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1 **High survivability of discarded invertebrates from bottom trawling fisheries**

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## 6 Abstract

7 The impacts of bottom trawling in coastal ecosystems are significant, not only for targeted species but also for  
8 non-commercial ones. However, the critical gaps in scientific knowledge associated with these impacts on  
9 untargeted but functionally important species remain to be filled. This is notably the case for a great proportion  
10 of discarded invertebrates, for which only a handful of studies have investigated their survival. In this study, 600  
11 individuals from six different benthic invertebrate species were collected in commercial conditions in the Bay of  
12 Biscay for short-term survival experiments. Overall, the observed survival after 100-130 hours and the predicted  
13 survival via mixture models were very high (>93%) for *Asterias rubens*, *Aphrodita aculeata*, *Buccinum undatum*  
14 and *Pagurus* sp. Survival of *Maja brachydactyla* was lower though still high (>80% overall) and *Atelecyclus*  
15 *undecimdentatus* was more vulnerable to trawling and handling, with ~50% of survival. Both showed 100%  
16 mortality when presenting carapace cracks and survival of *M. brachydactyla* was lower when missing  
17 appendages. No biotic nor abiotic parameters were correlated to survival, except injury class for *M.*  
18 *brachydactyla* and *A. undecimdentatus*. This study shows an overall high survival but highlights the fact that  
19 otter trawl fisheries may differentially affect discarded benthic invertebrates, therefore bringing light for future  
20 studies on longer-term impacts on benthic communities and coastal ecosystems. Furthermore, we recommend  
21 incorporating survival rates of discarded invertebrates in ecosystem-level modelling studies and encourage the  
22 use of detailed information and biomass reports of benthic invertebrates for a better management of natural  
23 populations and fisheries resources.

24 **Keywords:** fisheries management, benthic invertebrates, physical injuries, discard mortality, survival mixture  
25 models

## 26 1. Introduction

27 Understanding how human activities and more particularly fishing pressures are impacting the different  
28 components of marine ecosystems is crucial to predict their dynamics (Barange et al., 2010; Botsford et al.,  
29 1997). Among fishing practices, bottom trawling is widely used and profoundly disrupts benthic habitats and  
30 communities (Hiddink et al., 2019; Olsford et al., 2008; Van Denderen et al., 2015). Indeed, the direct footprint  
31 of bottom trawling on the seafloor is thoroughly documented (Amoroso et al., 2018; de Juan et al., 2011; Hinz et  
32 al., 2009; Rijnsdorp et al., 2016), as well as its direct and indirect impacts on targeted commercial species  
33 (Hiddink et al., 2011; Thurstan et al., 2010). The resources harvested by bottom trawling fisheries are  
34 economically important, and understanding the ecosystem-level footprint of the latter is necessary to provide  
35 efficient management (Pikitch et al., 2004). One of the important aspects for such management is the  
36 characterization of the fate of fisheries discards (Suuronen and Gilman, 2019; Zeller et al., 2018).

37 Recently, the European Union legislated a landing obligation for all fisheries discards of commercial species  
38 under quota management, except for those that show a high survivability to the fishing process. As a result,  
39 many recent studies focused their efforts on the estimation of survival rates for commercial species of fish  
40 (Morfin et al., 2017b, 2017a; Van Der Reijden et al., 2017) and invertebrates (Campos et al., 2015; Méhault et  
41 al., 2016; Mérillet et al., 2018). The knowledge of survival rates is not only important for the targeted species,  
42 but also to determine which proportion of individuals maintain their ecological roles in the ecosystem after being  
43 discarded, and which part of discards biomass is available for both consumers and scavengers (Catchpole et al.,  
44 2006; Depestele et al., 2019, 2016; Groenewold and Fonds, 2000).

