Behaviour of adult sea trout *Salmo trutta* that survive or die at sea

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1 **Title:**

2 Behaviour of adult sea trout *Salmo trutta* that survive or die at sea

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14 **Declaration of interest:** None

15

16 **Abstract**

17 We tagged 125 sea trout kelts (460 – 925 mm) in seven Danish rivers with positively buoyant DSTs. Fifty-
18 three (42 %) tags were recovered, enabling a comparison of behaviour in kelts that survived the marine
19 period and kelts that did not. Data revealed an estimated mean survival time at sea of 14.3 days (range 1-
20 65 days) for fish that died at sea. Fish that did not survive had lower weight/length ratios when tagged than
21 survivors ($P = 0.005$) but exhibited a similar diel diving pattern while at sea. Both surviving and non-
22 surviving fish gradually increased diving activity and the daily visited maximum depths after sea entry, but
23 some performed fewer dives and resided in shallower depths than others. This difference was pronounced
24 when comparing surviving fish (most active divers) with fish caught by anglers (least active divers). The
25 results show that the first weeks at sea are critical for kelt survival and that physical status of kelts may
26 affect behaviour and probability of survival. The preference for shallower waters and less diving activity in
27 some individuals indicate that coastally based fisheries and recreational angling may select against specific
28 behavioural phenotypes which should be investigated more intensively.

29 **Key words:**

30 Sea trout; kelts; telemetry; survival; behaviour

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38 1. Introduction

39 The iteroparous nature of anadromous brown trout *Salmo trutta* L. (hereafter referred to as *sea trout*)
40 allows individuals to enter freshwater multiple times to spawn (Klemetsen et al. 2003), and large repeat
41 spawners may contribute with a disproportionately high production of juveniles (L'abée-Lund 1989). This
42 makes survival and success of repeat spawners important for the overall success of a given brown trout
43 population (Jensen et al. 2012). Spawning is energetically costly (Hendry et al. 2004), and the re-entry to
44 marine environments may be associated with high mortality for post-spawned individuals (termed as *kelts*,
45 Bendall et al. 2005; Thorstad et al. 2012; Aarestrup et al. 2015). Condition and physiology of kelts has been
46 shown to affect their migratory behaviour during this phase (Bordeleau et al. 2018; Birnie-Gauvin et al.
47 2019). Part of a decline in sea trout populations observed worldwide may be attributed to reduced marine
48 survival (Butler and Walker, 2006; ICES 2013) but detailed reports on kelt mortality at sea have not been
49 published so far (Thorstad et al. 2016). Studies have found overall marine survival of sea trout kelts ranging
50 from 18 to 86% with high mortalities in the early marine habitats like fjords and estuaries while mortality at
51 sea is unknown (Bendall et al. 2005; Bordeleau et al. 2018). It is estimated that 32 % of sea trout smolts
52 produced in Denmark eventually end up dying as a consequence of recreational angling from the coast or in
53 rivers (Nielsen and Koed 2016). Predators may also play a crucial role in sea trout mortality in the early
54 marine environment (Jepsen et al. 2018; Kristensen et al. 2018a) but their impact on kelts is unknown.
55 Danish (Aarestrup et al. 2015), Swedish (Aldvén et al. 2015) and British (Bendall et al. 2005) sea trout
56 generally migrate to sea in a relatively direct manner as opposed to their more northern conspecifics (e.g.
57 Eldøy et al. 2015; Jensen et al. 2014) and knowledge of aspects related to their mortality at sea are
58 therefore important for the management of the species (Drenner et al. 2012).

59 We therefore tagged 125 sea trout kelts with positively buoyant data storage tags (DSTs). This enabled us
60 to recover tags from fish that had died at sea (hereafter referred to as fish lost at sea) and compare the
61 observed behaviour in these with the behaviour in surviving individuals (hereafter referred to as returning

62 fish). The tagged fish had survived at least one successful marine period and were large in size compared to
63 adult sea trout studied in marine environments elsewhere (e.g. Bendall et al. 2005; Rikardsen et al. 2007;
64 Eldøy et al. 2015). The DSTs measured depth and temperature, and the aim of the study was to compare
65 these measurements to document behavioural traits in returning fish and fish lost at sea to reveal possible
66 differences between the two groups. We hypothesized that fish lost at sea would display different activity
67 levels and migratory tactics than returning fish.

68 2. Methods

69 2.1 Experimental area

70 The fish were caught and tagged in seven Danish rivers (Figure 1). Five of the rivers ran into fjords or
71 estuaries with outlets to either the southern North Sea or the Kattegat while rivers Liver and Uggerby ran
72 directly into the Skagerrak (Table 1, Fig 1.).

River	Runs into	River mouth to sea outlet	Outlet location	Tagged individuals
Ribe	Estuary	14.9 km	North Sea	4
Varde	Estuary	13.6 km	North Sea	39
Skjern	Estuary	19.1 km	North Sea	3
Uggerby	Sea	0 km	North Sea	10
Liver	Sea	0 km	North Sea	40
Villestrup	Fjord	22.1 km	Kattegat	13
Gudena	Fjord	31.7 km	Kattegat	16

73

74 **Table 1.** River information. The distance from the river outlet to the sea, name of the sea of entry and the number of fish tagged in
75 each river is given.

