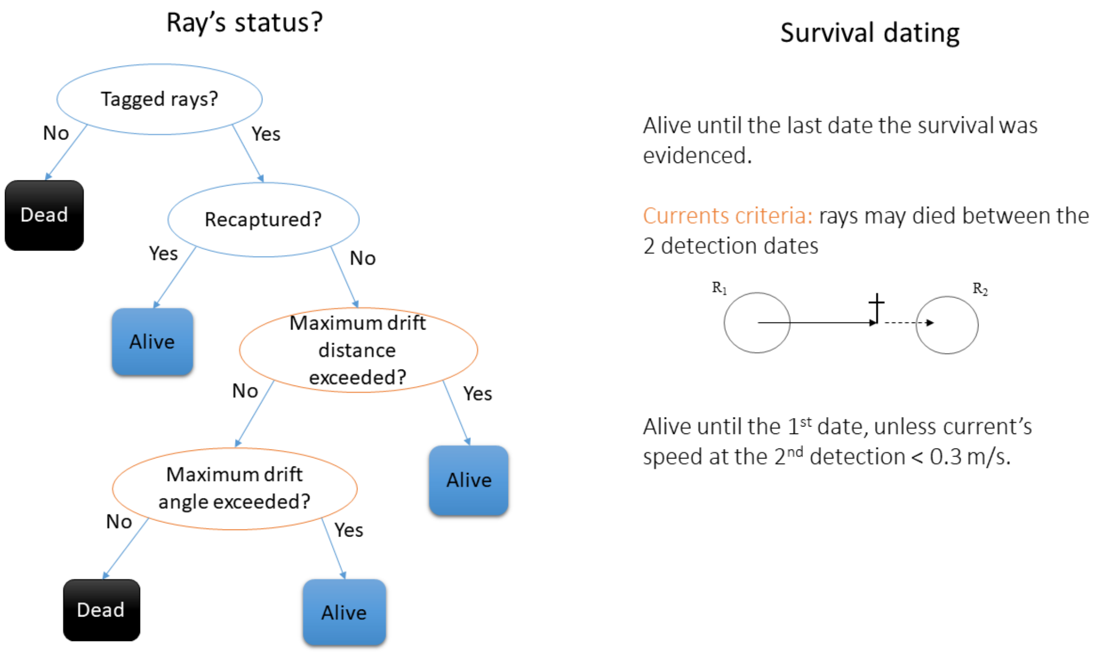

Figure 2. Flow chart describing the decision criteria on the ray's alive/dead status. In this conservative approach, a ray was considered dead from the date of its release to water unless its alive status could be demonstrated after this date. In this case, it was considered alive until this date.

When a ray was recaptured alive and its capture reported, its status as "alive" was confirmed on that date. Otherwise, survival determination was based on travel distances and directions between receivers relatively to the bottom current. The locations of rays detected at least once were known at the time of detection and at the spatial resolution of the receiver's detection range. Based on their large sizes and geographical distributions, seals (*Halichoerus gripus* and *Phoca vitulina*), bottlenose dolphin (*Tursiops truncatus*), tope (*Galeorhinus galeus*), and meagre (*Argyrosomus regius*) were identified as the only potential predators of large skates in the Bay of Biscay. However, examination of stomach contents revealed no consumption of skates and rays by this group of species (Hauksson and Bogason, 1997; Hubans et al., 2017; Mikkelsen et al., 2002; Morato et al., 2003; Pierce et al., 1991; Santos et al., 2001). This suggests that only scavengers would have eaten dead rays, leaving tags undamaged. Therefore, a tag from a dead ray would either remain on the bottom or drift with the current. A dead ray from one of the haul was tagged and released at a receiver location to explore the potential drifting of dead rays, but this receiver was unfortunately not found at the end of the experiment. The mobile receiver, however, detected the ray in the same location 11 days later.

An experiment was conducted in the Lorient flume tank (Vincent et al., 2018) to measure drift speeds of a tag with its anchoring device at 9 current speeds from 0-0.8 m/s. Due to the smoothness of the bottom of the flume tank, the resulting tag drift speeds were considered maxima.

Bottom-current data in the study area were available for the entire experimental period, as predicted by the regional ocean model MARS-3D (Model for Application at Regional Scale), which estimates the hourly speed and direction of the current in a 4 × 4 km grid (Lazure et al., 2009). The model also generated maps of daily residual currents (i.e. those not influenced by tides). Currents in the Bay of Bourgneuf appeared to be driven mainly by tides; thus, a drifting tag should start moving in the opposite direction each time the tide changes.