45 However, because a majority of benthic invertebrate species are not commercially exploited, only a small  
46 number of studies recently examined their post-capture survival. High survival rates were previously reported for  
47 starfish and brittlestars, sea mice, hermit crabs and whelks (*e.g.* Bergmann and Moore, 2001b; Depestele et al.,  
48 2014; Kaiser and Spencer, 1995), while lower survival was reported for other species, notably small crustaceans  
49 (*e.g.* Bergmann and Moore, 2001a; Mérillet et al., 2018). Survival was found to be dependent on the fishing  
50 conditions (*e.g.* gear type, haul duration, sorting procedure) and subsequent injuries (Depestele et al., 2014;  
51 Mérillet et al., 2018). However, the information on survival rates for unwanted and unregulated benthic  
52 invertebrates remains very scarce despite their well-documented ecological importance in coastal ecosystems  
53 (Boudreau and Worm, 2012; Demestre et al., 2018) and their significance in terms of catch biomass (*e.g.* 35.6%  
54 of total catch for French bottom trawlers in the Eastern English Channel ; Leforestier, 2018). The importance of

55 assessing survival rates has thus been under-appreciated for benthic invertebrates despite the potential usefulness  
56 of their knowledge, notably in terms of modelling (*e.g.* ecosystem-level functioning). Indeed, the use of  
57 integrative approaches relies on the assessment of variations in discard flows and their consequences on marine  
58 food webs (Depestele et al., 2019; Fulton et al., 2011; Link et al., 2010), with important considerations for future  
59 management (Fulton et al., 2014; Mackinson et al., 2018).

60 In this study, we lay the groundwork towards a better characterization of benthic invertebrates survival for future  
61 management recommendations and applications in ecosystem modelling, by focusing on the post-capture  
62 survival in captivity of six functionally different species (*Asterias rubens*, *Maja brachydactyla*, *Atelecyclus*  
63 *undecimdentatus*, *Aphrodita aculeata*, *Pagurus* sp. and *Buccinum undatum*). The objectives are multiple: (i) the  
64 quantification of overall discard survival; (ii) the quantification of injury-dependent survival rates to assess the  
65 potential of an injury index as a proxy of discard survival; (iii) the assessment of the influence of technical,  
66 environmental and biological conditions related to fishing activity on survival, to identify the potential direct  
67 measures that could be taken to improve discard survival.

## 68 **2. Materials and Methods**

### 69 *2.1. Sampling procedure*

70 Sampling of benthic invertebrates was conducted in commercial fishing conditions in April 2019 in the Bay of  
71 Bourgneuf (Bay of Biscay; 2.30°W 47.05°N ; ICES subarea 8.a) onboard the *Déesses de l'Océan*, a 10.95 m-  
72 long French coastal trawler equipped with a 150 kW power engine and a single otter trawl (20 m headline and 70  
73 mm diamond mesh codend). During three daily trips, a total of eleven hauls were performed with a maximum  
74 duration of 2.4 hours at a speed of  $3 \pm 0.5$  knots in shallow coastal habitats (5-22 m; Table 1). Technical and  
75 environmental conditions were recorded for each haul (Table 1), as well as the total catch (number of crates as a  
76 proxy, each crate weighing approximately 45 kg of catch). The hauling process usually took less than 10 minutes  
77 and total air exposure, corresponding to the sorting process, varied between 16 and 54 minutes, mainly  
78 depending on the total catch volume. Air exposure duration was measured for each batch of handled  
79 invertebrates and therefore differs among hauls and between species. The described fishing conditions and  
80 handling process are representative of typical commercial fishing conditions by small bottom trawlers (< 12 m)  
81 in the area. The invertebrates fished by such process are hereafter called 'trawled' individuals.

82 **Table 1** Fishing conditions and size of the 'trawled' invertebrates with mean ( $\pm$ SD), minimum and maximum for  
83 the total number of hauls. Measurements are the following: total length for *A. rubens* and *A. aculeata*, shell

84 length for *B. undatum* and cephalothorax length for *M. brachydactyla* and *A. undecimdentatus*. Thermal shock is  
85 the difference between air and water temperature

