Marine Policy
March 2017, Volume 77 Pages 23-29
http://dx.doi.org/10.1016/j.marpol.2016.12.003
http://archimer.ifremer.fr/doc/00362/47281/

Narrowing down the number of species requiring detailed study as candidates for the EU Common Fisheries Policy discard ban

Morfin Marie [1, *], Méhault Sonia [1], Benoît Hugues P. [2], Kopp Dorothée [1]

[1] IFREMER, Unité de Sciences et Technologies halieutiques, Laboratoire de Technologie et Biologie Halieutique, 8 rue François Toullec, F-56325 Lorient Cedex, France
[2] Gulf Fisheries Centre, Fisheries and Oceans Canada, Moncton, NB, Canada, E1C 9B6

* Corresponding author : Marie Morfin, email address : marie.morfin@ifremer.fr

Abstract :

By 2019, the Common Fisheries Policy will prohibit discarding in all European fisheries of any pelagic, demersal or shellfish species for which removals are managed by TACs and quotas or minimum sizes. However, the regulation allows for exemptions from the prohibition for species for which scientific evidence demonstrates high survival rates associated with discarding. Producing reliable evidence of high survival typically requires long and costly studies involving tagging or captivity. This paper proposes to use the capacity to resist air exposure, a key stressor for discarded animals, as a proxy for survival that can be used to prioritize candidate species for more in-depth discard survival studies. The time required to induce mortality (TM) in air-exposed fish was estimated for ten discarded species under commercial fishing conditions for two artisanal French otter trawlers in the Bay of Biscay and in the English Channel. European seabass, plaice, sole and skates had extended TM values on average, suggesting that these species are good candidates. The three species observed in both regions (plaice, sole and skates) had larger TM values in the English Channel experiment compared to the Bay of Biscay experiment. Among the four measured external conditions that could influence TM (air temperature, fish length, tow depth and tow duration), the air temperature was the most important and the factor that most distinguished the two experiments.

Highlights

► Discard survival was investigated in small-scale bottom trawl fisheries. ► Mortality due to air exposure was used as a proxy of discard survival potential. ► Air exposure mortality was higher in the Bay of Biscay than in the English Channel for three common species. ► High survival potential was demonstrated for sole, plaice, seabass and skates.

Keywords : Landing obligation, Discard mortality, Hypoxia, Artisanal bottom trawl fishery, Bay of Biscay, English Channel

1. INTRODUCTION

The discards from commercial fisheries are of particular concern as they can represent a substantial part of the catch. Though the long-term consequences on populations and ecosystems are not well-understood [1], fisheries management policies recommend their reduction [2]. Several approaches are already being used to decrease discards rates such as gear modifications [3,4], area closures [5], acoustic and optical detection [6] and local discard bans [7]. The European Union recently modified its Common Fisheries Policy (CFP) and has enacted a landing obligation under which discarding of species under quota management will be prohibited (Official Journal of the European Union, December 28th 2013). However, the regulation acknowledges that there may be net benefits to conservation of allowing discarding in certain instances where there is strong potential for successful live release. Specifically, article 15 paragraph 4(b) of the regulation allows for the possibility of 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". While no threshold has been defined for a "high survival rate", exemptions will be allowed for species and fisheries with the highest discard survival probabilities.

Capture in trawls is known to be highly stressful for fish, involving injury by abrasion and crushing, scale loss and exhaustion by sustained swimming [8], with severity depending on the gear type and how it is fished (e.g. haul duration, towing speed) [9,10]. When the trawl is hauled back, overcrowding of fish in the net, along with changes in environmental conditions such as pressure, salinity and temperature may induce additional stress and injuries [8,11–13]. As a result, many individuals may be already dead upon arrival on deck. For those that survive the catching process, air exposure during catch handling is amongst the strongest stressors contributing to mortality [9,14–16]. Temperature and light conditions have also been found to influence survival [17,18]. Among fish that are still alive when thrown back to the sea, weakened individuals are at greater risk of avian and marine predation [19].

Depending on fishing conditions, species [20] and body size [14,17], individuals may withstand stress and injury very differently [21], resulting in variable post-release survival of discards. The Expert Working Group 13-16 (EWG13-16) from the Scientific, Technical and Economic Committee for Fisheries (STECF, 2013) established a general methodology to accurately estimate the survival rate and identify the associated external factors, based on captive observation [4,21], vitality and reflex assessments [22–24] and tagging or biotelemetry experiments [25,26]. These methods typically require experiments that can be of long duration, cost-prohibitive or unfeasible for areas where discard composition may be very diversified [27,28]. Thus there is a need for methods for prioritizing cases where high discard survival is likely and where further study can be targeted. Several studies have shown that air exposure is one of the greatest contributors to discard mortality within and among species [14,15,29,30], particularly in trawl fisheries where fish can spend considerable time on deck. Differences in resistance to hypoxia among species and sizes of fish have been shown to be good proxies of discard mortality rates for trawl caught individuals [14]. The time required to induce mortality (TM) in air-exposed fish is therefore a simple metric that can be used to identify candidates for a possible landings obligation exemption.

This study analyzed the TM for a number of discarded fish species from the French artisanal otter trawl fishery. Selected species were those that constituted a large part of the discards in these fisheries [28] and represent a diversity of taxonomic orders (Gadiformes, Perciformes, Pleuronectiformes, Rajiformes and Scorpaeniformes). The association of TM with four external factors (tow depth, tow duration, air temperature and fish length) that have been shown to affect discard survival (reviews in [8,31]) was also investigated in order to identify factors potentially influencing discard mortality in the French fisheries.