76 The seas surrounding Denmark are generally shallow with depths of 10-30 meters dominating the southern
77 parts of the Kattegat and North Sea, while depths exceeding 100 meters can be found in the Northern
78 North Sea, in Skagerrak and in the central Baltic Sea (Figure 1). A complex mixing regime and an almost
79 constant stratification is present in the Kattegat-region due to differences in salinity between the saline

80 North Sea (32-35 on the Practical Salinity Scale) and the brackish Baltic Sea (8-10 on the Practical Salinity
81 Scale) (Rasmussen 1995).

82
83 **Figure 1.** Maps of the study area with depth contour lines for 30 and 100 metres (left panel). Open circles represent the location of
84 the seven rivers where tagging took place. The 27 crosses on the right panel represent the pickup or capture location of the 25
85 recovered tags from fish lost at sea and the two corrupted tags that were found outside rivers and fjords.

86 **2.2 Data storage tags**

87 We used CEFAS Technology Ltd G5 long life archival tag (<http://www.cefastechnology.co.uk/>) fitted with a
88 string of 11mm diameter floats (the same diameter as the tag). Total length with floats was approximately
89 140 mm, weight in air was 9.8 g and the net buoyancy in full salinity sea water was 0.009 N, corresponding
90 to a negative weight in water of 0.9 g. The floating device was covered in silicon rubber (Dow Corning, 734)
91 that is biologically inactive and harmless to the fish (Thorstad et al. 2013). The tag type has not been used
92 in salmonids before, but studies of tagged European eel (*Anguilla anguilla*) found only few cases of partial
93 tag expulsion (12 %, but none were actually expelled) after six months (Thorstad et al. 2013).

94 The tags were programmed to record temperatures and pressure at 5-min intervals. Internal tag memory
 95 was sufficient to record a two-year period. Temperature range for the tags was -5 C to 35° C with an
 96 accuracy of at least 0.1° C and resolution of 0.03° C. Pressure, a proxy for depth, was measured in dbars (1
 97 dbar is equivalent to approximately 1 m in depth) to a maximum of 2000 dbars and an accuracy of $\pm 1\%$
 98 (20m) and resolution of 8 cm. Tags were fitted with a reward notice and address asking people to return
 99 the tag upon recovery. Data was downloaded from the tags on their return.

100 **2.3 Fish capture and tagging**

101 Sea trout kelts were electro-fished or captured in traps during downstream migration in the rivers during
 102 winter or spring (Table 2). The fish were anaesthetized (benzocaine 300 ppm) and the total body length and
 103 body mass was measured. The DST was inserted into the body cavity through a mid-ventral (8-10 mm)
 104 incision anterior to the pelvic girdle. The incision was closed with 2-3 separate sutures. The operation lasted
 105 between 1 and 2 min and the recovery time was 2-5 min. The tagging process was carried out in
 106 accordance with the guidelines described in permission 2012-DY-2934-00007 from the Danish Experimental
 107 Animal Committee.

108 In total, 125 kelts were tagged: 45 were tagged November 28th and December 12th 2012, while the
 109 remaining 80 kelts were tagged between March 13th and April 13th in the years 2012-2015.

110 Tagging data from fish that died before sea entry are presented in Table S1.

Tag ID	Type	Origin	Weight (g)	Length (cm)	Fulton's condition	Gender	Date of tagging	Date of sea entry	Marine period (d)
A08546	Returning	Liver	7150	91.5	0.93	F	16-03-2012	27-04-2012	47
A08609	Returning	Varde	1650	54	1.05	F	08-04-2013	10-04-2013	94
A08634	Returning	Varde	1650	57	0.89	F	08-04-2013	14-04-2013	87
A08579	Returning	Gudenaa	1850	56.5	1.03	M	27-03-2013	24-04-2013	105
A08534	Returning	Gudenaa	2400	58	1.22	F	27-03-2013	02-05-2013	89
A08577	Returning	Liver	1736	55	1.03	M	12-12-2012	06-05-2013	142
A08549	Returning	Gudenaa	2480	58	1.27	F	27-03-2013	09-05-2013	87
A08640	Returning	Villestrup	1860	60.5	0.84	F	13-04-2015	28-04-2015	118