	Mean (SD)	Min	Max
Depth (m)	11 (5.4)	5	22
Air temperature (°C)	14.6 (3.6)	8.3	21.8
Water temperature (°C)	11.5 (0.3)	11.0	11.9
Thermal shock (°C)	3.1 (3.5)	-3	10.4
Atmospheric pressure (hPa)	1013 (4.2)	1001	1017
Environmental humidity (%)	55 (4.2)	50	62
Haul duration (min)	116 (16)	85	141
Catch (crates)	4.5 (0.9)	3	6
Air exposure (min)	-	16	54
Size (cm)			
<i>Asterias rubens</i>	13.2 (2.1)	9	19
<i>Maja brachydactyla</i>	10.6 (1.38)	5.4	13.2
<i>Atelecyclus undecimdentatus</i>	4.1 (0.4)	3.0	5.1
<i>Aphrodita aculeata</i>	7.3 (1.4)	5	11
<i>Pagurus</i> sp.	-	-	-
<i>Buccinum undatum</i>	6.4 (1.1)	4.5	10.6

86 The onboard observers collected six species for further examination and survival experiments (Table 1). These  
87 species were selected for their abundance in observed catches in the area and their taxonomic diversity,  
88 representing different functional traits and various phyla. Among them, one annelid (sea mouse, *Aphrodita*  
89 *aculeata*), three crustaceans (spider crab, *Maja brachydactyla*; great circular crab, *Atelecyclus undecimdentatus*;  
90 and hermit crab, *Pagurus* sp.), one echinoderm (common starfish, *Asterias rubens*), and one mollusc (common  
91 whelk, *Buccinum undatum*).

92 Individual size was measured to the nearest mm, depending on species (Table 1): total length for starfish and sea  
93 mice, shell length for whelks and cephalothorax length for spider crabs and great circular crabs. Hermit crabs  
94 were not measured. Sex was determined for spider crabs and great circular crabs.

95 The benthic invertebrates were randomly selected among the discarded part of the catch. Their physical injuries  
96 potentially linked to the fishing process were visually assessed as the crew was sorting the catch, following the  
97 classification described in Veale et al. (2001) and also used in Depestele et al. (2014) (Table 2).

98 **Table 2** Injury classes used to characterize invertebrate species physical damage

	Injury class 1	Injury class 2	Injury class 3	Injury class 4
<i>Asterias rubens</i>	No visible damage	Arms missing	Minor disc damage	Crushed
<i>Maja brachydactyla</i>	No visible damage	Legs missing	Major carapace cracks	Crushed
<i>A. undecimdentatus</i>	No visible damage	Legs missing	Major carapace cracks	Crushed
<i>Aphrodita aculeata</i>	No visible damage	Visible damage	Crushed	-
<i>Pagurus</i> sp.	No visible damage	Edge of shell chipped	Shell cracked/punctured	Crushed
<i>Buccinum undatum</i>	No visible damage	Edge of shell chipped	Shell cracked/punctured	Crushed

99 2.2. Survival experiments in captivity

100 Directly after the sorting process (16 to 54 minutes), the invertebrates were placed in onboard tanks with  
101 continuous water flow in baskets to distinguish between hauls. Onboard captivity lasted from 1 to 8 hours.  
102 Spider crabs were individually marked with coloured rubber brands and great circular crabs were individually  
103 placed in numbered perforated tubes. For the other species, biotic parameters (size, sex and injury class) were  
104 not only recorded during the sorting process, but also at the moment of their death to identify them *a posteriori*.  
105 Following landing, the sampled invertebrates were transferred as quickly as possible and within the same  
106 timeframe (10-30 minutes) into closed-loop tanks (7 m<sup>3</sup>) with continuous oxygenated water flow located in the  
107 harbor auction market to limit transport and handling time.

108 Sampled invertebrates were monitored every twelve hours and dead specimens were removed from the holding  
109 tanks to avoid contamination. In tanks, water parameters were monitored on a daily basis (Zolux® digital  
110 temperature, pH, nitrites, ammonium, silicates and phosphates using JBL® Testlab kits) and tank water was  
111 renewed two times during the whole experiment to avoid a detrimental high concentration of nitrites. Survival  
112 experiments were terminated at the same date for all the individuals, resulting in three to six days of captivity  
113 depending on the sampling day, as recommended before for survival studies (Wassenberg and Hill, 1993).

