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Survivorship of discarded sole (*Solea solea*) characterised via telemetry, vitality, and physiology

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Abstract :

While the discarding practices of commercial fisheries might greatly contribute to fish mortality, a better understanding of discard survival patterns and their drivers is crucial to assess fishing mortality and develop effective mitigation measures. Bottom trawling in particular is likely to induce multiple forms of stress in captured fish. In this study, we used three experimental methods to explore discard survivorship of the common sole (Solea solea). We focused on fish captured via a coastal bottom trawler of the Bay of Biscay and conducted sampling during commercial fishing operations. First, we used acoustic telemetry to determine the survival rate of 160 discarded soles. While this technique makes it possible to study discarded fish in their natural habitat, inferring fish fate from these data can be challenging, especially when acoustic receiver network coverage is fragmented. Second, we scored the vitality of the sole before their release. Third, we examined three plasma markers of fish physiological status over a 90-min period following capture. The method based on acoustic telemetry estimated a minimum discard survival rate of 41%. This metric was positively correlated to the vitality. Furthermore, both survival and vitality were associated to tow duration and the presence of algae in the catch consistently. The three physiological markers reflected the presence of various levels of stress and fatigue among discarded individuals, but also a fish's ability to recover after being discarded. Individuals with excellent vitality (33% of discards in this study) suffered less stress, were less fatigued and, therefore, were greater equipped to react to other sources of stress than individuals in lower vitality. The consistency of the results demonstrates the reliability of our approach to estimate post-release survival from acoustic tagging even from fragmented network coverage, and that vitality can serve as a proxy for discard survivorship.

Highlights

► Survivorship of discarded *Solea solea* was explored in a coastal otter trawl fishery. ► Three methods were used: acoustic telemetry, vitality, and physiological markers. ► At least 41% of discarded sole survived. ► Sole with good vitality post capture had greater chance of recovery. ► Survivorship was associated to tow duration and the presence of algae in the catch.

Keywords : Bycatch mortality, Physiological status, Acoustic tagging, Flatfish, Bay of Biscay

1. INTRODUCTION

Discarding practices occur in almost all commercial fisheries worldwide. Recent estimates situate total discarded catches at 9.1 million tonnes by year (2010-2014), approximately 10% of total recorded landings (Gilman et al., 2020; Kelleher, 2005). In the north-eastern Atlantic, high discard levels result because demersal trawling captures mixed assemblages of fish, crustaceans, and cephalopods (Kelleher, 2005; Zeller et al., 2018). In Bay of Biscay fisheries, the common sole (*Solea solea*) is one of the main species targeted by trawlers and netters because it has high commercial value (Bellanger et al., 2018 and references herein). While the discard rate for sole is currently quite low (mean of 1.8-3% depending on the fishery), 90-100% of the individuals discarded measure less than 24 cm (minimum conservation reference size [MCRS]) (Cornou et al., 2021). Additionally, inshore trawler fleets occasionally discard large number of young soles (age 1, mean length=18 cm) and mature soles (age 2, mean length=22 cm) of commercial size may also be discarded because of their lower value ('high-grading practices') (Cornou et al., 2021). Last but not least, the last stock advice led to a drop in 2022 of the total allowable catch (TAC; -37%) and could prompt management measures such as an increase in the MCRS, which would cause the sole discard rate to rise in the absence of improved gear selectivity (ICES, 2021; Lecomte et al., 2021). The effectiveness of management measures is affected both by fisher's ability to improve selectivity leading to fewer discards, and by discard survivorship. Indeed, it remains challenging to improve selectivity without generating excessive losses, such as in the case of bottom trawling, which generally targets several species.

The European landing obligation (LO) was introduced to incentivise more selective practices by fishers (Fitzpatrick et al., 2019; Guillen et al., 2018) (Council Regulations [EU] 1380/2013 and 2016/72). The legislation mandates that fishers bring ashore species subject to catch limits or minimum size regulations. This requirement causes issues related to storage capacity, fuel consumption and/or ice consumption when options for improving selectivity are limited. Furthermore, those working in mixed fisheries may be forced to stop their activity without having reached their quota for their target species if they have also caught species with lower quotas (i.e., choke species). Some exemptions may thus exist for fisheries where discards have high survival rates (Council Regulations [EU] 1380/2013). Since the impacts of discarding on fish stocks and marine ecosystems are heavily shaped by fishing practices, the species and the status of its population (Cook, 2019; Kopp et al., 2016), it is necessary to examine how fishing gear and practices influence discards mortality to optimise fisheries management strategies. According to Morfin et al. (2017b), the common sole is potentially equipped to survive both capture and discard because of its pronounced resistance to air exposure after being captured by coastal otter trawlers.

The scientific community has established a set of methods for accurately estimating the survival likelihood of discarded species during commercial fishing (Breen and Catchpole, 2021). The most common approach is captive observation where fish are directly and continuously monitored (van Marlen et al., 2021). Discarded individuals are transferred into tanks or cages (Méhault et al., 2016), and their status is assessed over a period of several days to several weeks, until all catch-related deaths has occurred. However, this methodology can bias the results because fish experience additional stress such as from confinement and transportation. Also, it is sometimes necessary to adapt luminosity, substrate or refugee availability, and the type of food to ensure fish welfare, all while maintaining good water quality (Madsen et al., 2022). Captivity related bias can be assessed by introducing control fish that have not experienced the stress from capture, but this is not always easy to get such fish nor clear how to correct the survival rate in case of mortality related to the captivity. Another approach to assessing discard survival utilises tagging, allowing discarded animals to be studied in their natural habitat; in this way researchers can limit logistical constraints and experimental biases (Breen and Catchpole, 2021). While mark-recapture methods are often ill suited to studying discard survivorship because of the low probability of fish recapture, acoustic telemetry tagging is an effective technique for determining the post-release survival rates of species, especially for large species carrying pop-up satellite archival tags (Afonso and Hazin, 2014) or for species that migrate over vast vertical distances that carry acoustic tags with pressure sensors (Capizzano et al., 2016; Curtis et al., 2015; Morfin et al., 2019b; Yergey et al., 2012; Zemeckis et al., 2020). For smaller individuals, such as sole below the MCRS, only external, acoustic tags are light and tiny enough to not induce stress and/or impede swimming (Jepsen et al., 2015) and Bégout Anras et al., (2003) did not record any mortality after a month on juvenile sole tagged with a similar tagging procedure. These tag types are generally used with a network of acoustic receivers to register fish locations. These networks record the position of the receiver next to which the fish passes, but not the position of the fish. Consequently, the precision and the census of trajectories depend on the receiver detection range (~100 m) on one hand, and the spatial coverage of the network on the other hand. As acoustic receivers are expensive, they can be restricted to locations where they are safe from trawling. As a consequence, the receiver network coverage might be very small in study areas with high levels of fishing activities, and can lead to very incomplete trajectories. In these conditions, it is not always straightforward to determine whether a fish in movement is still aliveness, given that dead fish can drift by in the current. Furthermore, living fish can remain in the range of a receiver for long periods. Therefore, inferring survivorship from such data remains challenging, as significant biases or uncertainties may exist. Vitality-based metrics are also commonly used as a predictor of discard survival once a clear relationship with survival have been established, for a given species and fishery (Benoît et al., 2012; Davis et al., 2021; Madsen et al., 2022). The semi-quantitative assessment (SQA) index (Benoît et al., 2010), is defined by ordinal scores assigned to the degree of visible injuries and the vigor of body movements. SQA has been found to be highly correlated with post-release survival rates of sole in two bottom trawling fisheries (Masnadi et al., 2020; van der Reijden et al., 2017). This index can be assessed for large samples at low cost while limiting harm to fish; in this way, to estimate survival can be estimated at broader scales and/or the main drivers of survivorship can be identified (Benoît et al., 2010; Morfin et al., 2017a). This kind of index are still more subject to inter-observer variability and might be correlated to environmental conditions.

