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Published in:
Ecology of Freshwater Fish

Link to article, DOI:
[10.1111/eff.12460](https://doi.org/10.1111/eff.12460)

Publication date:
2018

Document Version
Peer reviewed version

[Link back to DTU Orbit](#)

Citation (APA):
Birnie-Gauvin, K., Højrup, L. B., Kragh, T., Jacobsen, L., & Aarestrup, K. (2018). Getting cosy in freshwater: assumed-to-be brackish pike are not so brackish after all. *Ecology of Freshwater Fish*, 28(3), 376-384.
<https://doi.org/10.1111/eff.12460>

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Getting cosy in freshwater: assumed-to-be brackish pike are not so brackish after all

Accepted for publication in Ecology of Freshwater Fish

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Running title: pike movement in a coastal river

25 **Abstract:**

26 Pike (*Esox lucius*) occupy coastal streams and rivers of the Baltic Sea, where they attain large sizes
27 (>5kg). These large sizes are perhaps due to the fact that they can tolerate relatively high salinities
28 and can thus forage in the nearby more productive brackish environments. In an attempt to quantify
29 the extent to which pike utilize brackish environments, and to provide some insight on the
30 underlying causes for brackish water migrations, we tagged 30 pike from a western Baltic river with
31 acoustic transmitters and were able to track 21 individuals for one year. Based on local anglers, this
32 population was assumed to be brackish in nature, where individuals underwent freshwater
33 migrations to spawn. Our findings however suggest that the smallest and most active individuals
34 make short exits into brackish waters, and do so on rare occasions. Our results further indicate that
35 neither sex nor size are related to activity level. We suggest that these patterns reflect two distinct
36 behaviours – active and passive – and that large pike can be supported by the food availability in
37 the river, without the need to venture into coastal zones, thus defying the conventional view that
38 Baltic pike are all brackish in nature.

39
40 **Keywords:** brackish, *Esox lucius*, ecosystem functioning, freshwater, reproductive migrations

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49 **Introduction:**

50 Northern pike (*Esox lucius*, Linnaeus) is a signature apex predator of many freshwater ecosystems
51 in the Northern Hemisphere. As such, this species has a great top-down impact on the structure,
52 abundance and composition of prey fish within a system (Johnson 1966; Skov *et al.* 2002; Craig
53 2008), and thus acts as an important regulator of fish assemblages, including on nutrient levels and
54 cycles. Evidence suggests that pike can affect the behaviour and movements of prey fish (Jacobsen
55 and Perrow 1998), and alter foraging activity (Bean and Winfield 1995; Jacobsen and Perrow
56 1998), with important ecosystem-scale impacts, including nutrient levels and cycles (Skov *et al.*
57 2011). The role of pike in local ecosystem functioning implies its ecological importance in
58 temperate freshwater systems.

59 Recently however, pike populations – like many other freshwater fish populations – have
60 been exposed to extensive habitat changes and other perturbations, largely stemming from
61 anthropogenic pressures (Craig 2008). This has resulted in considerable research on pike ecology in
62 recent times, especially geared towards investigating the implications of habitat and food chain
63 alterations for conservation and management purposes. Furthermore, given their prized value as a
64 sport fish, Northern pike have received much attention for their performance associated with
65 various fishing gear, as well as their survival during catch-and-release practices (*e.g.* Arlinghaus *et*
66 *al.* 2009).

67 Northern pike have been found living in both fresh (*i.e.* rivers and lakes) and brackish
68 waters (low salinity, estuary-like; Harvey 2009). Despite their common use in research and
69 widespread distribution however, few aspects of the species' life history appear constant across all
70 populations. Instead, research on pike seems to support a more diverse and flexible life history, with
71 different populations behaving differently in space and time. For example, there is evidence
72 suggesting that under laboratory conditions pike activity peaks at approximately 20°C and

73 decreases gradually at lower temperatures (Casselman 1978). Given these findings, a lower activity
74 level during winter (in comparison to summer) is expected. This is both corroborated (*e.g.* Kobler *et*
75 *al.* 2008) and contradicted (Jepsen *et al.* 2001; Koed *et al.* 2006), supporting the idea that pike can
76 display flexible behaviour, perhaps as a function of their specific environment.

77 Fish movement is arguably the most important behaviour, as it regulates foraging activity
78 and efficiency, predator avoidance and refuge seeking, as well as habitat selection (Shreck *et al.*
79 1997). Movement is thus an important determinant of fish fitness as it is associated with various
80 fitness endpoints such as growth, reproductive success and survival (Scherer 1992; Schreck *et al.*
81 1997; Barton *et al.* 2002). Understanding the spatial and temporal movements of a species can thus
82 focus management efforts and make them more profitable. To that effect, understand the
83 underpinning mechanisms behind the flexibility in pike life history may also help improve the
84 current management approach.