2. MATERIAL AND METHODS

2.1 At-sea experiments

Fish mortality following capture and air exposure

A first trial was held in the Bay of Biscay (BB; East Atlantic, ICES subarea VIIIa) in June 2014 onboard a 10.3 m long trawler and a second trial was held in July 2015 in the eastern English Channel (EC; ICES subarea VIId) onboard a 10.95 m long trawler (Figure 1). Both commercial vessels were rigged with a single bottom trawl, which is commonly used to target multispecies fish assemblages. The codend mesh sizes were 70 mm in the BB and 80 mm in the EC, and the headline lengths were 20 m and 17.5 m respectively. The crew aboard each vessel was asked to maintain usual on-board handling practices in order to obtain samples that were representative of normal commercial fishing conditions. The same observers participated in commercial fishing trips aboard these vessels prior to and during the experimental trips and confirmed that there were indeed no changes in fishing or catch handling practices. Furthermore, the protocol for the study is not expected to induce any change practices.

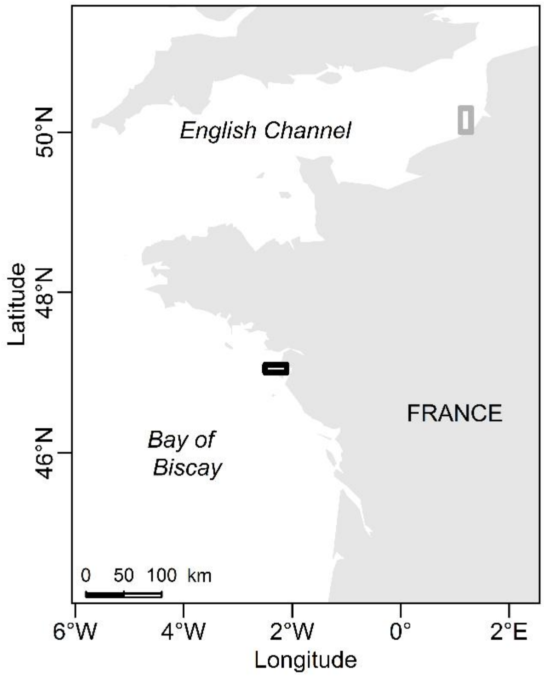

Figure 1: **Study areas**

Map of the two study regions along the French coast, in the Bay of Biscay and in the Eastern Channel. Hauls were located in the in shaded lines rectangles.

Eight hauls were performed in the EC and fourteen in the BB. For both sea trials, experiments were conducted by the same two experienced on-board observers. Discarded fish were obtained during catch sorting by the harvesters. In both trials the sorting time varied from 10 to 50 min, with a mean duration of 30 min, which is representative of practices in the commercial fishery. The time elapsed between the arrival of the catch on the deck and the first observation times varied between 5 and 49 min. Subsequently each individual was monitored regularly at least every five minutes for body and operculum movements. Unresponsive individuals were manipulated to try to elicit a response, failing which they were placed in seawater to determine if ventilation would resume. Fish that failed to ventilate were considered dead, and the duration of their period of air exposure (i.e. their TM) was recorded, as was their total length (cm). Fish that resumed ventilation were kept out of water for further monitoring.

Data on TM for ten species or groups of species were analyzed: European seabass (*Dicentrarchus labrax*), European hake (*Merluccius merluccius*), whiting (*Merlangius merlangus*), horse mackerel (*Trachurus trachurus*), black seabream (*Spondyliosoma cantharus)* in the BB; gurnard (Triglidae family) and pouting (*Trisopterus luscus*) in the EC; and plaice (*Pleuronectes platessa*), skates (Rajidae family) and common sole (*Solea solea*) in both areas.

The exact time of death was unknown for 42% of individuals (from 6% for skates in the EC to 100% of hake in the BB) that were dead when first observed. The TM for these individuals is referred to as "interval-censored" in that their time of death is known only to have occurred between the start of the haul and the first observation. Furthermore, two skates and seven plaice in the EC were still alive when the sea trip ended. The TM for these individuals is termed "right-censored" in that their time of death is known only to have occurred after the last monitoring observation.

Table 1: Mean and range for environmental variables measured across hauls and fish lengths across species for each region.

		Censoring			Covariates			
	Haul	None	Left	Right	Depth (m)	Tow duration (min.)	Air temperature (°C)	Fish length (cm)
Bay of Biscay								
Plaice	8	18	9	0	9 [4-25]	113 [99-130]	20 [16-25]	23 [16 - 35]
Skates	6	15	3	0	14 [4-25]	120 [99-130]	18 [16-25]	40 [24 - 60]
Sole	11	20	2	0	12 [4-26]	117 [99-130]	22 [16-25]	21 [15 - 37]
European seabass	12	44	8	0	9 [4-25]	115 [99-130]	22 [16-25]	31 [21 - 39]
Hake	12	0	48	0	10 [4-26]	120 [100-130]	22 [16-24]	27 [22 - 45]
Whiting	7	14	16	0	13 [4-17]	120 [100-130]	21 [16-23]	25 [20 - 30]
Horse mackerel	6	8	8	0	17 [13-26]	120 [120-124]	19 [17-22]	20 [15 - 33]
Black seabream	8	11	8	0	14 [8-26]	122 [99-129]	22 [19-25]	27 [19 - 37]
English Channel								
Plaice	6	39	1	7	20 [17-28]	99 [56-122]	16 [15-18]	24 [17 - 29]
Skates	5	32	1	2	24 [17-28]	99 [72-122]	17 [15-18]	34 [20 - 50]
Sole	7	21	0	0	20 [17-28]	101 [72-122]	16 [15-18]	20 [17 - 26]

Gurnard	5	4	15	0	22 [17-28]	86 [72-122]	16 [16-17]	24 [18 - 29]
Pouting	2	10	2	0	20 [17-22]	114 [105-122]	17 [15-18]	21 [18 - 24]