114 Control individuals that have not experienced the whole fishing process, as opposed to the ‘trawled’ individuals,  
115 were sampled using two different techniques. Crustaceans and whelks were collected using creels, whereas sea  
116 mice and starfish were collected during short trawl hauls (< 25 min). This sampling for controls resulted in intact  
117 individuals that were put in the same tanks as the ‘trawled’ individuals but in separate baskets. Mortality of  
118 controls was also assessed every twelve hours at the same moment than the ‘trawled’ individuals.

### 119 2.3. Survival estimation of discarded invertebrates

120 Experimental survival data is longitudinal (*i.e.* measured at several times) and related to varying monitoring  
121 periods (between 3 and 6 days). Furthermore, some data are right-censored, meaning that the time of death is  
122 unknown for individuals still alive at the end of the monitoring period. To account for these features, the  
123 empirical Kaplan-Meier curves were performed and provided a non-parametric estimation of survival probability  
124 over the duration of the experiment (Kaplan and Meier, 1958). Kaplan-Meier curves were compared between  
125 ‘trawled’ individuals and controls via a log-rank test (Harrington and Fleming, 1982).

126 Then, parametric survival mixture models (SMMs) were applied to estimate the survival rate of each species.

127 Indeed, these models are based on the hypothesis that only a proportion of individuals are affected by the fishing

128 process (capture, handling and release). While the death of affected individuals is assumed to follow a survival  
 129 function  $S_A$  (here a Weibull law), the overall survival curve converge to an asymptote equal to  $(1 - \pi)$ , the overall  
 130 survival rate (Benoît et al., 2012; Morfin et al., 2017a):

$$131 \quad S'(t) = \pi S_A(t) + (1 - \pi) S_I(t) = \pi \exp[-(\alpha t)^\gamma] + (1 - \pi) \quad (1)$$

132 In Eq. (1),  $(\alpha, \gamma) > 0$  and  $0 \leq \pi \leq 1$ .

133 It is worth noting that the limit of  $S'(t)$  when  $t \rightarrow \infty$  is equal to  $(1 - \pi)$ . Such model is appropriate for the study of  
 134 discards survivability as it does not assume that all fish die as a result of fishing but rather divides the survival  
 135 function in two terms in Eq. (1): the first related to the affected individuals,  $S_A(t)$ , and the second to the  
 136 unaffected ones,  $S_I(t)$ . The latter equals one because unaffected individuals are considered immune to the fishing  
 137 process and natural mortality is supposedly negligible compared to the time period mortality related to the  
 138 fishing event may occur (Benoît et al., 2012).

139 For each species, Weibull SMMs parameters  $(\alpha, \gamma, \pi)$  in Eq. (1) were fit to the benthic invertebrates survival data  
 140 by maximisation of the model likelihood using a quasi-Newton optimisation algorithm as described in Byrd et al.  
 141 (1995) and Morfin et al. (2017a). When the algorithm for Weibull SMMs did not converge to a solution,  
 142 exponential SMMs ( $\gamma = 1$  in Eq. (1)) were investigated with the same maximum likelihood approach, also  
 143 checking AICc values for differences in model fit (Burnham and Anderson, 2002). The best model for each  
 144 species was then visually compared to the non-parametric Kaplan-Meier curves for a quick validation.

#### 145 *2.4. Relationship between discard survival, injuries and fishing conditions*

146 A correlation between discard survival probability and injury class can intuitively be expected, as severely  
 147 injured individuals would theoretically have fewer chances of survival. To quantify this association for each  
 148 species, the injury class was then tested as a covariate on the three parameters  $(\alpha, \gamma, \pi)$  describing the Weibull  
 149 SMM, also checking AICc values for model fit.

150 Correlations between abiotic (tow duration, air exposure, air and water temperatures, thermal shock, atmospheric  
 151 pressure, humidity and volume of capture), biotic parameters (sex, size) and invertebrate survival probabilities  
 152 were explored using multivariate mixed-effects Cox proportional hazards models (Cox, 1972) with a backward  
 153 AIC selection of variables.