Mean, returning fish		-	2597	61.4	1.03	-	-	-	96.1
A08565	Lost	Ribe	2525	67	0.84	F	14-03-2012	05-04-2012	19
A08563	Lost	Liver	4900	82.5	0.87	F	16-03-2012	10-04-2012	5
A08553	Lost	Liver	3190	71	0.89	F	16-03-2012	14-04-2012	4
A08539	Lost	Liver	1130	53	0.76	F	16-03-2012	20-04-2012	18
A08544	Lost	Ribe	1296	53	0.87	F	14-03-2012	20-04-2012	2
A08636	Lost	Varde	1550	58	0.79	F	08-04-2012	20-04-2012	10
A08643	Lost	Liver	3159	78	0.67	F	28-11-2012	17-12-2012	20
A08573	Lost	Liver	3630	75.5	0.84	F	28-11-2012	18-12-2012	2
A08758	Lost	Uggerby	2082	62	0.87	F	12-12-2012	21-12-2012	9
A08576	Lost	Liver	1289	54	0.81	F	12-12-2012	03-01-2013	1
A08762	Lost	Liver	2150	62.5	0.88	F	12-12-2012	15-01-2013	65
A08620	Lost	Varde	3900	73	1.00	F	08-04-2013	13-04-2013	17
A08601	Lost	Varde	2600	62	1.09	F	08-04-2013	15-04-2013	10
A08615	Lost	Varde	2620	64	1.00	F	10-04-2013	03-05-2013	46
A08590	Lost	Varde	1900	59	0.93	F	08-04-2013	05-05-2013	17
A08552	Lost	Gudena	1750	55	1.06	F	27-03-2013	11-05-2013	2
A08556	Lost	Varde	1823	57	0.98	F	04-04-2014	05-04-2014	22
A08576	Lost	Varde	2305	66	0.80	F	03-04-2014	06-04-2014	16
A08565	Lost	Varde	3508	74	0.87	F	04-04-2014	07-04-2014	3
A08556	Lost	Villestrup	3488	73	0.90	F	06-05-2015	13-05-2015	11
A08605	Lost	Villestrup	902	49.5	0.74	F	13-04-2015	23-05-2015	1
Mean, fish lost at sea		-	2462	64.2	0.88	-	-	-	14.3
A08549	Angled	Skjern	4070	78	0.86	F	13-03-2012	04-04-2012	26
A08640	Angled	Varde	4220	74	1.04	F	08-04-2013	17-04-2013	42
A08758	Angled	Villestrup	1539	60.3	0.70	F	27-03-2015	18-04-2015	8
A08543	Angled	Villestrup	1526	54.5	0.94	F	27-03-2015	07-06-2015	75
Mean, fish angled at sea		-	2839	66.7	0.89	-	-	-	37.8

111 **Table 2.** Tagging data for the eight returning fish, the 21 fish lost at sea due to unknown causes and the four fish caught by anglers
112 from the coast. The table contains tag ID, origin of the fish, weight, length, condition, gender, date of tagging and sea entry along
113 with marine period. Fulton's condition is given by $K = 100 \frac{Weight(g)}{Length(cm)^3}$.

114 2.4 Determining the duration of the marine period

115 Internal temperature and depth recorded by the recovered DSTs were downloaded from the tags and
116 analysed in R Studio version 1.0.136 (www.r-project.org).

117 Time of entry and exit to the marine environment was based on analysis of depth measurements. The fish
118 appeared to initiate the dive pattern described in Kristensen et al. (2018b) when reaching the marine
119 environment. Some of the fjords and estuaries entered by the fish in the present study are, however, only a
120 few metres deep, making it impossible for the fish to initiate the behaviour before reaching deeper waters.
121 It was therefore not possible with certainty to segregate between residency in rivers or marine
122 environments before the fish entered areas with deeper waters. We therefore focused on the sea, and
123 defined entry to and exit from the sea as the period between the first and last visit to a depth of 10 metres.
124 All fjords and estuaries except the fjord that River Villestrup runs into are shallower than this (a threshold
125 of 15 metres was used for fish from this river).

126 In some cases, fish would initiate their dive/surface residency behaviour with dives to 5-10 meters for 1-4
127 days before breaking the 10 metre threshold (Figure S1), indicating that the fish had entered the sea but
128 was not yet residing in areas with depths exceeding 10 metres. Close inspection of temperature data for all
129 fish revealed a decline in surface temperatures 0-4 days before sea entry (defined by the 10 metre
130 threshold), suggesting that the fish may have entered the sea 0-4 days sooner. We maintained the uniform
131 definition of first and last visit to a depth of 10 metre in spite of the possible 0-4 days of error associated
132 with doing so in order to maintain an unbiased data treatment.

133 **2.5 Determining mortality events**

134 Time of mortality of fish lost at sea was defined by visual inspection of temperature and depth plots. In
135 three tags, temperatures increased to 37° C for 1-2 days, suggesting that the tags had been ingested by a
136 marine mammal (Figure 2a). Eight tags sunk to the bottom and recorded small cyclic depth changes caused
137 by the tide (Figure 2b), suggesting that the tag had sunk with the fish or parts of it. Thirteen tags reported a
138 constant depth of 0 metres (Figure 2c), leaving few clues as to the cause of mortality.

139

140 **Figure 2.** Examples of mortality events with depth (blue line) and temperature (red line) records of different mortality profiles. 2a:
 141 Temperature increases to 37° C and returns to ambient levels 1-2 days later, suggesting marine mammal predation. 2b: The tag
 142 drops to the bottom where it records tidal amplitudes for two days before returning to the surface. 2c: Recorded depths suddenly
 143 stabilizes at 0 m until the tag reaches shore a day later (temperature starts fluctuating).