Environmental, biological and technical covariates

For each haul, a series of potential explanatory variables likely to influence survival were recorded. These included biological (total fish length in cm), environmental (ambient air temperature) and fishing operation factors (tow duration and mean tow depth) (Table 1). The towing speed was maintained at 3 knots (+/- 0.5) in both trials and the tow durations varied from 56 to 130 min, at depths varying from 4 to 26 m (see Table 1 for more details). Collinearity amongst covariates is often unavoidable in discard mortality studies undertaken under commercial fishing conditions. Redundant covariates that were highly correlated with other covariates were not included in the analysis. Other retained covariates were associated with moderate levels of collinearity: the deepest hauls were associated with cooler air temperature, longer tows and longer fish in the BB experiment, and with shorter tows in the EC experiment. For both the highly and moderately collinear variables, associations with TM are interpreted in light of the confounding amongst explanatory variables. Details on the variation and covariation of these variables for each species are presented in the Supplementary Material (Figures S1.a-b).

2.2. Analysis

Time to Mortality

TM was studied for each species and region separately. The TM observed between individuals of the same species was considered as a random variable in the analyses. A widespread and useful way to describe this continuous variable is to estimate its survival function, i.e. the probability that an individual is alive as a function of time. Following the approach of Benoît et al. [15], parametric survival analysis models that can accommodate both interval and right censored observations were fitted to the TM data. Such models assume that the probability to die in the censored period follows the same probability distribution as in the observed period. As the death during the haul is a different process from the death due to air exposure, this assumption does not stand. Benoît et al. [15] proposed a model where the probability to die during the haul was accounted independently by a supplementary unknown parameter. Giving the sample size available in this study and the fact that except for hake only a few individuals were apparently already dead at their arrival on the deck in these trials, this model did not improve substantially the model fit compared to a model assuming that death occurred after the arrival on the deck. All individuals were assumed alive at their arrival on the deck and to die as a result of air exposure, thus the function takes the value one at time zero and decreases to zero after sufficient time has elapsed and all individuals have died.

The Weibull distribution was used as the basis for the models as it is consistent with observed empirical patterns. Under this hypothesis, the survival function *S* which depends on the time *t* has the following form:

$$S(t) = P(TM \leq t) = e^{-(\alpha t)^{\gamma}}$$

where *TM* is the time of death, and α>0 and γ >0 are respectively the scale and shape parameters of the curve. Note that the special case where γ=1 is an exponential distribution, meaning that the mortality hazard function, i.e. the probability of an individual dying at time *t+dt* conditional on it being alive at time *t*, is constant on time spent on the deck. This formula implies a linear relationship between the quantities $\ln(-\ln\big(S(t)\big)$ and $\ln(t)$. Plotting these two quantities using the non-parametric Kaplan-Meier estimates $\hat{S}(t)$ allowed *a priori* confirmation of the validity of the Weibull assumption (Figure S2.a).

Associations with environmental, technical and biological conditions

To study the potential impact of external conditions, covariates were introduced as a linear combination related to the scale parameter α as follow:

$$\ln(\propto) = X\beta$$

Where *X* is the matrix of covariates and β the parameters vector. In this form the model is a proportional hazards model, i.e. the effect of covariates on the hazard function is constant over time. As a result the relationship between $\ln(-\ln\left(\hat{S}(t)\right)$ and $\ln(t)$ for different covariates modalities/values should have the same slope if the assumptions are met (Figure S2.b).

For each species in each region Weibull and exponential distributions were tested with all the possible linear combinations of the four covariates, for a total of 16 models. For the species observed in both regions, models were also fitted to combined datasets, to increase sample size, test the consistency of covariate effects between experiments and to examine whether there are differences in survival between the experiments that were unaccounted for by the other covariates. An effect of “region” was therefore also tested to account for any effect that was not measured in the experiments, which could include vessel specific fishing and catch handling practices and other unquantified environmental conditions. For this study 32 candidate models were thus tested. The models were fit using package “survival” implemented in the R software [32].

The Akaike Information Criterion corrected AICc for small samples was used to evaluate relative model suitability and to rank the models, and is defined as *AICc= 2k-2log(L)+2k(k+1)/(n-k-1),* where *k* is the number of parameters and *L* is the maximum value of the likelihood function for the model [33].

For a given candidate model *k*, a Δ-AICc value Δ_k was calculated as:

$$\Delta_k = AICc_k - AICc_{min}$$

where AIC_{min} is the value for the model with the lowest AICc.

Models with $\Delta_k<2$ can be interpreted as having similar support in the data, while larger values suggest less support for the competing model . As very few models had a low Δ_k, and those that did resulted in similar survival predictions, only the model with the lowest AICc is presented. The fit of the selected models were considered suitable given that their predicted values fell within the 95%-confidence intervals of the estimated Kaplan-Meier survival curves, which are non-parametric estimates of survival probability as a function of time (Figure S3.a).

The Δ_k quantity was also used to calculate a relative weight (w_k) for each candidate model:

$$w_k = \frac{e^{-0.5\Delta_k}}{\sum_{l=1}^{K} e^{-0.5\Delta_l}}$$

The relative importance of each covariate (termed evidence weight, ranging from 0 to 1) was then measured as the sum of these weights for the models in which the covariate was present [34]. This weight takes into account model uncertainty; a value close to one means that the covariate is present only among the best models according to AICc. The time at which 50% and 95% of individuals died (TM_{50} and TM_{95}) were used to describe the survival curves and to compare the differences in survival potential between species or regional experiments. Only the covariates for which the evidence weight was greater than 0.75 and the TM_{50} greater than the minimum sorting time (15 min) are interpreted in the Results. Confidence intervals were estimated from 5,000 non-parametric bootstrap samples of the observed dataset [35,36].

4. RESULTS

4.1. Time to Mortality

For all species except hake, the estimated shape parameter $\hat{\gamma}$ was systematically greater than one (Table 2), meaning that the mortality hazard risk increased with time spent on the deck.