Several criteria were defined to identify live individuals based on currents and the trajectories between all the pairs of detections by receivers (including the mobile receiver at the release and during the active tracking). To determine whether a tag could have passively drifted into the detection range of a given receiver, a maximum-drift area was first bounded as a polygon that included all locations where a tag could have drifted after a detection, according to the strongest half-tide cycle of the entire study period (Fig. 1). For each pair of detections (i,j), the maximum distance $D^{max}(i,j)$ that a tag could have drifted after the first detection was estimated from the predicted currents and the results of the flume tank experiment (Fig. 3A). As tag location could not be recorded continuously, we assumed the highest current speed in the maximum-drift area as a conservative estimate. As current speed is not necessarily the same in both tide directions, we assumed an extreme situation in which the tag drifted in only one tide direction, making $D^{max}(i,j)$ equal to the longest drift distance in one of the two tide directions.

We also considered the deviation between the directions of all the currents that could have transported a tag and the straight line between two detections. A drifting tag could have reached the next receiver only if this deviation was smaller than the maximum deviation between the limits of the two receivers ranges $\theta^{max}_{(i,j)}$ (Fig. 3B).

Thus, if the distance between two detections minus 1700 m (i.e. two times the detection range of 850 m), $d_{min}(i,j)$, exceeded the maximum drift distance between the two detections $D^{max}(i,j)$, or if the maximum deviation between the positions of the detections, $\theta^{max}_{(i,j)}$, was lower than the minimal deviation between any currents that could have drift the tag and the straight line between two detections plus $\theta^{max}_{(i,j)}/2$, the ray was considered alive at the first detection (Fig. 3).

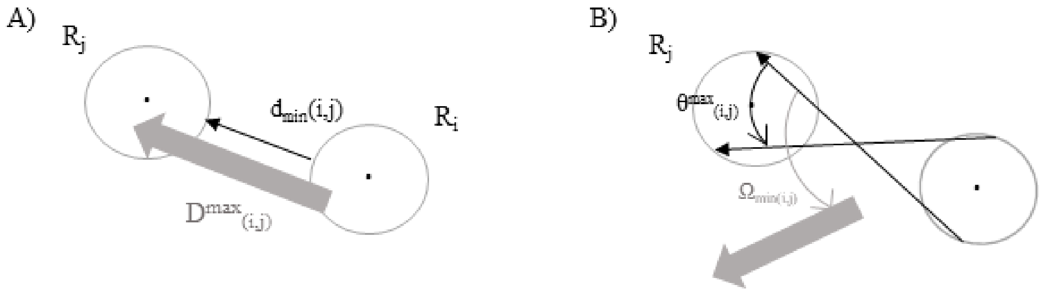

Figure 3. A) Illustration of the distance-based survival criterion. B) Illustration of the direction-based survival criterion. R_i and R_j are two different receivers and the grey circles are their detection range. $d_{min}(i,j)$ is the minimum distance between the two detection ranges and $\theta^{max}(i,j)$ the maximum deviations between any locations within both detection ranges. $D^{max}(i,j)$ is the maximum current speed between the detections from R_i and R_j. $\Omega_{min}(i,j)$ is the minimum deviation during the entire period between current directions and the extreme locations of the receivers detection ranges area.

Survival dating

Evidence for survival based on distance or direction criteria could not be accurately dated because the ray might have travelled toward the surrounding area of the second receiver, died and then drifted within its detection range. In this case, the currents around the receiver would have been strong enough for the tag to drift to the detection area on the date recorded. Thus, a ray considered alive between two detections was also considered alive until the second detection only if the currents in the range of the second receiver were lower than the minimum speed required for a tag to drift. Otherwise, it was considered alive until the first detection only (Fig. 2).

After release, an individual may eventually have died from its injuries. The period during which this delayed mortality occurs depends on the degree of injury and stress of the tagged individual, its robustness and the environment (Raby et al., 2014; Ryer, 2002; Ryer et al., 2004; Wood et al., 1983). In discard survival studies performed in captivity, the status of individuals is recorded every day until a stabilisation is observed in the survival rate. As the present study could infer only evidence of survival, this stabilisation was not observable.

We estimated the survival rate at 14 days, the maximum period over which discard mortality occurs, according to most of the published studies (Benoît et al., 2012; Mérillet et al., 2018; Morfin et al., 2017b; Uhlmann et al., 2016). To estimate survival conservatively, individuals that were not tagged because they were dead or too small to tag were considered dead on board.