144 The timing of mortality was easily distinguishable with a precision of a few measurements (<15 minutes) for
 145 23 of the 25 recorded mortalities. For the remaining two records, it was hard to determine with accuracy
 146 when mortality occurred as the fish was resident very close to the surface around the time of death.

147 2.6 Defining a dive

148 All individuals appeared to initiate a characteristic diving pattern (Kristensen et al. 2018b) once they
 149 reached the sea. The present study follows the definition of a dive that was used by Reddin et al. (2011)

150 and Kristensen et al. (2018b) where a dive is defined as an entry to depths deeper than 5.0 metres, and
151 each dive is logged at the time of the first measurement in depths deeper than 5.0 metres. The duration of
152 the dive is determined by the number of subsequent measurements at depths deeper than 5.0 metres,
153 while the dive is defined as terminated once the fish enters depths shallower than 5.0 metres again.

154 **2.7 Data analysis**

155 Weight/length relationships between different groups of fish were analysed with general linear models
156 where weight of the fish in grams was entered as response variable and length and type of fish were
157 entered as explanatory variables. Both weight and length were square root transformed to linearize the
158 relationship and to ensure model assumptions were met.

159 Generalised linear mixed effects models were used to analyse if returning fish behaved differently
160 compared to fish caught by anglers and fish lost at sea in terms of daily dive frequency and daily maximum
161 depths at sea. Only four fish were caught by anglers at sea, which technically is too few to include as a
162 separate group. The models, however, displayed some behavioural differences between the groups well,
163 and fish caught by anglers were therefore included as a separate group to illustrate this.

164 The models included data from the first 20 days at sea, as most fish lost at sea died within this period. The
165 33 fish that entered the sea are divided into four groups: Returning fish (group 1, $n = 8$), lost fish where the
166 tag started floating after mortality or the fish was predated (group 2, $n = 13$), lost fish where the tag sunk
167 to the bottom after mortality (group 3, $n = 8$) and fish caught by anglers (group 4, $n = 4$).

168 A negative binomial generalised linear mixed effects model was used to analyse for differences in diving
169 frequencies among the four groups of fish. Number of dives per day was entered as response variable while
170 days since marine entry and fish mortality type were entered as fixed effects and fish ID was entered as
171 random effect. Negative binomial was used for the amount of dives per day since the conditional variance
172 exceeded the conditional mean in Poisson-regression models due to high variation of the diving activity.

173 Model diagnostic by visual inspection of residuals plotted against the data showed no signs of violation of
174 model assumptions. The dispersion statistics of the model was 1.06, revealing no signs of over- or
175 underdispersion of the model (Zuur et al. 2009).

176 A gamma distributed generalised linear mixed effects model with a log link was used to analyse for
177 differences in daily visited max depth among the four groups of fish. Daily depths were entered as response
178 variable while days since marine entry and fish mortality type were entered as fixed effect and fish ID was
179 entered as random effect. The diagnostics of this model showed no patterns when residuals were plotted
180 against the data.

181 The R-package glmmTMB (Brooks et al. 2017) was used to run the models.

182 **3. Results**

183 **3.1 Tag return rates**

184 Six of the eight tags from returning fish were recovered by recreational anglers who caught the fish after it
185 had returned to the river. The seventh tag from a returning fish was recovered after the fish was electro
186 fished for stocking efforts while the eighth tag from a returning fish was found on the river bank (without
187 the fish).

188 Seven of the 21 tags from fish lost at sea were found along Danish shorelines, nine tags were found along
189 Swedish coastlines and the remaining five tags were found along Norwegian coastlines (Figure 1).

190 All five tags that contained corrupted data were found in the water or along coastlines.

Figure 3. Fate of the 125 tags. In total, 33 tags had recorded fish behaviour from the sea.

Inspection of the data from the 21 fish lost at sea but where mortality reasons were unknown (as exemplified on Figure 2b and 2c) suggested that the tags had been drifting in the water for a mean period of 24 days (range: 0 – 101 days) before reaching shore. Some tags were found almost instantly after reaching shore, while extensive temperature fluctuations suggested that other tags had been deposited on dry land for weeks or months before recovery.

3.2 Size and condition of the fish

The mean weight of all 125 tagged fish was 2640 g (range: 760 – 7250 g), the mean length was 65.3 cm (range: 46.0 – 92.5 cm) and the mean Fulton's condition was 0.88 (range: 0.66 - 1.28). Fulton's condition is given by $K = 100 \frac{Weight(g)}{Length(cm)^3}$. The distribution of the tagged fish is presented in Figure 4.

204 **Figure 4.** Distribution of the 125 tagged fish. 4a: Weight (g) of the fish in 500 g intervals. 4b: Length of the fish (cm) in 5 cm
 205 intervals, 4c: Fulton's K in intervals of 0.06.

206 Mean weight of the 72 fish where tags were not returned and the 53 fish where tags were returned was
 207 identical (2640 g) while mean length was nearly identical (65.3 cm for fish with non-returned tags and 65.2
 208 cm for fish with returned tags). The weight/length relationship for the two groups of fish displayed on
 209 Figure 5a was not significantly different according to the general linear model ($P = 0.24$, $R^2 = 0.91$).