Survival functions varied significantly among the ten species analyzed in both regional experiments (Figure 2). In the BB experiment, TM_{50} ranged from 0 min for hake to 54.1 min for sole (Table 2). For hake, whiting, horse mackerel and black seabream TM_{50} and TM_{95} were at or below 13 and 41 min respectively (Table 2). The exponential model form with zero mean for hake was expected as all the individuals were already dead at their first time of observation, resulting in an instantaneously decreasing survival function (Figure 2). Plaice, followed by European seabass, skates and sole survived much longer. Values for TM_{50} and TM_{95} ranged respectively from 33 and 62 min for plaice to 63 and 211 min for skates. This last result indicates more variability in TM among skates than other species, with a strong capacity to resist hypoxia in some individuals. In the EC experiment, gurnard and pouting died almost instantaneously on the deck after being removed from the water (TM_{50}=4 min and 6 min respectively), while the estimated TM for plaice, sole and skates were much longer. Values for TM_{50} ranged from 55 min for plaice to 97 min for sole, while TM_{95} ranged from 207 min for sole to 281 min for skates.

Sole, skates and plaice had extended TM values in both sets of experiments, though estimated means were approximately twice as long in the EC experiment compared to the BB experiment for all three species (Table 2, Figure 2).

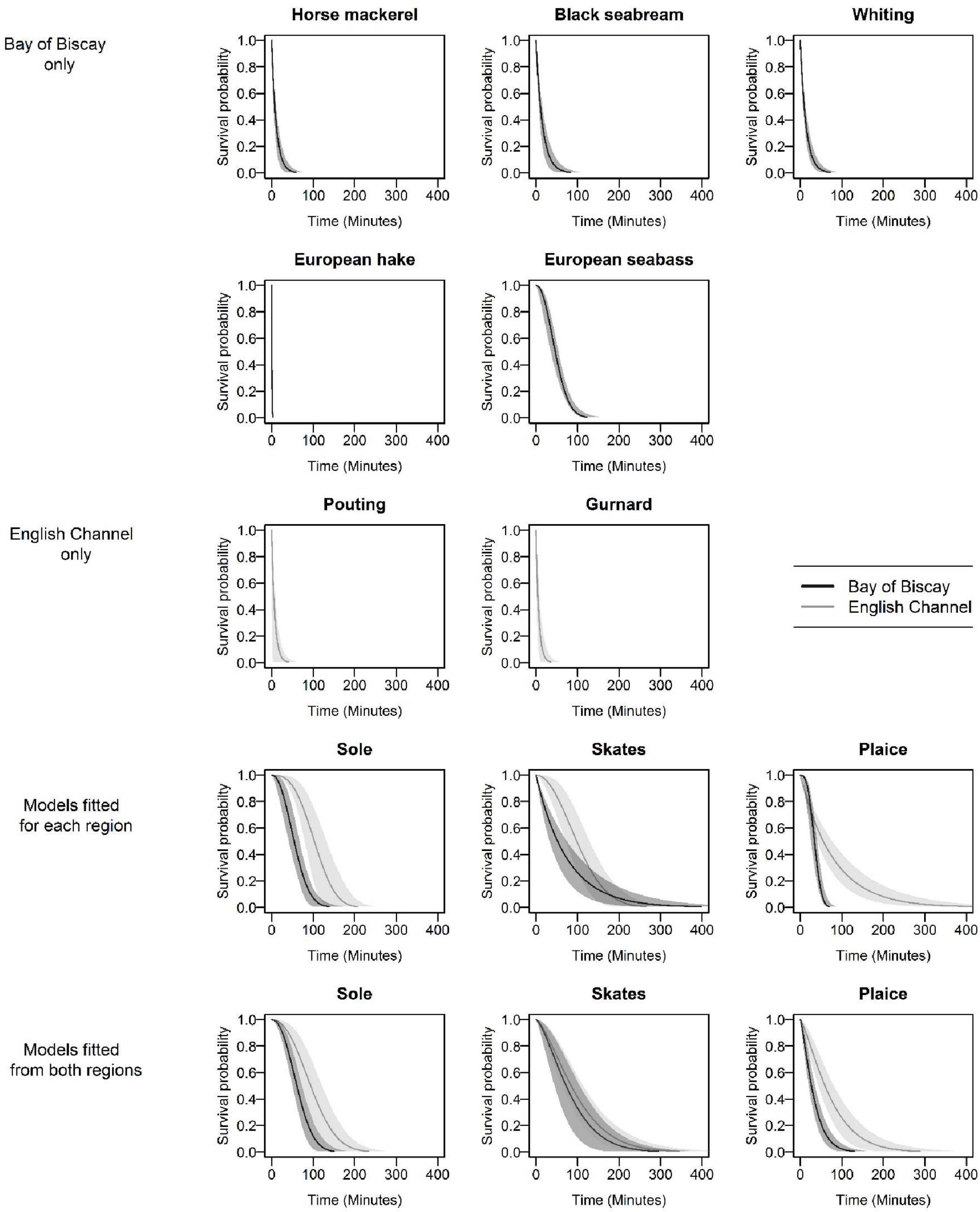

Figure 2: **Survival curves**

Curves of the survival probability function for each species in relation to time (min) spent on the deck. Lines are the predictions from the best models, while shaded areas are the bootstrapped 95%-confidence intervals.

Table 2: Description of best survival Time to Mortality (TM) models according to AICc. $\overline{\mathrm{TM}}$ is the estimated mean, TM_{50} and TM_{95} are the estimated time to 50% and 95% of mortality. 95%-confidence intervals are in square brackets. A value 1 for the shape parameter γ means that the estimated survival function followed an exponential law, while other values mean that a Weibull law provided the best fit.