Fish survivorship is affected by the technical characteristics of fishing operations such as haul duration, speed, depth, catch composition, fish overcrowding in the codend and sorting time, as well as environmental conditions such as the degree of thermal chock, air temperature and wind intensity (Depestele et al., 2014; Morfin et al., 2017b; Uhlmann et al., 2016; Van Beek et al., 1990). These stressors have a physiological impact on fish that is proportional to stressor severity and duration (Barton, 2002; Gesto et al., 2015). Fish may then display specific adaptive mechanisms to boost recovery. Thus, to predict the likelihood of species recovery following release using vitality, it is crucial to relate these metrics to physiological indicators that can accurately reflect stress levels in animals destined to be discarded. In fish, the physiological response to acute stress involves reallocating and mobilising the energy needed to cope with stressors and, thereby, restore homeostasis (Balasch and Tort, 2019). Alterations in fish physiology can be assessed by monitoring blood parameters (levels of glucose, lactate, and cortisol). These metrics are associated with exposure to acute stressors, such as staking, compression, exhaustion, handling, and hypoxia. Methling et al. (2017) proposed analysing blood markers (e.g., plasma cortisol and haematocrit) to quantify the physiological stress experienced by flatfish when exposed to air. They showed that, for plaice (*Pleuronectes platessa*) in an otter-trawl fishery, all the markers reflected profound levels of stress. More generally, fish experiencing stressful conditions (e.g., confinement in the codend and exposure to air) had increased levels of plasma cortisol first, and then of glucose, and lactate (Costas et al., 2011). These responses occur over a brief window of time, increase over the period of capture, reach peak levels, and then diminish as recovery proceeds (Cooke et al., 2013; Costas et al., 2011; Skomal and Bernal, 2010). The likelihood of recovery can be assessed by keeping fish in a water tank for a relatively short period of time and monitoring plasma levels of the above compounds. Studies conducted in bottom trawling and other commercial fisheries found that, if fish or crustaceans were released quickly, the metabolic recovery was possible (Barragán-Méndez et al., 2020; Farrell et al., 2001; Ruiz-Jarabo et al., 2021). Finally, measuring these markers in tandem with vitality indicators makes it possible to relate results from physiology to acoustic method, and validate their usefulness as proxies for survivorship.

Here, we investigated how well these different approaches characterised the survival of common sole that were captured and then discarded in a mixed bottom trawling fishery in the Bay of Biscay. We focused on vessel lengths comprised between 10 and 12 m, which account for the largest number of vessels of the sole fishery in ICES divisions 8a-b (60 of the fishery's 360 vessels; Bellanger et al., 2018). First, we adapted the method proposed by Morfin et al., (2019b) to estimate the survivorship of small sole using telemetry and a fragmented receiver network. To evaluate whether measured discard survival of tagged individuals was correlated with their vitality and blood plasma levels, we also analyzed these two other survivorship indicators. As plasma markers cannot be sampled on tagged fish, we conducted a second experiment to measure the kinetics of cortisol, glucose and lactate in captured fish immediately after the trawl was hauled in, and over 90 minutes in captivity. We assessed vitality in both experiments to relate the three indicators. We also analysed the influence of fishing conditions to identify to which extent fishing practices could be mitigated to enhance discard survival but also to assess the consistency of both vitality and survival of tagged individuals.

2. MATERIALS & METHODS

2.1. Acoustic telemetry

Tagging and onboard data collection were conducted in April 2021 in the Bay of Bourgneuf (Bay of Biscay, France, north-eastern Atlantic, ICES division 8a, Fig. 1). This 320 km² bay is shallow (depth: 0-34 m) and its bottom currents are essentially driven by tides, which can be quite strong (tidal range up to 7 m in the spring). The climate is temperate and oceanic (humidity, wind, and low gradients in temperatures). Mean daily air temperature varies from 4°C in January to 23°C in August.

2.1.1. Receiver deployment

Before the tagging operation, 14 fixed acoustic receivers were established in the bay. They were left moored for four months, from April to August. Although we do not know the migratory route followed by sole each month at a fine spatio-temporal scale, past research has shown that, starting at age 1, sole in the Bay of Biscay seasonally migrate offshore in the late summer and return to the coast in the spring (Dorel et al., 1991; Koutsikopoulos et al., 1995). We relied on fishers' knowledge to strategically place acoustic receivers along the sole's seasonal migration path, avoiding zones where trawling could cause damage on the receivers (Fig. 1). Two divers deployed the receivers on the seafloor using a protocol described in Morfin et al., (2019b). The receivers stored all successfully decoded pings (see 2.1.2), which contained information on the transmitter identity, detection date, and detection time. The receivers were equipped with lithium batteries that had low self-discharge rate (<1% after 1 year at +20°C) and that displayed stable voltage across most of their lifetime.

A preliminary 'range test' experiment was carried out *in situ* to assess the receivers' detection range. To do this, we established the relationship between the detection probability and the distance separating the receiver from the transmitter (see S1). This relationship was used to estimate the mean distance between the receiver and a detected individual (D_{mean}=203 m).

In addition, at the beginning of the experiment, eight dead sole were tagged and released within the detection range of eight different receivers (50-500 m from the receiver), to evaluate the potential drift of dead fish.

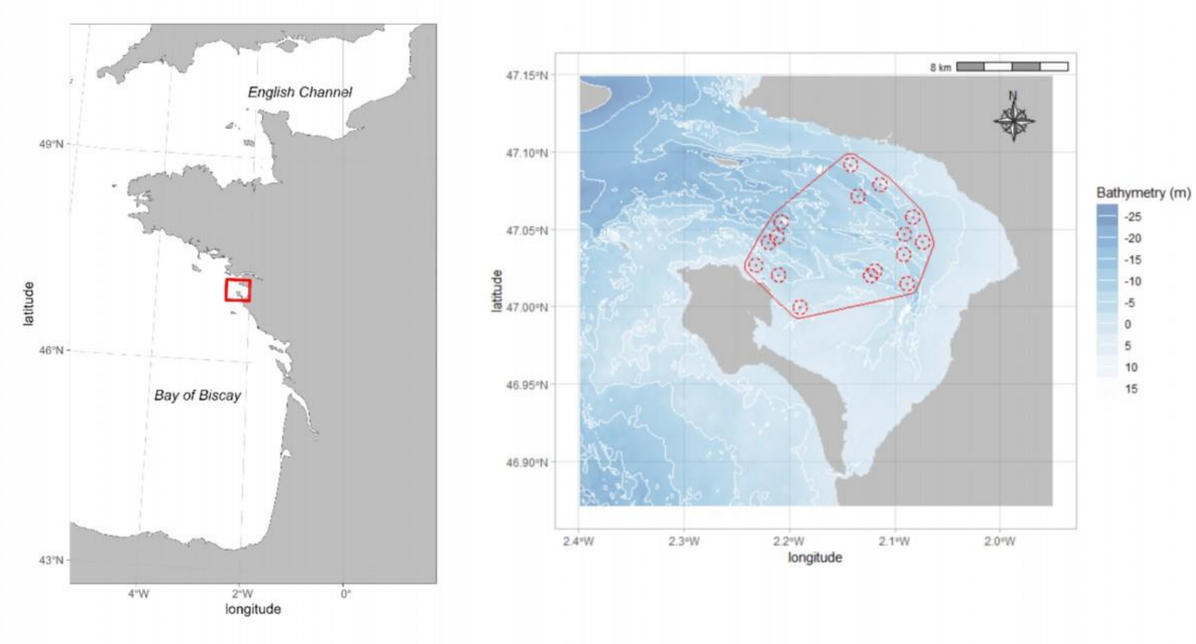

Figure 1. Map of the study area showing the receivers' locations (red dots), mean detection ranges (dashed red circles) and the maximum area of drift (solid red polygon) as defined in (Morfin et al., 2019b).