210 The present study mainly focuses on comparison of the eight returning fish, the 21 fish that were lost at sea
 211 and the four fish that were caught by anglers at sea. Fish lost at sea at had a significantly lower
 212 weight/length relationship ($P = 0.005$) than returning fish. Fish caught by anglers were similar to fish lost at
 213 sea, but the difference between fish caught by anglers and returning fish came out with a higher P-value of
 214 0.089 (Figure 5b), likely due to the much smaller sample size of fish caught by anglers. The R^2 of the model
 215 was 0.93.

217 **Figure 5.** Linear model of weight/length relationship for different groups of fish. Shaded areas represent 95 % confidence intervals
218 and points represent individual fish. 5a: Fish where the tag was returned vs. fish where it was not. 5b: Returning fish vs. fish lost at
219 sea and fish caught by anglers at sea.

220 **3.3 Survival and duration of marine period**

221 Fifteen returned tags contained data suggesting mortality prior to sea entry. Eight of these tags did not
222 record depths greater than 2.0 metres before the fish died, while four recorded max depths between 2-9
223 metres before fish mortality, suggesting that the fish could have reached the fjord or estuary. The
224 remaining three tags had recorded max depths between 2-8 metres before the fish that carried them were
225 caught by anglers in the fjords. A total of seven kelts could therefore have reached the marine environment
226 without entering the sea before mortality.

227 The present study only analyses data from fish that certainly made it to sea (based on the 10 metre
228 threshold). It therefore disregards these seven fish that either could have or certainly did reach the marine
229 environment due to the uncertainty associated with their fate and possible timing of marine entry.
230 Including these seven fish in the analyses does not change the output and conclusions, but it introduces
231 additional uncertainty.

232 The tagged fish spent a mean of 26.3 days (range: 1-142 days) in the river or fjord/estuary between tagging
233 and sea entry. Fish lost at sea spent a mean of 22.0 days (range: 1-72 days) in river/fjord/estuary before
234 entering the sea, and survived for a mean period of 40.0 days (range: 6-99 days) after tagging.

235 Mean duration of the period spent at sea for the eight returning fish was 96.1 days (range: 47 – 142 days,
236 Table 2), while fish caught by anglers survived 37.8 days (range: 8-75 days) at sea and fish lost at sea
237 survived 14.3 days (range: 1-65 days) at sea. It was not possible to determine the duration of the marine
238 period (including fjords/estuaries) with the present dataset. Using kelt movement rates of Aarestrup et al.
239 (2015) of 1.6 km d^{-1} during outmigration through a Danish fjord on the fish that had to migrate through

240 fjords on estuaries adds 6.4 days to the mean time spent at sea, resulting in a mean marine survival time of
241 20.7 days for the present dataset.

242 Three of 21 natural mortalities at sea had mortality profiles similar to Figure 2a, where a warm blooded
243 animal presumably ingested the tag. Eight mortality profiles were similar to Figure 2b, where the tag sunk
244 to the bottom for a period of time and 10 mortalities were similar to Figure 2c where the tag started
245 floating.

246 Of 21 natural mortalities at sea, 19 could be determined with a precision of 5-10 minutes. Eight of these
247 mortalities (42 %) occurred during daytime, seven (37 %) occurred within one hour from sunrise and sunset
248 and four mortalities (21 %) occurred during nighttime. Mean day length on the day of mortality was 13.7
249 hours for the 19 precisely determined natural mortality events at sea, corresponding to a mean of 57 %
250 daytime, 17 % crepuscular hours and 26 % nighttime at the time of death. The three recorded predation
251 events from warm-blooded animals occurred during daytime (n =1) or crepuscular hours (n = 2).

252 **3.4 Behaviour at sea**

253 All fish exhibited a distinct diel behavioural pattern with pronounced diving activity during daytime and
254 residence close to the surface with very little vertical movement during night time (Figure 6). Although
255 large variation occurred between individuals and in time, the typical pattern was for the fish to perform a
256 dive of 10-25 minutes duration and return to shallow depths of 0-3 metres for 30-40 minutes before diving
257 again. The behaviour has previously been described for the returning fish of the present study by
258 Kristensen et al. (2018b). Most dives peaked at depths between 10-20 metres, though the record dive of
259 the dataset was 88 metres. Some individuals only rarely visited depths deeper than 10 metres, possibly due
260 to dive depth restriction caused by the sea floor in the area of residence.

261

262

263 **Figure 6.** a) Example of diel behaviour during June 2013 with depth (blue line) of a returning fish (A08549) where shaded areas
 264 represent night time (20-04 hours). Note how the fish dives repetitively during daytime but is almost constantly residing at the
 265 surface during nighttime b) Proportion of the 20 first days at sea where each individual fish performed at least one dive during a
 266 given hour of day. The eight rows in the bottom represent returning individuals, the next four rows are fish caught by anglers and
 267 the top 17 rows are fish lost at sea. The blue colours dominating before 4 and after 19 hours reveal that the fish generally perform
 268 few or no dives during evening and night time while the yellow and orange colours between 4 and 19 hours reveal that the fish dive
 269 more frequently during these hours. Four fish resided <3 days at sea before dying and are not included.