Species	$\overline{\mathbf{TM}}$	$\mathbf{TM_{50}}$	$\mathbf{TM_{95}}$	$\hat{\gamma}$
Bay of Biscay				
European hake	0.0 [0.0;0.0]	0.0 [0.0; 0.0]	0.0 [0.0; 0.0]	1.0
Horse mackerel	11.5 [6.8; 16.4]	9.9 [5.0;15.2]	27.2 [17.9;33.0]	1.5
Whiting	14.3 [9.7; 19.2]	11.1 [5.5 ;17.0]	38.9 [29.1;46.3]	1.2
Black seabream	15.9 [10.8; 22.4]	13.0 [8.2;19.3]	41.0 [22.4;58.6]	1.3
Plaice	34.4 [27.9; 40.9]	33.3 [25.9 ;40.8]	61.9 [45.9;68.4]	2.4
European seabass	48.6 [41.3; 55.9]	44.9 [35.5 ;54.0]	100.0 [80.5;111.3]	1.8
Sole	56.6 [45.3 ; 68.1]	54.1 [40.7;67.4]	106.2 [83.4;127.3]	2.2
Skates	75.4 [47.8; 106.8]	62.7 [31.7;90.0]	210.9 [104.5;292.1]	1.1
Eastern Channel				
Gurnard	8.3 [3.1; 14.4]	4.3 [1.8;12.2]	31.2 [6.2;21.5]	2.1
Pouting	8.1 [4.1; 15.5]	6.4 [1.6;15.0]	21.8 [15.5;27.1]	1.2
Plaice	76.5 [56.0; 107.9]	54.5 [43.5;82.0]	229.3 [135.1;296.8]	1.2
Sole	103.5 [80.1;128.9]	96.7 [79.4;130.1]	207.1 [117.4;210.4]	2.9
Skates	105.5 [78.5; 137.2]	84.2 [71.4;130.1]	281.4 [147.0.3;252.0]	2.0

4.2. Associations with environmental, technical and biological conditions

Associations with external conditions were also investigated for the four species with the highest estimated TM values, European seabass, plaice, sole and skates.

TM for European seabass in the BB experiment was longer for deeper and shorter tows (Table 3, Figure S4.a), which also happened to be where the longest specimens were found. For skates, sole and plaice air temperature was selected at least once and was systematically negatively associated with TM. The other selected covariates differed from one species to another and between the two regional experiments. For plaice in the BB experiment and for sole in the EC experiment, TM was shorter for longer specimens which happened to also be found in deeper hauls. TM for skates in the BB experiment was shorter in shallow areas, where smaller specimens were also found. For skates and plaice in the EC experiment, depth and fish length were not correlated, and longer TM values were associated with shallower water for both species, and with longer specimens for skates.

In the EC experiment the hauls were shorter, in deeper waters and the ambient air temperature was colder (Table 1, Figures S1.a-b). For sole, the negative association of TM with air temperature was sufficient to explain the differences between the two experiments, while for plaice and skates, there was evidence for a "region" effect, with higher TM values predicted for the EC experiment (Table 3, Figures S4.a-b). For the combined data, TM was longer for longer plaice and in shallower waters. Overall, the proportions of the model deviances explained by the selected covariates were very low (5.1% on average, Table 3).

Table 3: Covariates that were retained in the best survival models according to AICc for species whose TM_{50} was above 30 min. The sign +/- indicates the trend of the effect (positive/negative) on the TM, and covariates in bold are those that had an evidence weight greater than 0.75. %ExpDev is the percentage of deviance explained by the covariates in the models.

Species	**Covariates**	**Signs**	**Evidence weight**	**% Exp Dev**
Bay of Biscay				
European seabass	**Tow duration**	**-**	**86.3**	**0.1**
	Depth	**+**	**97.0**	**0.2**
	Air temperature	-	45.3	1.6
Sole	1			0.0
Plaice	**Length**	**-**	**87.6**	**5.4**
	Air temperature	**-**	**81.8**	**1.2**
Skates	**Depth**	**+**	**86.1**	**3.9**
English Channel				
Plaice	**Depth**	**-**	**98.0**	**2.1**
	Air temperature	**-**	**81.0**	**0.0**
Sole	**Air temperature**	**-**	**97.2**	**2.1**
	Length	**-**	**97.4**	**13.4**
Skates	**Length**	**+**	**98.2**	**1.0**

	Depth	**-**	**78.5**	**10.8**
	Air temperature	**-**	**91.0**	**8.0**
Both regions				
Plaice	**Region EC**	**+**	**98.0**	**4.1**
	Length	**+**	**96.5**	**0.4**
	Depth	-	35.5	1.3
Sole	**Air temperature**	**-**	**99.2**	**6.9**
	Depth	-	70.8	0.5
Skates	**Tow duration**	**+**	**97.2**	**2.5**
	Region EC	**+**	**83.7**	**0.6**
	Length	+	71.8	0.7

5. DISCUSSION

The present study investigated the TM of ten species currently discarded by French coastal bottom trawl fisheries. The experiments were held in summer as exposure to high light intensity and warm air temperature are expected to increase the fish mortality rates [8]. As other external conditions (tow depth and duration, handling practices) were representative of the fisheries, the present results on TM are thus expected to be in the lower boundary of the annual range, suggesting that the most resilient fish would be so regardless of season.