2.1.2. Tagging fish and measuring vitality

The tagging operation was carried out using a 10.95-m-long commercial trawler equipped with a 150-kW engine and a single bottom trawl (5-m vertical opening, 18-m headline, 70-mm diamond mesh codend), a set-up that is commonly used to target multispecies fish assemblages in the Bay of Bourgneuf. Over the course of 3 days, 14 hauls were performed by the crew under standard commercial conditions.

Three observers measured a range of environmental, technical, and biological conditions likely to influence sole survivorship: air temperature, sea state, mean tow depth, tow duration, catch weight, presence of injury-inducing elements in the catch, presence of algae in the catch, duration of fish air exposure onboard and total fish length (Table 1). Towing speed was maintained at 3±0.5 knots.

As the crew sorted the catch, the vitality of each discarded sole was immediately assessed individually using a SQA index, at the time they would have been discarded into the sea. The ordinal categories were as follows: excellent= vigorous body movement, with minor or no external injuries; good= moderate body movement, with minor or no external injuries; poor= weak body movement and/or substantial injuries; dead= no movement of the body or head (adapted from Benoît et al., 2010). Dead sole were directly discarded into the sea. Live sole were externally tagged with an acoustic tag before being released as well. The intent of external tagging was to avoid the need for surgery and its potential confounding effects. A VEMCO ultrasonic transmitter (modelV7-4x-BLU-1, 69 kHz, 141 dB, ping interval of 80-160 seconds, 114 days of expected battery life, 0.9 g in water) was attached to each fish in the same way as in Morfin et al., (2019b). A unique identification code and the institute's phone number were printed on the top laminated disk so that fishers could report the capture of any tagged individuals.

	Min-Max (Mean)
Tow duration (min)	78 – 109 (93)
Tow depth (m)	5-15 (9)
Sea state (Beaufort scale)	Calm to light breeze
Atmospheric pressure (hPa)	1006-1011 (1009)
Humidity (%)	50-54 (52)
Catch weight (kg)	45-360 (243)
Air temperature (°C)	10.2-18 (13.5)
Presence of injury-inducing elements in the catch	0-1 (0.23)
Presence of algae in the catch	0-1 (0.47)
Duration of air exposure (min)	6-40 (18)
Total fish length (cm)	14-24 (21)

Table 1: Summary of the technical, environmental and biological conditions during the 14 fishing operations

2.2. Estimating discard survivorship

2.2.1. Conservative estimation of discard survival rate

The records from the 14 receivers and the data obtained from fisher recaptures of tagged fish were combined to provide the sole's spatiotemporal trajectory over the four months of study. Then, we used a methodology described in sections 2.6 and 2.7 in Morfin et al., (2019b) to estimate survival rate. Fish were considered to have survived if one of three conservative potential criteria were met: 1) the fish was recaptured alive; 2) the distance between two detection events was greater than the distance predicted by drift; 3) the minimal deviation predicted by drift between two detection events (Ω_{min} in Fig. 2) would involve a tag outside the range of the second receiver (Fig. 2). The relationship between dead sole drift and current speed was measured during an experiment conducted in a flume tank (Vincent et al., 2018) detailed in (S2).

In our approach, the sole were assumed alive at least until the last date on which one of the criteria was fulfilled. Therefore, we estimated a minimum survival rate. It is important to note that we made two modifications to the original methodology to limit the chance of underestimating the expected survival rate. First, the preliminary range test experiment made it possible to employ the mean detection range (D_{mean}) instead of the nominal maximal range. Second, in the original methodology, the dating of trajectory-based survival proof was considered unknown between the two recorded dates in Morfin et al., (2019b) because a tagged individual could have died in the vicinity of the second receiver, and then drifted within detection range. As this scenario is extremely unlikely, we considered the sole alive until the second date systematically.

Because the receivers were removed after four months and the sole began migrating in the summer, the probability of demonstrating the survival of a live sole obviously decreased over time. As a result, it is impossible to confidently identify the entire period over which there was delayed mortality arising from capture and discarding. Two other studies have measured sole survival under similar fishing conditions as the present study, based on captivity experiments (Depestele et al., 2014; van der Reijden et al., 2017). They found that discard mortality occurred within 5 days. With other flatfish, such as plaice, this time frame was 5, 7, 8, 10, or 15 days (Eskelund et al., 2019; Morfin et al., 2017a; Savina et al., 2019; Uhlmann et al., 2016). Consequently, we went with the assumption that delayed mortality is certainly more driven by the species than other external conditions, and we assumed that a period of 10 days was reasonably sufficient.

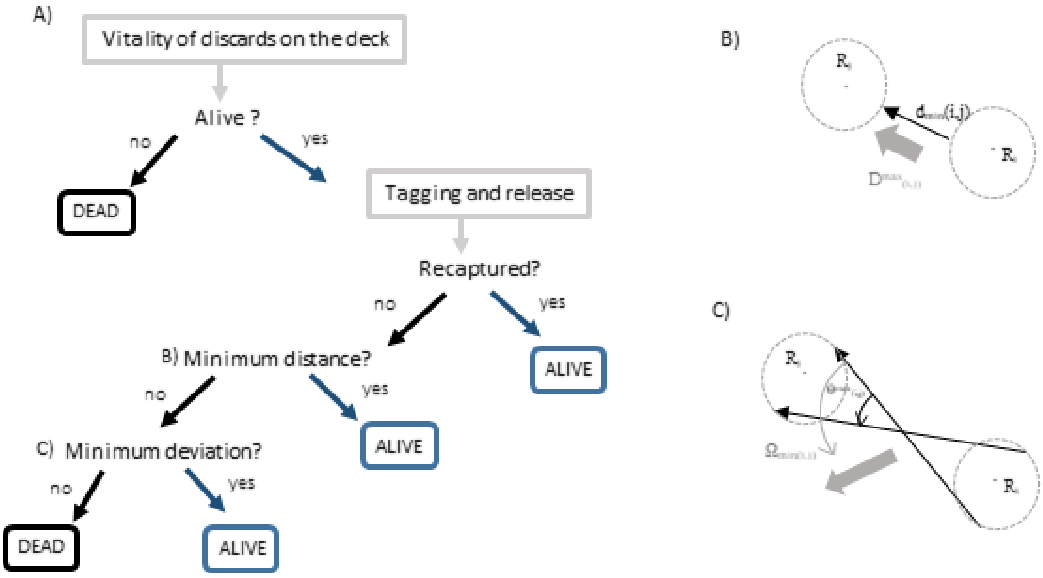

Figure 2: A) Flow chart describing the decision criteria used to classify a sole as alive or dead (based on Morfin et al., 2019b). B) Illustration of the distance-based survival criterion. C) Illustration of the direction-based survival criterion. R_i and R_j are two different receivers, and the grey circles around them are their detection ranges. $dmin(i,j)$ is the minimum distance between the two detection ranges and $\theta_{max}(i,j)$ is the maximum deviation between two locations within both detection ranges. $D_{max}(i,j)$ is the maximum current speed occurring between detections events at R_i and R_j. $\Omega_{min}(i,j)$ is the minimum deviation between currents directions and extreme points within the receivers' detection ranges.

2.2.2. Methodological validity

To validate the above approach, we estimated how well individuals were correctly classified as alive (true positive/sensitivity) or dead (true negative/specificity) using the trajectory-based criteria. Sensitivity was estimated using the alive fish that were recaptured at least 10 days after release: we counted how many of these soles were classified as alive for at least 10 days using only the trajectory-based criteria. Specificity was estimated the using the data for the eight 'dead controls fish' released within the range of receivers.

2.3. Measuring survivorship with physiological indicators

Over the course of five additional fishing operations discarded sole were sampled from each vitality category (excellent/good/poor) (total n = 60). They were immediately placed in separate cages in a tank supplied with running sea water. Using heparinized syringes, we took blood samples from four samples of sole (from 10 to 24 individuals) at different time points over a 90-min period (0, 30, 60, and 90 min). Each sole was sampled only once as the sole were immediately euthanised after their blood has been drawn. Plasma was recovered using centrifugation (10 min at 3000 g) and then frozen at -20°C until the analyses could be performed.