270 The fish caught by anglers were the least active in terms of diving activity and had also resided at the most
 271 shallow depths (Figure 7). The diving activity generally increased with time after sea entry for all fish. Mean
 272 number of dives per day for all kelts was 14.3 (range: 2.3 – 27.2).

Figure 7. Histograms of daily measurements at depths of 0-3 m (light blue), 3-6 m (medium blue) and deeper than 6 m (deep blue) for returning and fish caught by anglers during the first 40 days at sea. Fish caught by anglers reside more in shallow (0-3 m) waters than returning fish, thus suggesting that these fish were more likely to get caught in the first place due to the high coastally based fishing pressure in the area.

We investigated the diving activity and daily visited max depth with generalized linear mixed models, although the sample size of the fish caught by anglers was not sufficient for an ideal investigation of this.

The modelled output for diving activity (Figure 8) indicated a lower diving activity in fish caught by anglers ($P = 0.035$) while days since marine entry had an overall significantly positive effect on the diving activity ($P < 2e^{-16}$, Table 3).

283

284 **Figure 8.** Modelled daily dives since sea entry (8a) and daily visited max depth (8b) for returning fish (1), fish lost at sea where the
 285 tag floated immediately after mortality (2), fish lost at sea where the tag sunk after mortality (3) and fish caught by anglers (4).
 286 Shaded areas represent 95 % confidence intervals of the model, while points represent actual observations. Diving activity is higher
 287 for returning fish and gradually increases for all types after marine entry though less pronounced for fish caught by anglers. The fish
 288 caught by anglers also visited more shallow max depths.

289 The model for daily visited max depth (Figure S3) revealed a tendency for increasing max depths after
 290 marine entry, while the fish caught by anglers appeared to have visited the shallowest max depths (Table
 291 3).

Diving activity					Max depths				
	Value	SE	z-value	P		Value	SE	z-value	P
Intercept	1.989	0.300	6.638	<0.0001	Intercept	2.285	0.169	13.546	<0.0001
Days at sea	0.321	0.034	-2.110	<0.0001	Days at sea	0.008	0.005	1.472	0.141
Returning	0	-	-	-	Returning	0	-	-	-
Lost, floats	-0.125	0.378	-0.330	0.741	Lost, floats	0.353	0.206	1.714	0.087
Lost, sinks	-0.371	0.476	-0.778	0.436	Lost, sinks	0.039	0.242	0.162	0.872
Angler	-1.110	0.526	-2.110	0.035	Angler	-0.415	0.276	-1.502	0.133

292 **Table 3.** Summary of the mixed models analyzing diving activity and daily max depths for the first 20 days at sea. Model parameter
 293 estimates, associated SE, z-values and p-values are given. A negative binomial distribution was used for the diving activity while a
 294 gamma distributed model was used for maximum depths.

295 4. Discussion

296 Large repeat spawning sea trout may contribute with a disproportionately high production of juveniles
 297 (L'abée-Lund 1989) thus making them important for the overall success of a given brown trout population
 298 (Jensen et al. 2012). We used positively buoyant data storage tags to generate the first detailed records of
 299 behaviour in adult sea trout that either died at sea or survived their marine period and returned to spawn.
 300 Our aim was to investigate whether the two groups behaved similarly in terms of activity levels and
 301 migratory behaviour.

302 4.1 Return rate and effects of the positively buoyant DSTs

303 The 6.4 % return rate (8/125 tagged fish) for tags from returning fish is low compared to other studies,
 304 while the total return rate of 42 % (53/125 tagged fish) is within the normal ranges achieved by other
 305 studies relying on active recapture methods for non-floating DSTs as discussed by Kristensen et al. (2018b).

306 The method of the present study was, however, mainly passive, and a total of 43 tags (34 %) were returned
307 by citizens who had found the tag without the fish. The floating characteristic of the tag therefore
308 succeeded in enabling collection of a dataset with behavioural reports from both returning fish and fish lost
309 at sea. This is unique compared to other DST-studies where the reported behaviour is based exclusively on
310 surviving individuals and therefore does not contain analysis of behavioural differences between surviving
311 and non-surviving fish.

312 The number of tags returned due to the floating characteristic is high compared to Righton et al. (2016)
313 that is the only existing study in the literature to have used positively buoyant DSTs on other species and
314 recovered 9 % of tags from ocean-going European eels (*Anguilla anguilla*).

315 A tag with the size of the DSTs used in the present study could have affected both fish behaviour and
316 survival, and the reported mortalities should therefore be considered a pessimistic estimate. The tagged
317 fish were, however, post-spawned with plenty of room in the body cavity for the tag, and there were no
318 reports on tag-related wounds or infections from fish that were caught alive. The fish lost at sea spent 22.0
319 days in river/fjord/estuary before entering the sea, and the distribution of recorded mortalities in this
320 phase (31 % or 15/48 recovered, non-corrupted tags) was below that observed in studies of kelts in
321 Denmark using smaller acoustic tags. Aarestrup et al. (2015) recorded a loss of 37 % in the river/fjord phase
322 for kelts from the River Gudenaa using 29 mm tags. A study from 2017 and 2018 recorded a river/fjord loss
323 of 62 % in kelts from rivers entering a different fjord system (the Limfjord, Kristensen et al. 2019) using 13
324 mm tags.