The estimated TM was very small (TM_{50} lower than 13 min and TM_{95} lower than 41 min) for hake, gurnard, pouting, horse mackerel, whiting and black seabream. In both fisheries, the catch sorting durations implied that discarded fish are exposed to air for durations ranging from 15 to 50 min, with an average of 30 min. These species would thus clearly have little chance of being alive once released to the water. Among the four other species, plaice and European seabass had TM_{50} greater than 30 min, and skates and sole hadTM_{50} values that significantly exceeded the longest sorting duration observed in the study (50 min). For these four species, it would be worthwhile undertaking more thorough studies to better estimate the discard mortality rate required to justify an exemption. TM had already been demonstrated to be a good proxy of discard mortality for a wide variety of species caught during a bottom-trawl survey in the Gulf of

St. Lawrence (NW Atlantic) [14]. Furthermore, the results are largely consistent with those from a recent study that used captive observation to estimate the mortality of discards from beam trawlers in the North Sea and Western Channel [22]. In that study, 100% of whiting and pouting died within 24h, while plaice, sole and skates had much better survival rates (48%, 14% and 72% respectively). Our findings are consistent with those results, except that survival of plaice exceeded that of sole, which may reflect differences in external factors between the studies.

Benoît *et al.* [14] found that the inter-species variability in TM was explained by taxonomic order, body size, presence of gas bladder or deciduous scales and sedentariness, a proxy for hypoxia resistance. Although there were no species in common with the present study, the general taxonomic rankings in TM from low to high were quite similar: Gadiformes (hake and pouting), Perciformes (black seabream, horse mackerel and European seabass), Pleuronectiformes (sole and plaice) and finally Rajiformes (skates). The exception was Scorpaeniformes which generally had elevated values of TM in[14], but for which the only representative, gurnard, produced a very low TM estimate. Otherwise, European seabass appeared to be much more resistant than other Perciformes. As in Benoît *et al.* [14], species lacking a gas bladder (as plaice, sole and skates) appeared to have greater TM. Due to their low number, individuals of small-spotted catshark (*Scyliorhinus canicula*) were not included in this modelling study. Nevertheless, the six observed individuals survived between 102 and 252 min, which also suggests high resistance to hypoxia, consistent with the results of Revill *et al.* [4]. Benoît *et al.* [14] found that relatively more sedentary species were generally associated with greater TM, which they ascribed to enhanced metabolic adaptation to hypoxia. Though our results for plaice, sole and skates are consistent with those findings, our results for gurnard are not, suggesting that other factors may be responsible for low survival potential in this species.

Overall, the significant covariates did not explain much of the variability in TM based on explained deviances, suggesting that species based differences are largely consistent across a range of conditions. This result is further supported by consistent ranking of species robustness across studies. This important finding suggests that the use of TM to identify candidate species for further discard mortality study appears robust to the particularities of different fisheries and therefore to have general applicability. Nevertheless, TM significant differences were demonstrated between the two experiments. Though only three species were observed in both experiments, the differences were substantial and all suggest enhanced TM in the EC experiment, with TM_{50} values that were about 1.5 to 2 times longer than in the BB experiment. As the experiments were held aboard different commercial trawlers, these differences might partly be due to fishing and catch handling techniques and other external factors. Though the smaller codend mesh size in the BB experiment may have induced more injuries, as observed anecdotally by the two observers that conducted both trials, the other technical fishing conditions were very similar.

Air temperature was sufficient to explain the TM difference for sole. For plaice and skates, while the temperature had a significant effect in each experiment, the "region" effect was selected instead of the temperature with the combined data, suggesting that additional unquantified factors may have also contributed to the estimated differences. These may include biological factors that have been shown to affect discard mortality, such as sex and species for skates [37,38], and catch related factors such as catch size and composition which may also induce stress and injuries [8,15,21]. Enever *et al.* [37], examined the factors affecting health status indicators in skates following capture and exposure to air for 10 to 20 min. The most important factors were the codend weight, species and tow duration. In the present study, tow duration appeared to be negatively associated with TM for European seabass only, a species which is known to swim hard to attempt to escape capture by trawls [39]. The effects of fish length and depth were significant, though it was not possible to tease the effects apart because the variables were positively correlated. Smaller individuals typically have greater susceptibility to injury due to crushing during the haul or to changes in barometric pressure when the trawl is brought to the surface, or greater fatigue from swimming to escape the trawl [8,31]. Furthermore, smaller fish are probably more susceptible to hypoxia due to their higher mass-specific metabolic rate [40,41] and often higher energy cost for breathing [42]. Fish length was positively associated with TM in skates and plaice, consistent with the results of Depestele *et al.* [21].

Other indicators such as vitality and reflex action mortality predictor (RAMP) scores have also been shown to be good proxies of species-specific discard survival [15,22,23]. Like TM, these indicators are easily obtained during commercial fishing operations and can be used to explore the effect of technical, environmental and biological factors affecting discard survival (e.g., [15]). However, the relationships between values of these proxies and discard survival are typically species-specific (e.g., [45]), and therefore, unlike TM, it is not possible to undertake inter-species comparisons based on these proxies alone. Direct estimation of discard survival is only possible from much more expensive captivity and tagging experiments, which are evolving and now better enabling the estimation of survival after capture and release [43–45]. It is these types of more elaborate experiments that will be required to confirm the high survival potential for candidate species. However, cost and logistical constraints preclude undertaking experiments for all discarded species in all areas. TM experiments therefore have an important role in targeting those studies to the most likely candidates for a landing obligation exemption.

Acknowledgments

This work was part of the ENSURE project supported by *France Filière Pêche* and the *Direction des Pêches Marines et de l'Aquaculture*. The authors thank the crews of the *Déesses de l'Océan* and *Mon Petit Celestin* for their help to conduct the experiments and Camille Vogel and Fabien Morandeau for their help onboard the fishing vessels.