Glucose and lactate levels were assayed using commercial kits (Randox #GL2614 and Randox # LC3980 respectively, Randox, Antrim, UK). Cortisol levels were determined via ELISA (ELISA kit #500360, Cayman Chemicals, Michigan, USA).

2.4. Relationships between minimum survival, vitality, fishing conditions and physiology

2.4.1. Relationship between discard survival, vitality, and fishing conditions

First, we assessed the relationship between the two indicators of discard survivorship — minimum survival at 10 days and vitality — using Kendall's rank correlation coefficient and its associated two-sided test for variable independence.

Then, we analysed the influence of the fishing conditions on each survivorship indicator independently. Among the technical, environmental, and biological conditions that were measured during the experiment, eight displayed enough variability to potentially explain differences in survivorship: tow duration, tow depth, catch weight, presence of injury-inducing elements in the catch, presence of algae in the catch, air temperature, duration of air exposure, and fish length. As suggested by individual relationships observed between both responses and the covariates, all the linear combinations of these variables were assessed as covariates, as well as the interaction between fish length and the air exposure, in multivariate regression models. For minimum survival at 10 days, a binomial model with a logistic link function was used. Since the vitality is measured as an ordinal variable, a proportional-odds cumulative logit model was used (Agresti, 2007; Benoît et al., 2010). To identify the potential multicollinearities, we examined pairwise correlations between all the covariates and looked at the Variance Inflation Factors for the full regression model. As the goal of this analysis was to explain survivorship rather than predict it, we looked at the results for: 1) the full model after removing any covariates causing major multicollinearity issues; 2) the model selected based on the Akaike criterion (AIC). To account for potential additional sources of variability between the catches, fishing operation was tested as a random effect in both of the above models, using the Likelihood Ratio Test. Shapiro-Wilk normality tests were performed using the Randomized quantile residuals (Dunn and Smyth, 1996) and the Surrogate residuals (Liu and Zhang, 2018) to validate the binomial and ordinal regressions, respectively.

2.4.2. Physiological responses and relationship with vitality

Levels of cortisol, glucose, and lactate were analysed independently in relation to vitality and time. At the discarding time (T0), the strength of the association with vitality was measured by the Pearson's r correlation coefficient. Then, a multivariate Gaussian regression was fitted to each blood marker; vitality, time, and their interactions were the independent variables. We ensured residual normality by log-transforming cortisol and lactate levels and square-root-transforming glucose levels. Normality was assessed using the Shapiro-Wilk normality test (W). Vitality was treated as a categorical variable, and time was modelled using a polynomial relationship (until the 3rd order). Finally, fitted candidate models were selected based on AIC values. While a random effect related to the fishing operation would have been interesting to be tested, the sample sizes by time duration and vitality category were too small to fit correctly this additional effect.

3. **RESULTS**

3.1. Estimating discard survivorship

Per haul, 1 to 38 undersized soles were discarded. The total sample was 160 soles, whose body length measured from 14 to 24 cm. Most had excellent vitality (33%) or good vitality (49%); 17% had poor vitality. Only one sole (0.6%) was dead upon arrival on board. Four months later, all the receivers were retrieved (with battery power remaining). For the 159 soles that were alive and thus tagged, we recorded a total of 189,722 detection events. Eleven soles (7%) were recaptured alive after release (within a few hours or up to 68 days later), and 136 soles (86%) were detected at least once by a receiver. Per individual, summed distances between detection events varied from 564 m to 68 km per sole (mean = 13.5 km), and 125 soles (78%) could confidently be assumed to be alive at least one time (1 to 120 days after release) according to the trajectory-based criteria. These results were combined to estimate a minimum survival probability over time (Fig. 3). The abrupt decrease in survivorship at time 0 was due to the fish that were never detected (24%). The curve then levelled off between 5 and 10 days before declining to 0 at a slow, steady rate and reaching 0 at the end of the monitoring period (120 days after release). This final drop to 0 was expected since the probability of detecting tagged sole decreased over time. Overall, 41% ($CI_{95\%}$ = [0.34, 0.49]) of the discarded soles were found to be alive after 10 days.

None of the eight 'dead control soles' remained continuously in receiver range. Two of them were detected once at another receiver, at distances of 482 m and 2.11 km, respectively. However, these detection events in no way met the trajectory-based criteria for categorising the fish as alive. This result means that 100% of the eight controls were correctly assigned a status of dead. Nine soles were recaptured alive at least 10 days after release, and 7 of could be categorised as alive up until 10 days using trajectory-based criteria. This result means there was a true positive rate of 78%. The two other soles could not be classified as alive using trajectory-based criteria because they had not been detected by any receivers after 10 days.

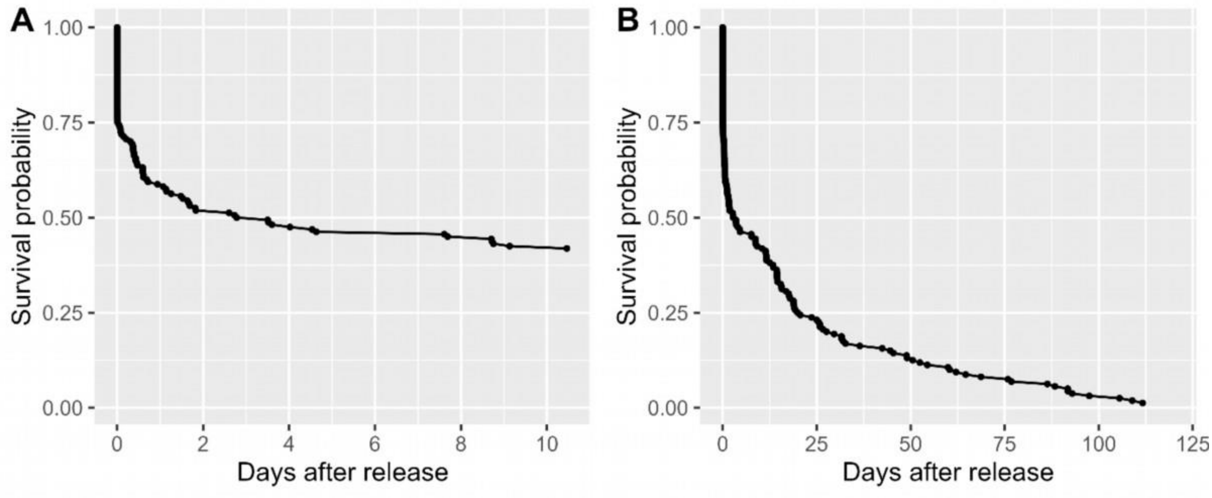

Figure 3: Minimum survival curve A) over the 10 days following release and B) over the whole monitoring period.

3.2. Relationships between survival, vitality, and fishing conditions

A positive, weakly significant relationship was observed between minimum survival at 10 days and vitality: 30%, 41%, and 49% for soles with poor, good, and excellent vitality, respectively (Kendall's rank correlation = 0.13, p-value=0.096). The dynamics of the survival curves for these three categories were generally similar, except that the final decrease in the curves (after the level-off) started earlier for soles in excellent vitality (S3).

The strongest pairwise correlations occurred between fish length and duration of air exposure (Pearson's r = -0.41). Fishing operation did not have a significant influence on either minimum survival at 10 days or vitality (p-value = 1 for both cases), even recognizing that the chi-squared test tends to yield conservative results for GLMMs. Consequently, only the fixed effects were included in the models for the two response variables. In the full models, VIF values were all lower than 5. The highest VIF was associated to the catch weight (VIF = 4.4 associated to the catch weight (VIF =4.4 for the survival model and VIF = 3.7 for the vitality model).

The full model and the model selected by AIC arrived at the same results (i.e., size effects and statistical significance) for survival at 10 days as well as for vitality (Table 2).

Four covariates were retained in the model selected by AIC to explain minimum survival at 10 days. Tow duration and the presence of injury-inducing elements in the catch had negative though not very significant effects (p-values=0.11 and 0.07 respectively). In contrast, the presence of algae in the catch and fish length were positively and significantly associated with survival (Table 2).