### 154 **3. Results**

155 3.1. Overall survival rates

156 A total of 600 individuals of the six benthic invertebrates was sampled, including 456 ‘trawled’ and 144 control  
 157 individuals (Table 3). Sex ratio M/F of the ‘trawled’ individuals was 0.7 for spider crabs and 1.6 for great  
 158 circular crabs. Mortality of controls was negligible for all species except great circular crabs (Table 3), for which  
 159 six control individuals died over a total of 22. However, their Kaplan-Meier estimates were significantly  
 160 different between ‘trawled’ and control individuals (log-rank test,  $\chi^2_{df=1} = 7.7$ ,  $p$ -value = 0.005).

161 **Table 3** Summary of survival data. The predicted survival corresponds to the estimation of  $1 - \pi$  ( $\pi$  = proportion  
 162 of adversely affected individuals) in survival mixture models (SMMs). IC = Injury Class

	$n_{\text{total}}$ ( $n_{\text{dead}}$ )	$n_{\text{control}}$ ( $n_{\text{dead}}$ )	Time for KM survival (min)	KM survival in % (SE)	Overall SMM survival in %	IC-dependent SMM survival in %
<i>Asterias rubens</i>	72 (4)	19 (1)	114	93 (4)	94	-
<i>Maja brachydactyla</i>	71 (8)	18 (1)	126	84 (6)	-	82
<i>A. undecimdentatus</i>	83 (40)	22 (6)	120	45 (7)	47	45
<i>Aphrodita aculeata</i>	64 (2)	4 (0)	179	96 (3)	-	-
<i>Pagurus</i> sp.	94 (5)	62 (2)	102	94 (3)	93	-
<i>Buccinum undatum</i>	72 (1)	19 (2)	124	95 (5)	-	-

163 The overall survival of all the species was high (Table 3). This pattern is confirmed by the values of Kaplan-  
 164 Meier survival estimates, which take into account right-censored data (Table 3, Supplementary Material 1).  
 165 Great circular crabs showed a KM survival estimate of 45% (SE  $\pm$  7%) after 120 h, 84% (SE  $\pm$  6%) after 126 h  
 166 for spider crabs, 89% (SE  $\pm$  7%) at 123 h for sea mice, 93% (SE  $\pm$  4%) at 114 h for starfish, 94% (SE  $\pm$  3%) at  
 167 102 h for hermit crabs and 95% (SE  $\pm$  5%) after 124 h for whelks (Table 3).

168 Survival mixture models with Weibull-type survival functions well fitted the survival data of great circular crabs,  
 169 hermit crabs and starfish, with respective predicted longer-term survival of 47, 93 and 94% (Table 3, Fig. 1,  
 170 Supplementary Material 2). For great circular crabs, the AICc for the Weibull-type SMM ( $\gamma > 0$ ) was lower  
 171 ( $AICc_{\gamma>0} = 393$ ) than the one for the exponential-type SMM ( $AICc_{\gamma=1} = 479$ ), but a visual assessment of the fit  
 172 allowed to choose the latter over the former. The maximization of model likelihood procedure was unable to  
 173 converge for the other species.

174 3.2. Survival considering physical injuries

175 In terms of physical injuries, only one sea mouse showed minor visible damage and 94% of hermit crabs were  
 176 intact (Table 2, Fig. 2A). 60% of whelks were intact and 40% showed minor damage. 68% of starfish were  
 177 intact, 22% showed arms missing and minor disk damage, whereas 7% were crushed. All the dead starfish at the  
 178 end of the experiment showed missing arms and minor disk damage (Fig. 2B). Intact spider crabs and great

179 circular crabs represented respectively 65% and 51% of the sampled individuals, while 32% and 36% had  
180 missing appendages, and 3% and 13% had major carapace cracks or were crushed (Table 2, Fig. 2A). Further  
181 analyses are however limited for all the species except spider crabs and great circular crabs because of the low  
182 number of death events ( $n \leq 5$ ).