References

[1] K. Kelleher, Discards in the world's marine fisheries: an update, Food and Agriculture Organization of the United Nations, Rome, 2005.
[2] T.L. Catchpole, C.L.J. Frid, T.S. Gray, Discards in North Sea fisheries: causes, consequences and solutions, Mar. Policy. 29 (2005) 421–430. doi:10.1016/j.marpol.2004.07.001.
[3] N. Madsen, R.P. Frandsen, R. Holst, L.A. Krag, Development of new concepts for escape windows to minimise cod catches in Norway lobster fisheries, Fish. Res. 103 (2010) 25–29. doi:10.1016/j.fishres.2010.01.008.
[4] A.S. Revill, N.K. Dulvy, R. Holst, The survival of discarded lesser-spotted dogfish (*Scyliorhinus canicula*) in the Western English Channel beam trawl fishery, Fish. Res. 71 (2005) 121–124. doi:10.1016/j.fishres.2004.07.006.
[5] A.D. Rijnsdorp, A.M. Buys, F. Storbeck, E.G. Visser, Micro-scale distribution of beam trawl effort in the southern North Sea between 1993 and 1996 in relation to the trawling frequency of the sea bed and the impact on benthic organisms, ICES J. Mar. Sci. J. Cons. 55 (1998) 403–419. doi:10.1006/jmsc.1997.0326.
[6] M. Breen, B. Isaksen, E. Ona, A.O. Pedersen, G. Pedersen, J. Saltskår, B. Svardal, M. Tenningen, P.J. Thomas, B. Totland, others, A review of possible mitigation measures for reducing mortality caused by slipping from purse-seine fisheries, ICES CM. 100 (2012) 12.
[7] B. Diamond, B.D. Beukers-Stewart, Fisheries discards in the North Sea: waste of resources or a necessary evil?, Rev. Fish. Sci. 19 (2011) 231–245.
[8] M.W. Davis, Key principles for understanding bycatch discard mortality, Can. J. Fish. Aquat. Sci. 59 (2002) 1834–1843. doi:10.1139/f02-139.
[9] W.G. Macbeth, M.K. Broadhurst, B.D. Paterson, M.E.L. Wooden, Reducing the short-term mortality of juvenile school prawns (*Metapenaeus macleayi*) discarded during trawling, ICES J. Mar. Sci. J. Cons. 63 (2006) 831–839. doi:10.1016/j.icesjms.2006.03.008.
[10] T.J. Wassenberg, D.A. Milton, C.Y. Burridge, Survival rates of sea snakes caught by demersal trawlers in northern and eastern Australia, Biol. Conserv. 100 (2001) 271–280. doi:10.1016/S0006-3207(01)00031-3.
[11] R.R. Harris, M. Ulmestrand, Discarding Norway lobster (*Nephrops norvegicus* L.) through low salinity layers – mortality and damage seen in simulation experiments, ICES J. Mar. Sci. J. Cons. 61 (2004) 127–139. doi:10.1016/j.icesjms.2003.08.002.

[12] M. Tenningen, A. Vold, R.E. Olsen, The response of herring to high crowding densities in purse-seines: survival and stress reaction, Ices J. Mar. Sci. 69 (2012) 1523–1531. doi:10.1093/icesjms/fss114.

[13] S.S. Uhlmann, M.K. Broadhurst, Mitigating unaccounted fishing mortality from gillnets and traps, Fish Fish. 16 (2015) 183–229. doi:10.1111/faf.12049.

[14] H.P. Benoît, S. Plante, M. Kroiz, T. Hurlbut, A comparative analysis of marine fish species susceptibilities to discard mortality: effects of environmental factors, individual traits, and phylogeny, ICES J. Mar. Sci. J. Cons. 70 (2013) 99–113. doi:10.1093/icesjms/fss132.

[15] H.P. Benoît, T. Hurlbut, J. Chassé, Assessing the factors influencing discard mortality of demersal fishes using a semi-quantitative indicator of survival potential, Fish. Res. 106 (2010) 436–447. doi:10.1016/j.fishres.2010.09.018.

[16] M. Castro, A. Araújo, P. Monteiro, A.M. Madeira, W. Silvert, The efficacy of releasing caught *Nephrops* as a management measure, Fish. Res. 65 (2003) 475–484. doi:10.1016/j.fishres.2003.09.033.

[17] M.W. Davis, B.L. Olla, Mortality of lingcod towed in a net as related to fish length, seawater temperature, and air exposure: a laboratory bycatch study, North Am. J. Fish. Manag. 22 (2002) 1095–1104. doi:10.1577/1548-8675(2002)022<1095:MOLTIA>2.0.CO;2.

[18] F. Giomi, S. Raicevich, O. Giovanardi, F. Pranovi, P.D. Muro, M. Beltramini, Catch me in winter! Seasonal variation in air temperature severely enhances physiological stress and mortality of species subjected to sorting operations and discarded during annual fishing activities, Hydrobiologia. 606 (2008) 195–202. doi:10.1007/s10750-008-9336-x.

[19] J. Depestele, G. Dorémus, P. Laffargue, E.W.M. Stienen, M.-J. Rochet, Favorites and leftovers on the menu of scavenging seabirds: modelling spatio-temporal variation in discard consumption, Can. J. Fish. Aquat. Sci. (2016). doi:10.1139/cjfas-2015-0326.

[20] M.K. Broadhurst, P. Suuronen, A. Hulme, Estimating collateral mortality from towed fishing gear, Fish Fish. 7 (2006) 180–218. doi:10.1111/j.1467-2979.2006.00213.x.

[21] J. Depestele, M. Desender, H.P. Benoît, H. Polet, M. Vincx, Short-term survival of discarded target fish and non-target invertebrate species in the “eurocutter” beam trawl fishery of the southern North Sea, Fish. Res. 154 (2014) 82–92. doi:10.1016/j.fishres.2014.01.018.

[22] M.W. Davis, Fish stress and mortality can be predicted using reflex impairment, Fish Fish. 11 (2010) 1–11. doi:10.1111/j.1467-2979.2009.00331.x.