325 A total of 17 tags were recovered from anglers who had caught the fish (n=3 from rivers, n=3 from fjords,
326 n=4 from the sea, n=7 from returning fish back in the river), none of which had observed tag related
327 damage or disease in the fish. One of the returning fish was handed over for dissection, revealing no
328 inflammatory response to the tag that had been encapsulated in tissue. We have therefore observed no

329 particular negative effects related to using positively buoyant tags compared to other tag types, although
330 future studies could ideally investigate this further.

331 The high early mortality at sea observed in the present study could in principle be due to the fish most
332 likely being closer to shore in the first weeks after reaching the sea (Kristensen et al. 2018b) if tags from fish
333 that die here have a higher chance of being found. 67 % of the tags that were found from fish lost at sea
334 were, however, found on Swedish or Norwegian coastlines, most likely after being moved there by
335 dominating W-SW winds in the region. The mean drifting time from expel-time to reaching the shore was
336 24 days (range: 0 – 101 days), and tags therefore appeared to be capable of surviving marine conditions for
337 long enough to reach shore and be found as long as the fish resided within the seas surrounding Denmark.
338 The fish may have moved into open sea during July and August as suggested by Kristensen et al. (2018b)
339 and Klemetsen et al. (2003) but likely not into the actual ocean as for Righton et al. (2016).

340 **4.2 Size and condition of the fish**

341 The size of the fish that were tagged in the present study (46.0 – 92.5 cm) have some size overlap with the
342 kelts tagged by Aarestrup et al. (2015) that measured between 30 and 87 cm. The fish were, however,
343 considerably larger than adult sea trout studied outside Denmark, e.g. 27.5 – 58.0 cm in Eldøy et al. (2017)
344 and 37.0 – 51.2 cm in Rikardsen et al. (2007). The difference is likely attributed to a general size difference
345 between Danish and more northern sea trout populations.

346 The low condition factor of the tagged fish (mean = 0.88) reflects that only post-spawned individuals were
347 tagged to avoid spawning-related tag loss and to ensure that there was room for the tags in the body
348 cavities. The statistically significant difference ($P = 0.005$) between condition factor of returning fish (mean
349 = 1.03) and fish lost at sea (mean = 0.87) indicates that condition may influence chances of survival.

350 Other physiological parameters such as levels of cortisol stress hormones may also affect migration timing
351 according to a recent study including Danish sea trout kelts (Birnie-Gauvin et al. 2019). Further investigation

352 of the effect of physiology on behaviour may therefore broaden our understanding of drivers behind
353 migratory behaviour and survival chances in salmonids.

354 **4.3 Survival and duration of marine period**

355 Timing of outmigration to the sea is within the normal period for fish that migrated during spring
356 (Aarestrup et al. 2015). Migration timing of the 45 fish tagged on November 28th or December 12th are
357 incomparable, as no other published or unpublished studies on Danish sea trout kelts have tagged fish
358 during that time of year.

359 The early marine stage is generally risky for downstream migrating salmonids, and high early mortality is
360 frequently observed in the marine environment (Thorstad et al. 2016). The present study reinforces
361 previous findings on kelt survival, but also adds to it because no previous studies have identified at-sea
362 mortality events. The 15 fish (31 % of the 48 returned, non-corrupted tags) that died before sea entry are
363 the ones that should be compared with e.g. the early mortality of other studies, like the 37 % in Aarestrup
364 et al. (2015) and 38 % in Bendall et al. (2005). Even these values are not entirely comparable, as the fish
365 from rivers Liver and Uggerby entered the sea directly. Pre-sea mortality was, however, 26 % for the
366 remaining systems as river-mortality was quite high in rivers Liver and Uggerby. Biases related to the
367 likeliness of people finding tags from dead fish in rivers versus fjords and the sea, however, means that the
368 setup used in the present study is not ideal for determining mortality rates.

369 Early marine mortality appeared high with 19 of 21 mortalities (not including fish caught by anglers)
370 occurring within the first 22 days after reaching the sea and mean survival time at sea being 14.3 days
371 (excluding fish caught by anglers). Adding the calculated time spent in fjords and estuaries increases the
372 marine survival time to 20.7 days excluding fish caught by anglers. This number is uncertain, but the first
373 three weeks after entering the marine environment appears to be a critical period for Danish sea trout
374 kelts.

375 Data revealed three incidents of tags being ingested by warm-blooded animals. Harbour seals *Phoca*
376 *vitulina* and grey seals *Halichoerus grypus* have become abundant in the seas surrounding Denmark (Larsen
377 et al. 2015), and may potentially predate on sea trout kelts as appeared to have occurred for these three
378 fish. Seals mainly hunt within 30 km from shore (McConnel et al. 1999, Tollit et al. 1998), and are therefore
379 capable of covering most of the seas surrounding Denmark. Harbor porpoises *Phocoena phocoena* is
380 another warm blooded predator that is present in the region, but these are not expected to catch prey
381 items larger than 26 cm in size and are thus less likely to have preyed on the trout kelts (Recchia and
382 Read, 1989).