183 The introduction of injury class as a covariate in the SMMs allowed to estimate the conditional survival  
184 probability of spider crabs according to their injuries (Fig. 1B). Survival was estimated to 96% for individuals  
185 with no visible injury, 61% for individuals with missing appendages, and down to 6% when showing major  
186 carapace cracks or completely crushed. Regarding the great circular crab, although the SMM including injury  
187 class as a covariate did not explain better their survival compared to the overall SMM ( $AIC_{injury} = 490$  vs.  $AIC_c$   
188  $= 479$ ), the predicted long-term survival is estimated at 53% for intact individuals, 51% for crabs missing  
189 appendages, and less than 1% when crushed or with major carapace cracks (Fig. 1B).

### 190 *3.3. Factors potentially influencing survival*

191 Among the biotic (sex, size) and abiotic parameters (tow duration, air exposure, air and water temperatures,  
192 thermal shock, atmospheric pressure, humidity and volume of capture) measured, the multivariate Cox  
193 proportional hazards models showed that no variable was correlated to survival for both great circular crabs and  
194 spider crabs.

## 195 **4. Discussion**

196 This experimental study was carried out for six benthic invertebrates for which survival rates after bottom  
197 trawling in commercial conditions and discarding were found very high (> 80%) except for a species of crab  
198 showing an overall survival rate around 50%. However, the mortality of damaged decapods was found very high.

### 199 *4.1. Discard survival rates experimentally inferred*

200 Previous studies have already investigated the survival of discarded invertebrates in bottom trawling fisheries  
201 (M. Bergmann and Moore, 2001b, 2001a; Demestre et al., 2018; Depestele et al., 2014; Kaiser and Spencer,  
202 1995; Mensink et al., 2000; Ramsay et al., 2001), but the most recent and thorough one, though very complete,  
203 has only been focusing on beam trawling (Depestele et al., 2014). The current study therefore brings  
204 complementary results with the use of an otter trawl. Overall, we find that the survivability of benthic  
205 invertebrates matches the results of Depestele et al. in 2014, but also that of other bottom trawling studies that  
206 were conducted in the 1990s and early 2000s.

207 Concerning starfish, 89% survived 29 days in captivity after bottom trawling (M. Bergmann and Moore, 2001b)  
208 and 93% after 14 days (Ramsay et al., 2001). Experiments with shorter durations showed that 97% of individuals  
209 of the same species survived for 65 h (Depestele et al., 2014), while Kaiser and Spencer (1995) showed 99% of  
210 survival after 48 h. The difference in survival rates between short and longer term experiments can be due to the  
211 development of *Vibrio* bacteria in the lesions of injured starfish, inducing death in several days (M. Bergmann  
212 and Moore, 2001b; Eckert et al., 2000).

213 The high survival rate (96% after four days of captivity) of sea mice has also been previously observed, with  
214 records of 90% survival after five days (Kaiser and Spencer, 1995) and 92% after three days (Depestele et al.,  
215 2014). Cannibalism among sea mice has already been observed in captivity (Kaiser and Spencer, 1995), which  
216 could be a potential explanation of the two death events near the end of the experiment.

217 *Pagurus bernhardus* showed high survival rates of 94% after 21 days (Bergmann et al., 2001), 100% after 6 days  
218 (Kaiser and Spencer, 1995) and 94% after three days (Depestele et al., 2014). Another species, *Pagurus*  
219 *prideaux*, showed a survival rate of 90% after six days (Kaiser and Spencer, 1995).

220 Finally, we show that 95% of whelks survived after five days of post-trawling experiment, which is consistent  
221 with another study using a beam trawl, showing 100% of survival after 65 days (Kaiser and Spencer, 1995).

222 To the best of our knowledge, this study is the first one to investigate the survival of discarded individuals of the  
223 *Maja* genus, showing a high overall survival probability, however dropping to 61% if legs are missing due to the  
224 trawling and handling process and to zero if crushed or with major carapace cracks. While the pattern is clear,  
225 the number of death events observed for spider crabs during the experiment was low ( $n = 8$ ), therefore nuancing  
226 the conclusions of further studies using these predicted survival rates depending on injury classes.