Effect of fishing conditions on survival

Once the survival status was determined for each individual, we analysed the influence of fishing and of the fish condition to identify the main drivers of post-release survival. A binomial model with a logistic link function was used to relate the survival status of rays after 14 days to any linear combination of potentially influential variables (Generalised Linear Model, GLM). Furthermore, a random "haul" effect was tested on the full model using a one-sided chi-square test; and when significant, a GLM with a mixed effect was used (GLMM). The explanatory variables tested were those with potential influence based on the literature and the conditions of this particular experiment (Table 1). To avoid overestimating the influence of fish length, the rays not tagged because of their small size were removed from the analysis because they were considered dead by default. Overall, 128 models, corresponding to all linear combinations of variables, were fitted. The relative performance of each was evaluated using the Akaike information criterion (AIC). All analyses were performed with R (software version 3.5.0), using the 'sp', 'raster' and 'rgeos' packages for spatial data treatments and the 'lme4' package to fit the GLMMs (R Core Team, 2018).

RESULTS

Among the undulated rays caught under commercial conditions, four were already dead on board, and 15 were too small or in too poor condition to tag. To remain conservative, these 19 rays were considered dead by default at time 0. Among the 144 rays that were tagged and released, eight ones were never detected or recaptured.

Among the 136 rays detected at least once, 132 rays were detected by the fixed receivers, 54 during the active tracking surveys and 16 were recaptured alive (one ray was recaptured twice the same year, six others once the next year). Overall, 215 259 detections were recorded throughout the experimental period, from 1-10 940 per ray, with each ray detected at 1-10 receivers. For each transmitter, the total distance estimated between detections (minimum distance for the tag) ranged from 0-30 km.

At many occasions, the frequency of detections for a single ray at a same receiver remained high for a long period (mean=17 days, 95th quantile=70 days). This demonstrates that the detection range (~750 m) was large compared to the rays average mobility, and that rays are prone to stay in the same place for a long time when conditions are suitable. The mean residence period within the detection range of a receiver for rays that were considered alive was 9 days and the 95th quantile 40 days.

Current-based criteria

The hourly speed of bottom currents in the Bay of Bourgneuf ranged from 0.00-0.51 m/s, peaking during new and full moon phases (Figure 4A). For this range of speeds, the experiment conducted in the flume tank provided a corresponding maximum speed for a drifting tag (Fig. 4B). In the flume tank, tags movements were not observed for currents speeds lower than 0.3 m/s. Furthermore, deviations between currents directions of speeds higher than 0.3 m/s never exceeded 62° during the entire study period (Fig. 4C). As mean daily residual currents in the study area never exceeded 0.06 m/s, this validates the current-based criteria used to infer survival.