Similarly, four covariates were remained in the model selected by AIC for vitality, including three of those mentioned above (Table 2). Notably, tow duration had a negative, slightly more significant effect, while the presence of algae in the catch had a positive, slightly less significant effect. Fish length was also retained, but its effect was negative. The fourth, unshared covariate was the duration of fish air exposure, which had a significant negative effect.

For both responses, fishing conditions had rather low explanatory power (from 7 to 8%).

	Minimum survival at 10 days		Vitality	
	Full model	Best AIC model	Full model	Best AIC model
Tow duration	-0.29	-0.29	-0.29.	-0.29.
Catch weight	-0.04		-0.01	
Tow depth	-0.04		0.05	
Presence of injury-inducing elements	-0.88.	-0.80.	0.01	
Presence of algae	1.39*	0.39***	1.21*	1.19**
Duration of air exposure	0.13		-0.74**	-0.74***
Air temperature	-0.26		-0.05	
Fish length	0.53*	0.18*	-0.58**	-0.60 ***
Duration of air exposure x fish length	-0.12		-0.04	

Table 2: Results of the multivariate regression models for minimum survival at 10 days and vitality. The estimated coefficients for the covariates selected are reported, as are the associated significance degrees: **.**: $p < 0.1$, *: $p < 0.05$, **: $p < 0.01$, ***: $p < 10^{-3}$. A positive/negative value means a positive/negative relationship with survival or vitality.

3.3. Physiological responses and relationship with vitality

At time T0, vitality displayed a significant negative linear relationship with cortisol levels (Pearson's r = -0.69, p-value = 0.003) (Fig. 4). The same was true for lactate levels, except that the relationship was exponential (Pearson's r = -0.63, p-value < 0.001): levels were much higher in the sole with poor vitality (4.8 and 5.5 times higher, respectively). In contrast, all three groups exhibited similar glucose levels (Pearson's r = -0.10, p-value = 0.64) (Fig. 4).

Over the next 90 min in captivity, the selected models indicated that the three markers were associated with vitality, a polynomial of the time, and the vitality-by-time interaction (Fig. 4B).

The group with excellent vitality had much more stable marker levels than did the other two groups, even though the former group did display a significant increase in cortisol (x 2.8) levels over time and in lactate (x 2.2) until 60 min before starting to precipitate (Fig. 4). However, even the highest cortisol plasma level of the group with excellent viability remains close to concentrations of sea bass in a non-stressed status (Servili et al., 2023).

For the group with poor vitality, markers were not measured at all time points (until 30 min for cortisol) and until 60 min for lactate and glucose) because of insufficient blood volumes or lack of fish. Both cortisol and lactate levels significantly decreased over time. Glucose levels has climbed slightly at 30 min (x 1.45) before decreasing at 60 min.

The group in good vitality displayed an intermediate pattern. Its marker levels at time 0 resembled those in the group with excellent vitality, and those 30 min were similar or even higher than the marker levels in poor vitality at time 0. Then, after 60 min, lactate and cortisol levels declined, reaching the same levels that the group with excellent vitality displayed at time 0; and even lower levels for glucose.

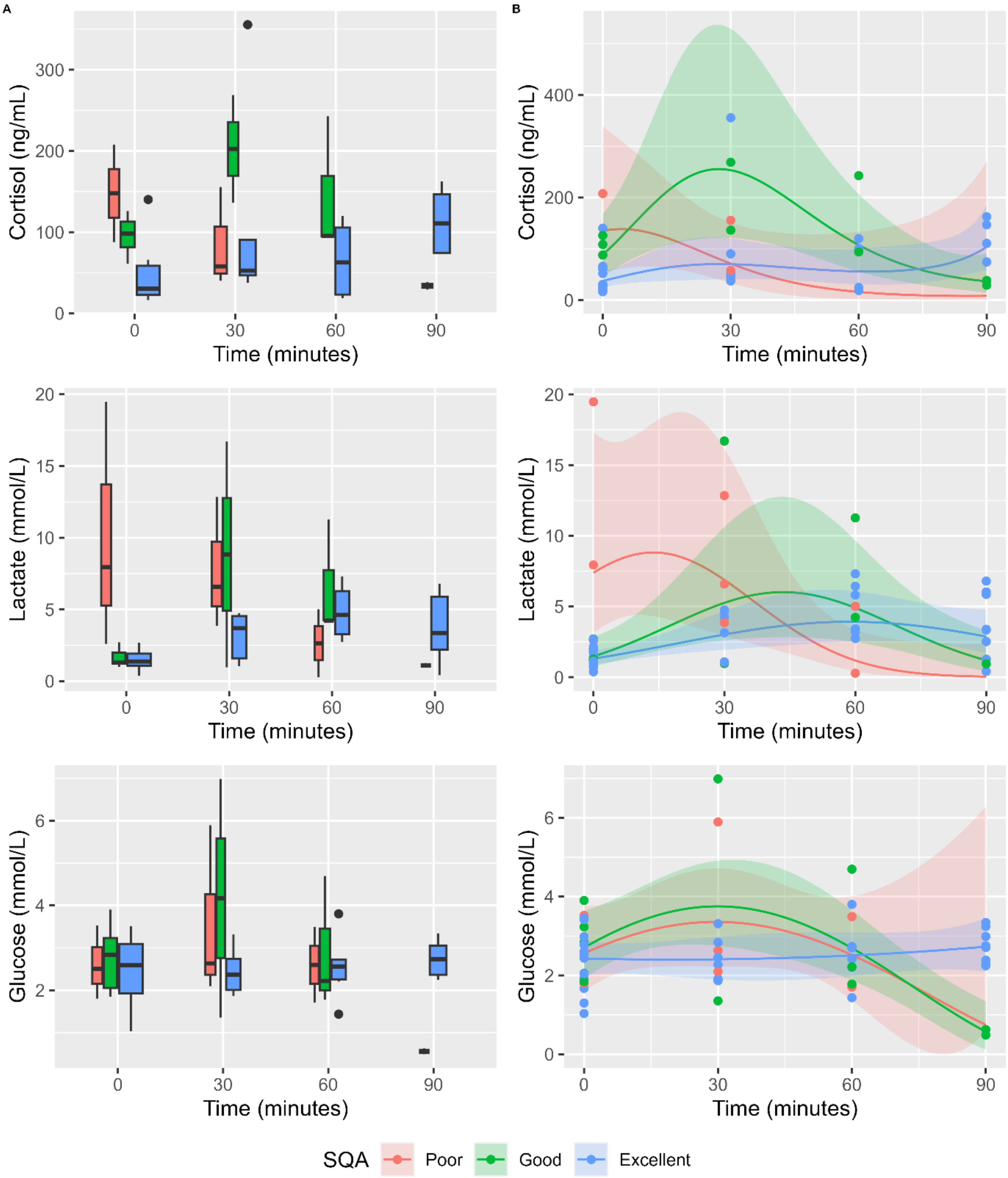

Figure 4. Plasma levels of cortisol, glucose, and lactate for sole in different vitality categories (excellent, good, and poor) over the 90-min recovery period. A): Boxplots of marker levels at each monitoring time. B): Marker values over time predicted by the fitted Gaussian regression models (lines) with their 95% confidence intervals (lighter areas) based on the observed marker levels (points).

4. DISCUSSION

4.1. Estimating discard survival with acoustic telemetry

In this study, we used an adapted methodological framework to infer sole survival based on data from a highly fragmented acoustic telemetry network. To this end, we compared the trajectories recorded with those expected to arise exclusively from drift.