227 Similarly to *Maja*, smaller decapods such as great circular crabs were also vulnerable to carapace cracks, with  
228 100% of quickly occurring mortality when punctured or crushed. Such severe damage induced by trawling may  
229 lead to the loss of bodily fluids detrimental to their survival (Ferner et al., 2005). Depestele et al. (2014) also  
230 found the same pattern on decapods (*Cancer pagurus* and *Liocarcinus* sp.) with almost no survivor when  
231 showing similar physical injuries.

232 Apart from direct and observable physical injuries, great circular crabs seem particularly subject to physiological  
233 stress due to the fishing and handling process, with a survival rate near 50% for intact individuals (Fig. 1B). We  
234 can hypothesize that this species is vulnerable to the stress induced by the whole fishing process, as observed in

235 other small crabs (Giomi et al., 2008; Raicevich et al., 2011). Thermal shock and air exposure during the sorting  
236 process, as well as changes in environmental parameters could be parameters influencing their survival, but Cox  
237 proportional hazards models did not show any effect. The lack of significance of such explanatory variables  
238 might be explained by the fact that individuals were only collected during one sampling period, resulting in a  
239 low variability of environmental variables between captured individuals. Six control individuals died during this  
240 study, but control and 'trawled' individuals showed significantly different Kaplan-Meier estimates, indicating a  
241 clear effect of the fishing process on survival. The main hypothesis explaining the mortality of intact individuals,  
242 additional to a potential captivity-induced mortality, could be the consequence of hyperactivity and stress  
243 induced when trapped in the trawl, that may be severe for this species potentially vulnerable to physiological  
244 stress like other decapods (Bergmann et al., 2001).

245 Overall, although globally high values were noted, variations in this study were observed in survival rates  
246 between species. Such variations might be explained by the great variability of biological traits of the  
247 invertebrate species considered, as well as their different vulnerabilities to crushing, increased activity when  
248 trying to escape the trawl, air exposure and thermal shock. For instance, whelks and hermit crabs have a very  
249 high resistance to mechanical damage (body crushing or cracked carapace) due to the presence of hard shells.  
250 Also, nearly all sea mice have survived the experiment, probably because of their specific anatomy showing no  
251 protruding elements and a dense and flexible body (Mettam, 1971). By contrast, decapods are not protected by  
252 hard shells, present protruding and fragile appendages, and are therefore more prone to injuries than other  
253 taxonomic groups. Starfish are also prone to injuries and subsequent bacterial infections because of their soft  
254 bodies, but their capacity for short-term survival and long-term regeneration render them less vulnerable to  
255 bottom trawling (M. Bergmann and Moore, 2001b; Ramsay et al., 2001).

#### 256 4.2. Methodological considerations regarding survival models

257 The overall survival models (SMMs) well fitted the data for three species: *Asterias rubens*, *Atelecyclus*  
258 *undecimdentatus* and *Pagurus* sp. Introducing the injury class as a covariate in SMMs for *M. brachydactyla*  
259 allowed the convergence of the optimisation algorithm that was non-convergent for the overall SMM. However,  
260 for the other species (*Aphrodita aculeata* and *Buccinum undatum*), the optimisation algorithm of SMMs did not  
261 converge to a single solution. This non-convergence is explained by the late death events just before the end of  
262 the experiment, combined with very high survival rates (hence a low overall number of death events) and non-  
263 negligible censorship. More samples and especially a longer experimental period, as recommended in previous

264 studies (M. Bergmann and Moore, 2001a, 2001b), would have been needed to better estimate their survival rates  
265 but this is difficult to achieve due to logistic constraints. However, depending on further use of such survival  
266 rates in other studies, the fact that they are very high is a crucial information by itself.