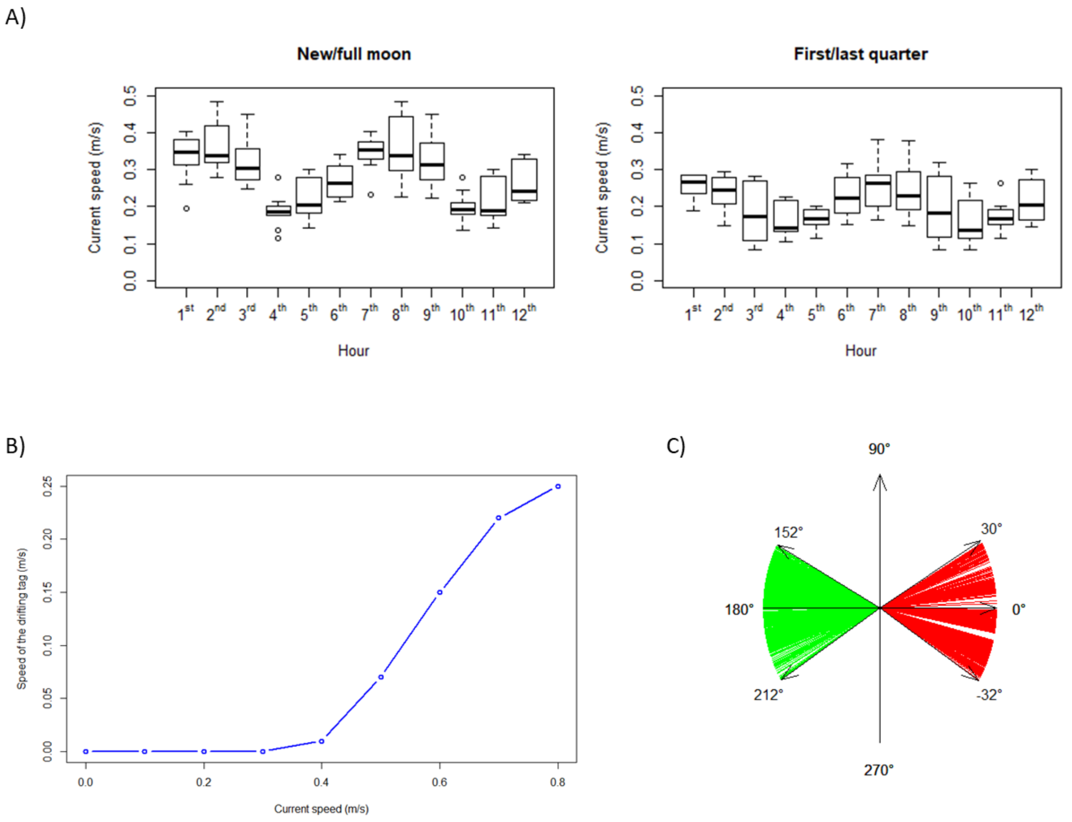

Figure 4. A) Boxplots of the hourly maximum currents speeds throughout the study area depending of the hour of the tides for different moon phases, B) Speed of a drifting tag with its anchoring device as a function of the water current speed, from an experiment in a flume tank in Lorient, France (Vincent et al., 2018), C) Directions of currents faster than 0.3 m/s in the tide's ebb (green) and flow (red) directions.

The number of detections slightly decreased over time and thus the potential to demonstrate the ray's alive status (Fig. 5A). However, 123 rays could be inferred alive according to the current-based criteria, allowing the calculation of a minimum survival rate during the first 14 days of underwater acoustic recording (Fig. 5B). For many rays, their survival could only be evidenced between the first detection (at time 0, during the release) and another detection. As a result, their minimum survival period were set to 0 and are confounded with individuals observed dead on the deck (only 4 out of 163 rays). At the end of this period, the minimum post-release survival rate was estimated at 49%, with a 95% confidence interval of [42%; 57%].

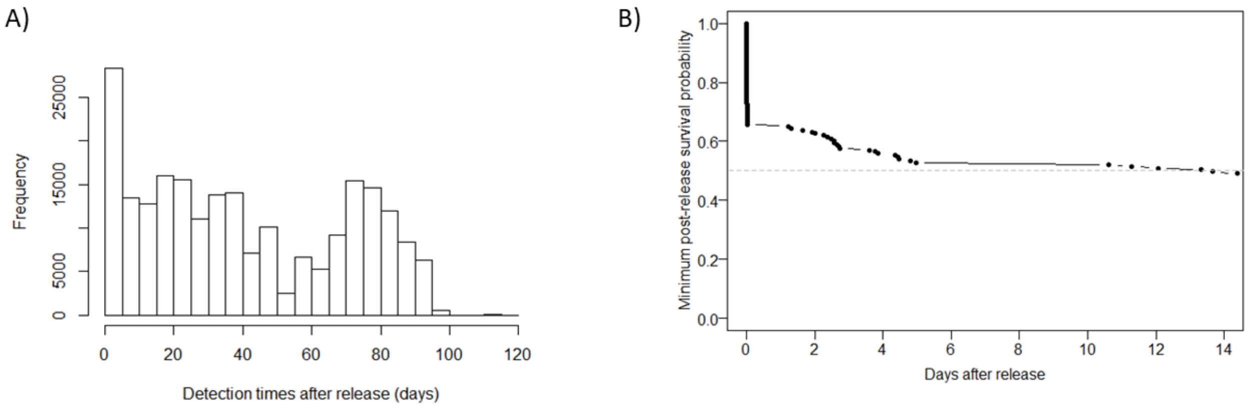

Figure 5. A) Histogram of the detection times for all rays, in days after the release of the tagged ray, B) Minimum post-release survival probability as a function of the number of days after release. The dotted grey line corresponds to y=0.5.

Effect of fishing conditions on survival

The best model selected according to the AIC indicated a positive relationship between survival and fish length; however, it explained only 1% of the deviance (Table 1).