383 Eight tags sunk (supposedly with the fish or parts of it) after mortality, while ten tags floated immediately
384 after mortality, suggesting the tag was no longer in the body cavity of the fish after the final measurement.
385 We consider it unlikely that these are all tag expulsions, as the size of the tag and the floats used in the
386 present study is quite large, and full expulsion were not documented in eels (Thorstad et al. 2013). Single
387 incidents of expulsion could, however, have occurred. Seal-predation cannot be ruled out as the final fate
388 of these fish either, as seals do not swallow large fish like sea trout kelts whole, but will tend to open the
389 fish and eat parts of it (Larsen et al 2015). Fish sinking with the tag could also be a consequence of mortality
390 due to energy depletion, infections or other late effects of spawning or the tagging procedure.

391 Four of 25 mortalities in fish that reached the sea were due to anglers catching the fish. Angling for sea
392 trout from the coast is popular in Denmark, and 32 % of produced wild sea trout are estimated to
393 eventually end their life due to angling (Nielsen and Koed, 2016). This makes angling an important factor to
394 consider in the management of the species.

395 **4.4 Behaviour at sea**

396 The behaviour with repetitive dives during daytime and a pause at the surface during night time described
397 for the returning fish in Kristensen et al. (2018b) was generally observed for all fish, although some of the
398 fish lost at sea fish had unstable diving patterns. The possibility that fish that die do not establish good diel

399 movements and stay closer to the surface, thus making them more vulnerable to predators and anglers and
400 potentially less able to find food, should be investigated further.

401 With 33 fish from seven Danish rivers following this diel behavioural pattern to a more or less pronounced
402 degree, we hypothesise that this behaviour could be widespread for sea trout outside the arctic region
403 where continuous light during summer may be responsible for the absence of diel patterns in sea trout
404 there (Rikardsen et al. 2007).

405 Although not finally proven, the repetitive diving strategy observed in sea trout kelts of the present study
406 and for other anadromous fishes in the Atlantic (Reddin et al. 2011) and Pacific (Walker et al. 2000) is likely
407 related to foraging, thus making it important for acquiring food leading to success at sea. If the energetic
408 status of the fish is too low to enable this behaviour, it may compromise the chance of survival. According
409 to the GLMM, the number of dives per day increased with date after sea entry for all fish as in Reddin et al.
410 (2011). Returning fish appeared to be more active, and were also significantly more active than fish caught
411 by anglers.

412 This difference could be related to foraging strategy or predator avoidance and suggests that condition may
413 affect migration behaviour as observed in Atlantic salmon in rivers by Halttunen et al. (2013) and in the
414 marine environment as observed in sea trout by Bordeleau et al. (2018). In Bordeleau et al. (2018), fish
415 condition was negatively correlated with the likeliness of it migrating to the outer parts of the fjord. The
416 data from the present study were, however, not conclusive in this sense, possibly due to the complexity
417 and general shallowness of the seas surrounding Denmark. A similar study with fish from a single river with
418 direct access to a sea area with deep waters close to shore may be more suited for future investigation of
419 differences in behaviour related to condition or physiological parameters.

420 The apparent preference for shallow depths and fewer foraging dives in some fish raises the possibility of
421 angler and fisheries-induced selection due to the pronounced angling and fisheries efforts from coastlines
422 in the region. Harvest based selection has been observed for other species (Philipp et al. 2008; Uusi-

423 Heikkilä et al. 2008), and could over time affect the distribution of sea trout phenotypes and have negative
424 effects for ongoing efforts to increase angling for sea trout from Danish coasts. The dataset from the
425 present study is too small to determine if residency in shallow depths occurs randomly or is a particular
426 preference of some individuals, thus possibly exposing sea trout to selection from coastal-based angling. A
427 more confined study setup with fish from a single river in collaboration with people angling on nearby
428 shorelines could generate a larger dataset on this.

429

430 In summary, we observed high early marine mortality in Danish sea trout kelts, consistent with other
431 studies on salmonids, but we also recorded mortality in the sea after a considerable period of time had
432 passed. Mortality appeared high for the first three weeks at sea, confirming that this period is critical for
433 the survival of salmonid kelts. Fish caught by anglers or fish lost at sea due to natural reasons were in
434 poorer condition when tagged than fish that survived the marine period and returned to the rivers again.
435 Once in the sea, the fish gradually increased their diving activity and to some extent also their daily visited
436 max depths. Surviving fish appeared to be more active than non-surviving fish in terms of diving activity,
437 which was particularly true when comparing with non-surviving fish caught by anglers that had also
438 preferred residency on shallower depths. This is the first study to provide detailed behavioural data of
439 surviving and dying sea trout kelts, and the results suggest the physical status of kelts prior to entering the
440 marine environment may affect their behaviour and survival chances at sea.

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444

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