267 Most of the time, the modelled survival functions are conditional probabilities that individuals survive the tank-  
268 holding period given that they had survived capture and handling (Benoît et al., 2012; Demestre et al., 2018). In  
269 this study, injury classes were used instead of vitality levels, so only the overall probabilities that individuals  
270 survived the whole process were considered. The individuals being randomly selected among the catch, such  
271 probabilities are representative of the total impact of bottom trawling on the survival of invertebrates.

#### 272 *4.3. Recommendations*

273 The results go beyond the scope of this experimental study with further recommendations in terms of  
274 management and ecological implications.

275 Based on the current study, a recommendation that can be made is linked to the result that all decapods with  
276 carapace cracks die as a result of such injury. In contrast, more than 50-60% of individuals would survive if their  
277 carapace was intact, even if showing missing appendages as a result of trawling. Additionally, almost all spider  
278 crabs survived when completely intact. Therefore, even if the number of individuals showing severe injuries was  
279 low in the commercial fishing conditions of our study, gentle handling of crustaceans is nonetheless  
280 recommended to drastically increase their survival. It is especially important to reduce the risk of carapace  
281 cracks which would induce a certain death, and special care is recommended when sorting the catch and clearing  
282 nets as to avoid loss of appendages, even if injuries are less likely to happen during sorting than during the  
283 hauling process.

284 The results of this study complement other experimental research (*e.g.* Depestele et al., 2014) which clearly  
285 show that survival rates of discarded invertebrates are variable but most importantly generally high. However,  
286 ecosystem-level modelling for trophic and resource management studies (*e.g.* Forrest et al., 2015; Fulton et al.,  
287 2011; Link et al., 2010 using Atlantis and EwE) consider that all invertebrates discards die as a result of fishing.  
288 As such, all the discarded invertebrates would be available as food for consumers (Depestele et al., 2016).  
289 Discarded benthic invertebrates quickly sink to the seabed (Garthe and Hüppop, 1998; Hill and Wassenberg,  
290 2000), where they represent a variable contribution to the energy needs of benthic scavengers (Catchpole et al.,  
291 2006; Depestele et al., 2016; Groenewold and Fonds, 2000). However, while the importance of discarded  
292 invertebrates in benthic food webs is undeniable (Demestre et al., 2018; Heymans et al., 2016), the total biomass

293 of such available resource for scavengers, dependent on their survival rates, may still be poorly estimated. As a  
 294 result, the biomass of supposedly dead invertebrates may probably be much lower than predicted by the models,  
 295 because we show a high survivability for different species. This clear mismatch would lead to an overestimation  
 296 of available resources for scavengers and to an underestimation of invertebrates' biomass (Depestele et al.,  
 297 2019).

298 Another key element to fisheries management via ecosystem-level modelling is the estimated biomass of  
 299 discards from fisheries observers and commercial data. It is common practice for onboard observers to record  
 300 non-commercial invertebrates by weighing their total catch without precise distinction between taxonomic  
 301 groups (Cornou et al., 2018). It would be recommended to detail the level of resolution of fisheries data to more  
 302 specific taxonomic levels, in order to further improve the models by incorporating the discards biomass/survival  
 303 duet as an input parameter. This is of particular importance for non-commercial invertebrates for which data is  
 304 lacking.

### 305 **Declaration of competing interest**

306 The authors declare that they have no known competing financial interests or personal relationships that could  
 307 have appeared to influence the work reported in this paper.

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#### 484 **Figure captions**

485 **Fig. 1** Curves of post-capture survival functions. Overall (A) and injury class-dependent (B) survival mixture  
486 models (SMMs) with Weibull-type functions fit over Kaplan-Meier curves. Dashed lines indicate KM 95%  
487 confidence intervals. Green = injury class (IC) 1 (no visible damage), orange = IC2 (legs missing), red = IC3  
488 (major carapace cracks) and black = IC4 (crushed)

489 **Fig. 2** Proportion of individuals belonging to the different injury classes among all the individuals (A) and  
490 among the dead ones (B). Injury classes are shown using grey shading, from light grey corresponding to injury  
491 class 1 (no visible damage), to dark grey (injury class 4, crushed). The darkest shade of grey corresponds to the  
492 unknown status of one *Pagurus* in a moulting phase

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