Variables	**Mean [min-max]**	**Best model coefficient ±** standard deviation
TL (cm)	64 [18-99]	0.23 ± 0.16
Tow duration (min)	93 [51-127]	0
Depth (m)	8.7 [4.6-17.8]	0
Thermal shock (°C)	4.1 [1.3-11.0]	0
Catch volume (crates)	4.4 [2-8.5]	0
Injuring elements (0/1)	0.18 [0-1]	0

Air exposure (min)	15 [1-40]	0

Table 1. Description of fishing conditions and outputs of models fitted to the minimum post-release survival after 14 days. Coefficient estimate from the “best model” according to the Akaike information criterion.

DISCUSSION

According to the criteria used to consider rays individuals alive, based on recapture or acoustic detection, this study demonstrated that at least 49% of undulate rays survived capture by a bottom trawl and discard for a minimum of 14 days. This minimum estimate of survival rate, the first under natural conditions for rays, agrees with those of previous studies performed in captivity with shorter retention times. For instance, similar survival rates (55% and 59.1%) were found for different species of ray caught on board commercial trawlers in United Kingdom waters (Enever et al., 2009) or off the Falkland Islands (Laptikhovsky, 2004), respectively. For studies that estimated ray survival in trawled areas, survival rates ranged from 72-81% for a captivity duration of 48-80 hours (Depestele et al., 2014; Mandelman et al., 2013; Saygu and Deval, 2014b). Only Kaiser and Spencer (1995) kept *Raja naevus* individuals in tanks for a longer period (5 days); they reported 59% survival, but for short tow durations, which were not representative of standard fishing practices.

This study and others found a positive relationship between fish length and ray survival (Depestele et al., 2014). When studying rays’ time-to-mortality (TM), a proxy of discard mortality (Benoît et al., 2013), Morfin et al. (2017b) demonstrated that small ray have shorter TM and do not survive capture as well as larger ones. As we used a conservative approach to infer a ray’s status, some rays considered dead might have been alive, which may have decreased the influence of certain factors. Other studies of ray discard survival, however, detected no influence of technical or environmental variables (Enever et al., 2009; Saygu and Deval, 2014b), suggesting that rays are highly resilient to trawl capture and handling. Furthermore, TM analysis demonstrated that rays survived a mean of 75 min on deck after capture under similar conditions (Morfin et al., 2017a).

The main advantage of using telemetry in this context is to be able to consider predation mortality, which does not occur in captivity. Using this technique in the wild is also especially suitable for large species such as rays, as experimental infrastructure limits fish density in captivity (Knotek et al., 2018; Saygu and Deval, 2014a). Although recapturing tagged rays alive after several weeks is proof of survival, using acoustic detection to infer survival is much more challenging. The main issues are (1) the potential for tagged individuals to leave the detection area, (2) the potential to loose detections due to tags collisions and (3) the risk of confounding detections of dead individuals with those of live ones. The first issue is minimised when the study area is a closed bay (Yergey et al., 2012) and when the acoustic network has a high coverage (Capizzano et al., 2016). These restrictive conditions could not be met in the present study, so the first issue was mitigated by deploying the acoustic network in a bay where rays are known to be sedentary during the experimental period, and by deploying a mobile receiver to increase coverage of the area. The method developed to determine survival addressed the other issues by considering only survival evidences and combining distance and angle criteria with current data. While these issues can be encountered in most of survival experiments using telemetry, this approach is easily transferable.

The rules used to determine whether an individual was alive were highly conservative because (1) the speed of drifting tags was estimated in a flume tank, whose bottom was smoother than the sea bottom; (2) the minimum distances and angles were used, based on the receiver's detection range; (3) the date of survival was inferred from the first of two detections if the current exceeded 0.3 m/s on the date of the second detection; and (4) the maximum drifting distances were based on maximum current speeds in a single direction per tide in the study area. Also, the experiment was conducted in summer, when environmental conditions are more stressful than those in other seasons. For all these reasons the average survival rate is likely much higher than 52%. While this result demonstrates a high survival rate, the approach developed may be improved to provide a closer estimate of the average rate. A specific detection range experiment could be realized to use a probability of detection depending on distances rather than a maximum range (Kessel et al., 2015; Mathies et al., 2014). Then a sample of dead rays could be tagged to potentially discriminate the detection pattern of any dead ray. Finally, the active tracking surveys could be performed more frequently to improve the detection coverage.

Currently, the undulate ray in ICES Division 8.a–b is under a small quota due to uncertainty in the status of its stock (ICES, 2016). Therefore, the strict application of the landing obligation will have substantial negative consequences for the related fisheries. Even if the undulate ray's TAC increases in the next few years and the conditions that likely decrease survival cannot be improved simply by changing fishing practices, these results demonstrate that landing rays instead of releasing them could cause great losses in the stock.

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