[23] M.W. Davis, M.L. Ottmar, Wounding and reflex impairment may be predictors for mortality in discarded or escaped fish, Fish. Res. 82 (2006) 1–6. doi:10.1016/j.fishres.2006.09.004.

[24] O.-B. Humborstad, M.W. Davis, S. Lokkeborg, Reflex impairment as a measure of vitality and survival potential of Atlantic cod (*Gadus morhua*), Fish. Bull. 107 (2009) 395–402.

[25] M.R. Donaldson, R. Arlinghaus, K.C. Hanson, S.J. Cooke, Enhancing catch-and-release science with biotelemetry, Fish Fish. 9 (2008) 79–105. doi:10.1111/j.1467-2979.2007.00265.x.

[26] M.E. Yergey, T.M. Grothues, K.W. Able, C. Crawford, K. DeCristofer, Evaluating discard mortality of summer flounder (*Paralichthys dentatus*) in the commercial trawl fishery: Developing acoustic telemetry techniques, Fish. Res. 115 (2012) 72–81. doi:10.1016/j.fishres.2011.11.009.

[27] A.-S. Cornou, M. Quinio-Scavinner, D. Delaunay, J. Dimeet, Goascoz, Nicolas, Dube, Benoit, Fauconnet, Laurence, Rochet, Marie-Joelle, Observations à bord des navires de pêche professionnelle. Bilan de l’échantillonnage 2014, (2015). doi:10.13155/39722.

[28] A.-S. Cornou, J. Dimeet, A. Tetard, O. Gaudou, B. Dube, L. Fauconnet, M.-J. Rochet, Observations à bord des navires de pêche professionnelle. Bilan de l’échantillonnage 2012, (2013). doi:10.13155/27787.

[29] J.D. Neilson, K.G. Waiwood, S.J. Smith, Survival of Atlantic Halibut (*Hippoglossus hippoglossus*) Caught by Longline and Otter Trawl Gear, Can. J. Fish. Aquat. Sci. 46 (1989) 887–897. doi:10.1139/f89-114.

[30] S.J. Parker, P.S. Rankin, R.W. Hannah, C.B. Schreck, Discard Mortality of Trawl-Caught Lingcod in Relation to Tow Duration and Time on Deck, North Am. J. Fish. Manag. 23 (2003) 530–542. doi:10.1577/1548-8675(2003)023<0530:DMOTCL>2.0.CO;2.

[31] P. Suuronen, Mortality of fish escaping trawl gears, Food and Agriculture Organization of the United Nations, Rome, 2005.

[32] R Development Core Team, R: A Language and Environment for Statistical Computing., R Foundation for Statistical Computing, Vienna, Austria, 2015. http://www.R-project.org (accessed February 4, 2010).

[33] H. Akaike, Likelihood of a model and information criteria, J. Econom. 16 (1981) 3–14.

[34] K.P. Burnham, D.R. Anderson, eds., Model Selection and Multimodel Inference, Springer New York, New York, NY, 2004. http://link.springer.com/10.1007/b97636 (accessed December 9, 2016).

[35] P.M. Dixon, Bootstrap resampling, Encycl. Environmetrics. (2002). http://onlinelibrary.wiley.com/doi/10.1002/9780470057339.vab028/full (accessed March 14, 2016).

[36] B. Efron, R. Tibshirani, An introduction to the bootstrap, CRC Press, 1993.

[37] R. Enever, T.L. Catchpole, J.R. Ellis, A. Grant, The survival of skates (Rajidae) caught by demersal trawlers fishing in UK waters, Fish. Res. 97 (2009) 72–76. doi:10.1016/j.fishres.2009.01.001.

[38] I.C. Stobutzki, M.J. Miller, D.S. Heales, D.T. Brewer, Sustainability of elasmobranchs caught as bycatch in a tropical prawn (shrimp) trawl fishery, Fish. Bull. 100 (2002) 800–821.

[39] S. Marras, G. Claireaux, D.J. McKenzie, J.A. Nelson, Individual variation and repeatability in aerobic and anaerobic swimming performance of European sea bass, *Dicentrarchus labrax*, J. Exp. Biol. 213 (2010) 26–32. doi:10.1242/jeb.032136.

[40] M. Jobling, Bioenergetics: feed intake and energy partitioning, in: J.C. Rankin, F.B. Jensen (Eds.), Fish Ecophysiol., Springer Netherlands, 1993: pp. 1–44. doi:10.1007/978-94-011-2304-4_1.

[41] R.H. Peters, The ecological implications of body size, Cambridge University Press, Cambridge, 1983. http://ebooks.cambridge.org/ref/id/CBO9780511608551 (accessed March 16, 2016).

[42] A.L. Kalinin, F.T. Rantin, M.L. Glass, Dependence on body size of respiratory function in *Hoplias malabaricus* (Teleostei, Erythrinidae) during graded hypoxia, Fish Physiol. Biochem. 12 (1993) 47–51. doi:10.1007/BF00004321.

[43] H.P. Benoît, C.W. Capizzano, R.J. Knotek, D.B. Rudders, J.A. Sulikowski, M.J. Dean, W. Hoffman, D.R. Zemeckis, J.W. Mandelman, A generalized model for longitudinal short- and long-term mortality data for commercial fishery discards and recreational fishery catch-and-releases, ICES J. Mar. Sci. J. Cons. (2015) fsv039. doi:10.1093/icesjms/fsv039.

[44] K.H. Pollock, W.E. Pine, The design and analysis of field studies to estimate catch-and-release mortality, Fish. Manag. Ecol. 14 (2007) 123–130. doi:10.1111/j.1365-2400.2007.00532.x.

[45] G.D. Raby, J.R. Packer, A.J. Danylchuk, S.J. Cooke, The understudied and underappreciated role of predation in the mortality of fish released from fishing gears, Fish Fish. 15 (2014) 489–505. doi:10.1111/faf.12033.