The approach is conservative, resulting in a minimum estimate of the survival. Indeed, the survival rate was estimated at 79% at the time fish were released, because 21% of individuals could not be affirmed to be alive afterwards; however, only a single death (0.7%) was observed. Furthermore, the degree of underestimation is expected to increase over time because the fish will ultimately either left the study area or the tags' batteries lost sufficient charge. This limits our ability to detect a threshold as recommended for discard survival studies (Breen and Catchpole, 2021). Indeed in most survival studies, post-release mortality occurs steadily until it reaches a threshold (Breen and Catchpole, 2021). Thus, the maximum period over which delayed, discard-related mortality may have occurred cannot be inferred from our data. On the one hand, establishing too short an observation period will tend to overestimate discard survival. On the other hand, establishing too long an observation period will tend to underestimate discard survival since chances are limited that the individual will be detected beyond the end. This phenomenon will be all the more pronounced when detection probability is low. Detections probabilities of alive fish are shaped by the degree of overlap between the receiver network coverage and distribution area occupied by the target population, as well as each individual's relative mobility. It was essential to draw upon fisher's to identify the best sites for receivers and the optimal window of time for our research, given the limited lifespan of the emitters. In areas with high levels of fishing activity where the number of potential locations for receivers is limited, it might be possible to obtain finer-scale trajectory-patterns by carrying out intensive tracking efforts using mobile receivers.

We defined our survivorship estimation period by making the assumption that the period for a fish to die from its injuries and stress is mainly driven by the species rather than other fishing conditions. This assumption was supported by past work which has consistently found a window of 5 days for sole (Depestele et al., 2014; van der Reijden et al., 2017), and 5-15 days for flatfish (Eskelund et al., 2019; Morfin et al., 2017a; Savina et al., 2019; Uhlmann et al., 2016). We thus defined a minimum survival at 10 days. That said, between 5 and 10 days, the estimated survival decreased by just 6%, suggesting it was relatively stable over this time period, which confirms the reliability of this approach.

Another source of uncertainty is receiver range, which may vary in space and time because it is influenced by many environmental factors, such as temperature, turbidity, depth, substrate, water flow, and biofouling (Kessel et al., 2014; Mathies et al., 2014). In this study, said conditions were likely similar across the entire experiment period. An additional source of uncertainty is that acoustic tags may emit signals from a fish's stomach if the original fish is preyed upon. A past study conducted in the same bay found that the species with the highest frequency of soles occurrence in their stomach contents were sea urchins, shrimps and crabs (Lejeune et al., 2021). If these scavengers would have eaten dead sole they would have left the tag undamaged.

To validate the ability of acoustic telemetry to reliably estimate discard survival, we looked at the method sensitivity, using tagged dead soles, as well as method specificity, using recaptured soles. Sensitivity was 100% and specificity was 78%, results that are consistent with our conservative criteria, and the mid-range survival estimates for fish with excellent vitality (49%). Correcting for possible misclassifications, this survival rate would rise to 63%. It is important to acknowledge that these metrics were based on very small samples. Directly placing the dead control fish within the range of receivers optimised the detection events; it is only possible to do so with a limited number of fish as greater numbers per receiver would increase the collision rate among tagged individuals, which is undesired when characterizing detection probabilities.

Using acoustic telemetry, we estimated that minimum sole survival at 10 days was 41%. While other studies have found survival rates between 10% and 69% for discarded sole, most have lacked controls for measuring captivity-induced mortality (Depestele et al., 2014; Masnadi et al., 2020; Revill et al., 2013; Van Beek et al., 1990; van der Reijden et al., 2017). The only one to do so estimated that the survival rate was 29% for sole discarded after a pulse trawling (van der Reijden et al., 2017). This level is consistent with what we found, given that the survival rate for plaice was only 15% in this same study, while other research focused on otter trawling discovered that plaice survival varied from 44% to 89% (Methling et al., 2017; Morfin et al., 2017a; Noack et al., 2020). Furthermore, two studies conducted under fishing conditions similar to ours found that sole better tolerate hypoxia and have higher vitality than do plaice (Morfin et al., 2019a, 2017b).

4.2. Predicting discard survival using vitality

Vitality was used to predict discard survival. There was a positive, but weakly significant relationship between vitality and minimum survival at 10 days. It may be that the current-based criteria used to infer sole survival were somewhat unreliable. The false negative rate of 22% resulted from the fact that some living fish were not classified as alive, owing to the low degree of spatial coverage of the receivers that has limited the number of detection events, while this phenomenon is potentially dependent on fish vitality. Indeed, fish with different levels of vitality differed in their survival curves: starting at 15 days, the group with excellent vitality displayed a steeper decline than did the other groups (S3). Sole tend to migrate towards the coast and thus outside of the receiver range. Consequently, it could be that impaired individuals spent more time in the study area because they were recovering, which could have improved their chances of being detected compared. Support to this hypothesis comes from prior research on the same excellent category that found survival rates of 57% for sole in the Mediterranean Sea (Masnadi et al., 2020) and of 90% for plaice in the Eastern Channel (Morfin et al., 2017a), both much higher than the survival rate in this study for sole in excellent vitality.

It could also be that vitality was a poor proxy for sole survival. Indeed, the SQA metric abstracts from a continuous spectrum of possible stress responses and injury levels. Though the same observers scored the fish in this experiment to prevent from the subjectivity of this kind of index, some 'scaling-effect' can also occur between fishing operations (i.e., fish from the same catch may tend to be overrated if all the discarded fish from this given were in bad conditions). Furthermore, the fish movements can be influenced by environmental conditions onboard and fish length.

We analysed the response of both minimum survival and vitality to the fishing conditions to identify influential factors in discard survival, but also to assess the consistency of the effects between these two proxy of discard survival. Two emerged as consistently relevant: tow duration and the presence of algae in the catch. Past research has already underscored the negative correlation between survival or vitality of flatfish, and tow duration as a proxy of the experienced stress during the catch (Morfin et al., 2019a; Van Beek et al., 1990). However, our work is the first to report a positive effect of the presence of algae. It is possible that the algae helped prevent injuries and favoured vitality by limiting crushing and abrasion. The presence of injury-inducing elements in the catch was negatively associated with minimum survival at 10 days, while the duration of air exposure was negatively associated with vitality. These effects have been seen in previous studies, especially that of air exposure (Breen et al., 2020; Cook, 2019). The latter stressor may be exacerbated by simultaneous exposure to direct sunlight, which can lead to overheating and rapid dehydration.

The association of fish length with the minimum survival at 10 days and vitality was significant but inconsistent in its sign: a positive association with survival and a negative association with vitality. It may be that larger soles tend to move less than smaller ones for the same level of vitality, which would limit the utility of the vitality index for sole. At the same time, smaller soles could be less mobile, decreasing their likelihood of being detected. Past research has found evidence of both relationships. For example, the positive association between fish length and survival has been attributed to smaller fish experiencing greater swimming-related fatigue during capture and, because of their lesser mass, a greater susceptibility to injuries (e.g., due to crushing, or abrasion) (Broadhurst et al., 2006; Depestele et al., 2014; Revill et al., 2013; Uhlmann et al., 2016). The negative relationship between fish length and vitality has also been reported elsewhere (Methling et al., 2017; Morfin et al., 2019a, 2017b). It has been attributed to a) larger fish having greater anaerobic energy expenditure and post-exercise metabolic disturbances and to b) smaller fish recovering more quickly recovery after air exposure, given the allometric scaling of the cardiovascular system, including larger relative gill surface areas (Hughes, 1984; Kieffer, 2000). Another possible explanation for this negative relationship could be that smaller fish were captured later because of their higher escape rate at the start of the tow. Indeed, as the codend fills up, the pressure of the catch stretches the mesh, which may allow early caught fish to escape.

That said, fishing conditions (i.e., tow duration, fish length, duration of air exposure, the presence of algae and injury-inducing elements in the catch) explain only a small part of the variance in both minimum survival at 10 days and vitality. This finding fits with the fact that conditions in the study fishery varied little. Given that there was no significant effect of the fishing operation, fish survival might have been mostly influenced by unmeasured factors related to individual fish, such as when fish entered the net (beginning/end of the tow) and proximity within the catch to injury-inducing elements.

Together, these results suggest that the weak significance of the relationship between minimum survival at 10 days and vitality could be driven more by a detection bias for higher-vitality fish rather than by vitality having poor predictive ability. These results also suggest that fishing conditions could be used as a proxy for survival once their relationship with survival or vitality has been established, but only at the scale of the fishing operation (Benoît et al., 2010). Although predictive performance should be assessed for broader ranges of conditions, such as among trips, vessels, and seasons, this approach could prove valuable for predicting delayed discard mortality and could allow a better stock assessment when such mortality is high (Cook, 2019).

4.3. Sole physiological status

To assess fish physiology and recovery potential in captured sole, three blood parameters were measured at the time fish would have been discarded and over a 90-min period. We examined the relationship between these three markers and the survivorship for soles displaying excellent, good, and poor vitality. At time 0, the three groups clearly differed in their cortisol and lactate levels, which were negatively correlated to vitality. The groups generally displayed similar patterns of cortisol, lactate, and glucose over time, which aligns with the literature, where levels have been found to peak 1-2 hours after the onset of stress (Costas et al., 2011; Methling et al., 2017; Mommsen et al., 1999; Wendelaar Bonga, 1997). In our study, these peaks did not occur at the same time for the different groups: they were observed at 30 and 60 min for fish with good and excellent vitality, respectively, while a decrease was seen in fish with poor vitality. This result suggests that fish with different vitality levels did not experience the stress of capture at the same time, which could mean that vitality primarily reflected fish's capture duration. Based on this assumption, fish with excellent vitality were the last to be caught. A past study on wild coho salmon arrived at a similar conclusion (Raby et al., 2012): fish's cortisol and lactate levels climbed higher the longer it remains in the fishing gear. It was further suggested that these high levels of cortisol and lactate signalled hypoxia-related muscle exhaustion, which would naturally result in lower vitality.

In this study, we observed a drop in cortisol and lactate levels for the sole over time, suggesting recovery was occurring. However, we did not obtain data for the poor vitality group at 90 min, which prevents us from knowing whether these fish were moving towards or away from homeostasis. In the latter case, a complete recovery would be less probable. It should also be noted that fish with excellent vitality displayed the lowest levels for all three markers during the recovery period. Nonetheless, these soles appear to have experienced some stress, given the group's relative increase in cortisol and glucose levels at 90 min, which could be due to the captivity. Indeed, the increase in glucose in parallel to cortisol would suggest a typical secondary stress response, as it has been observed in other fish species (Arends et al., 1999; Vijayan et al., 1994). This finding could call into question the practice of keeping discards onboard tanks, especially in the case of fish with good and excellent vitality. In contrast, this practice could benefit individuals with poor vitality because they would be safe from predators as they recovered (Cook et al., 2019). Furthermore, focusing exclusively on this group of fish would lowered the required tank volumes, which can be prohibitively large for small vessels.

Conclusion

In this study, the minimum survival rate of discarded sole was estimated to be 41%. This estimate was based on data collected under commercial fishing conditions representative of those for French coastal bottom trawling fleet targeting demersal fish. We relied on acoustic telemetry tagging, which allowed us to quantify sole survival in their natural environment. Survival displayed a positive, weakly significant correlation with fish vitality, which was semi-quantitatively scored while the fish were onboard. Some fishing conditions had significant effect on survival and vitality. The inconsistencies we observed in these relationships are likely due to an underestimation of the survival rate. In addition, we measured three plasma markers of fish physiological status over a 90-min recovery period. These markers indicated that the soles were experiencing varying levels of stress and fatigue. They also suggested that discarded sole have a capacity for recovery. Individuals with excellent vitality (33% of soles in this study) appeared to suffer less stress and fatigue. They were therefore more likely to be able to cope with to other stressors, compared to individuals with lower vitality. Taken together, our findings highlight the potential utility of vitality in predicting discard survival and validate the acoustic telemetry results obtained with our survival inference method.

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RANGE TEST

In addition to the characteristics of both receivers and tags, the probability that a ping is correctly detected by a receiver also depends on environmental conditions such as depth, noise, current speed (Huveneers et al., 2016). Though receivers were located in similar environmental conditions, an experiment was conducted on three out of the fourteen receivers to account for potential inter sites variability.

A sentinel tag emitting every 10 seconds was successively set on the seafloor for at least 5 minutes at different distances from the receivers from 50 m to 1000 m. The setting period was defined to obtain at least 30 pings by distance.

For each transmission, detection success or failure was modelled by a Bernoulli law Y whose probability $p(D)$ is a logistic function of the transmission distance to the receiver (D). Using Bayes' theorem (1) and the relationship between marginal and conditional laws (2), the random law of the distance D at which an individual is located when it is detected by a receiver can be defined (3). This result is based on the assumption that an individual has the same chance to be located at any distance from a receiver, and thus that its distribution law $[D]$ is a constant, c.

$$[D|Y=1] \times [Y=1] = [D] \times [Y=1|D] = c \times p(D) \tag{1}$$

$$[Y=1] = \int_D [Y=1, D]dD = \int_D [D] \times [Y=1|D]dD = c\int_D p(D)dD \tag{2}$$

$$[D|Y=1] = \frac{p(D)}{\int_D p(D)dD} \tag{3}$$

From this distribution estimated by simulation, the mean distance between the receiver and a detected individual (D_{mean}), as well as the quantile at 0.99 of the detection distance (D_{max}) were calculated.

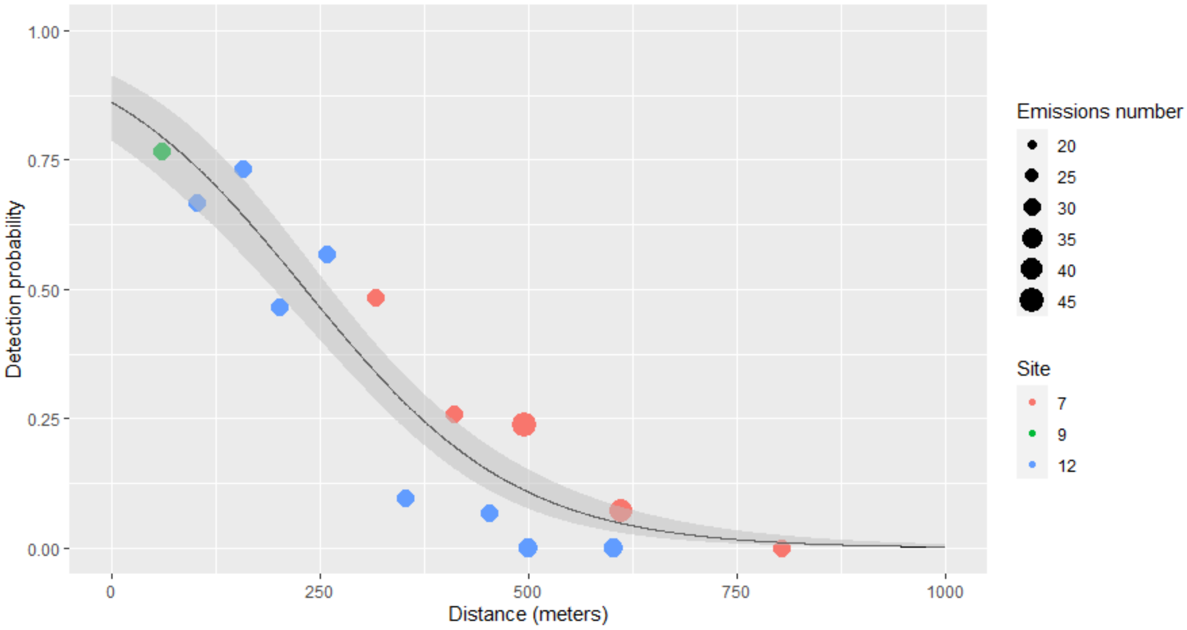

Figure S1-1: Results of the Range Test experiment. Probability of detection depending on the sentinel tag's distance in meters to the receiver. Coloured points are observed proportions and their size is proportional to the number of pings/emissions. Black line is the predicted probability by the fitted logistical model, and grey area is the corresponding 95%-confidence interval.

The fitted logistic model of the detection probability depending on the distance between the tag and the receiver was validated. Just next to the receiver, the probability is 0.80. Then, the decrease of the probability increases until an inflexion point at 69 m, then the probability declines to probabilities lower than 0.01 from D_{max} = 814 m. Finally, the mean distance of a random detection is estimated at D_{mean} = 202.8 m.

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Supplementary Material 2: Drifting speed of a dead sole

An experiment was conducted in a flume tank (Vincent et al., 2018) to measure the drift speed of a dead sole at height current speeds, from 0 to 0.7 m/s. The range of current speed was chosen to cover the range of the bottom current speeds in the study area. As the speed in the flume tank is not expected to be homogeneous in the entire tank owing to friction effects, especially on the floor, a speed sensor was located just next to the sole to measure the real speed. The speed of the sole was measured by the ratio between the total observed distance and the measured time.

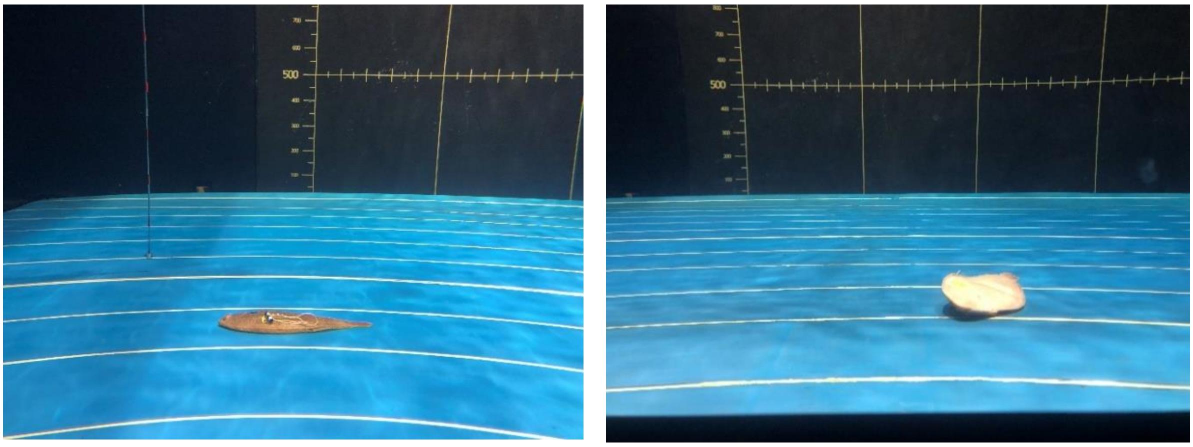

Figure S2-1: Pictures of the experiment in the flume tank.

For each speed, the experiment was replicated four times to measure the effect of different orientations of the sole in the current. Each replicate lasted for 30 seconds if the sole did not move at all, or until the sole crossed the entire tank (2 meters).

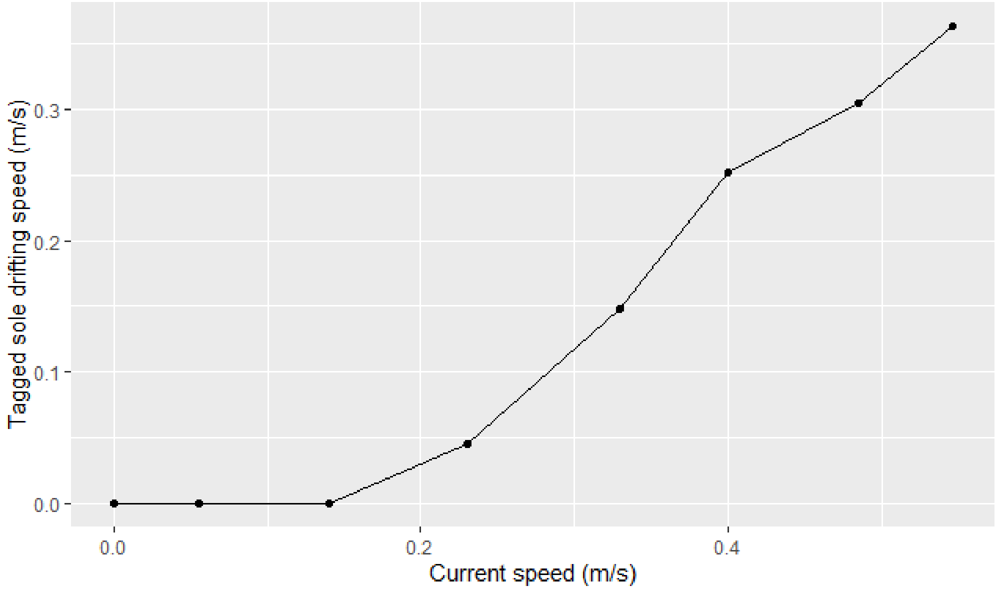

Figure S2-2: Speed of a drifting dead and tagged sole as a function of the water current speed.

Supplementary Material 3: Minimum survival curve depending on vitality

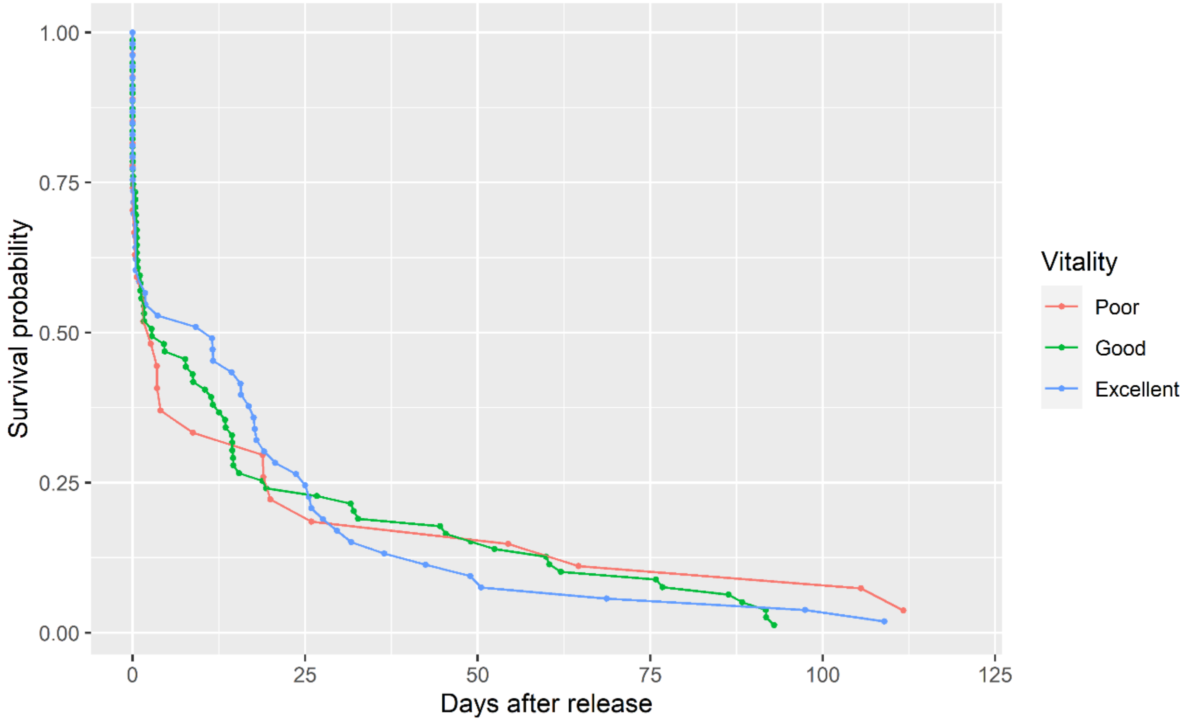

Figure S3: Minimum survival curve depending on vitality over the monitoring period (120 days).