85 Several studies have investigated pike movement, and have found that pike can be
86 abundant in coastal areas with low salinity. This is the case in Denmark, Finland, Sweden and
87 Germany for example, where pike are often found in coastal streams and rivers of the Baltic Sea
88 (Craig 2008), with salinities approaching their upper tolerance limit. In the Baltic Sea, two Swedish
89 pike populations were found to reproduce in different environments: one displaying an anadromous
90 behaviour, with obligate freshwater spawning, and the other spawning in brackish Baltic waters
91 (Westin and Limburgh 2002). This reproductive behaviour in brackish waters has also been
92 observed in Finland for example (Lappalainen *et al.* 2008). Pike eggs and fry have also been shown
93 to tolerate high salinities (Jørgensen *et al.* 2010). It is thus perhaps not surprising that pike spawn in
94 brackish waters. Nonetheless, understanding the drivers and the extent to which this flexible
95 behaviour is present in pike populations is necessary to understand population dynamics, and advise
96 adequate management measures. In this study, we aimed to investigate the movements of a Danish

97 pike population inhabiting a coastal river flowing into the Baltic Sea. Based on local angler
98 knowledge (from local angling clubs for example), brackish-water environments were expected to
99 be of considerable importance for this population. This idea stems from the fact that this pike
100 population is composed of very large individuals, and that feeding strictly in a small freshwater
101 river is thought to be insufficient for individuals to attain such sizes. In fact, this population has
102 long been assumed to be a brackish-water population, with individuals journeying into freshwater
103 only to spawn (*i.e.* anadromous). We tested this hypothesis by tagging and tracking pike with
104 acoustic transmitters over the course of one year.

105

106 **Materials and Methods**

107

108 *Study area*

109 River Tryggevælde, southeast Sealand, Denmark (**Figure 1**), is home to a population of Northern
110 pike comprising many large individuals (> 5 kg), supporting a valuable recreational angling
111 community. The pike population has long been assumed to consist of mainly brackish-water
112 individuals, driving the population's large individual mass and condition factor. The river is
113 approximately 45 km long, and flows into Køge Bay which gives into the Baltic Sea. Our study
114 focused on the 12 downstream-most river kilometres, and the river outlet (river mouth, where the
115 river exits into the bay).

116

117 *Fish*

118 Pike were caught between 9 March and 11 March 2014, either by electrofishing ($n = 18$) or angling
119 ($n = 12$) along the banks of the river between 500 and 5000 m from the outlet (within the receiver
120 range, see below). Individuals were kept in carp sacks or a large live-well placed in the river for up

121 to 24 hours. For the procedure, fish were anesthetized with 0.05mg l⁻¹ of 2-phenoxyethanol in
122 freshwater. Fish were then weighed, measured, sexed, and implanted with an acoustic transmitter
123 (V13-1L, Vemco, 13 mm in diameter, 36 mm in length, 11 g in air, Nova Scotia, Canada). The
124 incision was closed with two absorbable sutures (Vicryl 3-0 FS-2, Ethicon, Scotland). The
125 procedure took between 3 and 5 minutes. Fish were then placed in a tank with fresh river water, and
126 later released on either 10 March or 11 March 2014 at their site of capture. See *Table 1* for
127 summary data.

128

129 *Environmental variables*

130 Water temperature was monitored every 30 minutes using a temperature logger (HOBO Pendant
131 Temperature/Light Data Logger 8K, UA-02-08) at the outlet (82m from the outlet). Salinity was
132 measured once per hour using a conductivity logger (HOBO Conductivity Data Logger, UA-002-C)
133 at two positions (82 m and 2818 m from the outlet). Water discharge data were obtained from the
134 Ministry of the Environment using a logger situated approximately 16 km from the outlet.
135 Discharge was adjusted for size of the water catchment. Loggers were positioned in the river and
136 outlet on 25 June 2014, approximately 108 days after fish were tagged and released in the river.

137

138 *Tracking movements*

139 Movements were tracked with 12 automatic listening stations (VR2 receivers, Vemco, Nova Scotia,
140 Canada) placed strategically along the river and river outlet to detect fish movement within the river,
141 but also to detect fish as they moved in and out of the river and into the bay (*Figure 1*). Range testing
142 using a 'dummy' tag took place before fish were released, and ranged between 60 and 200m. Signal
143 detection efficiencies were between 70 and 100 %. At locations where detection efficiencies were

144 lower, two receivers were positioned nearby with overlapping ranges (see *Table 2* for details on
145 position and efficiency of receivers).

146 Of the 30 tagged pike, 21 (16 females and 5 males) were detected for one full year. Only
147 those individuals were used for movement analyses. The remaining 9 individuals either died (1 female
148 and 4 males) or disappeared from the study area (2 females and 2 males).

149 We measured the number of exits out of the river performed by each fish as periods when
150 fish were detected at receivers outside the river for 1 hour or more. One hour was chosen as the cut-
151 off after initial investigation of the data, which suggested fish seldom spent less than 1 hour when
152 venturing out. Furthermore, a shorter cut-off may not have been biologically significant in terms of
153 feeding, while a longer cut-off may have removed valuable data. Total distance moved was
154 determined as the sum of the distance between different receivers where the fish was detected in
155 sequence. At times when a fish was detected simultaneously at two receivers, the fish's position was
156 assumed to be midway between the two receivers. Mean daily activity was then calculated as the total
157 distance travelled, divided by the length of the study period for each fish (i.e., time between first and
158 last detection), regardless of days without detections. This approach results in the minimum mean
159 daily activity.

160

161 *Statistical analyses*

162 We first tested whether fish captured by angling differed from those being electrofished using a series
163 of ANOVAs to test for differences in mean daily activity and fate (i.e., survived, disappeared or dead).
164 Given the general size difference among males and females, sex was used as a covariate in the
165 subsequent analyses but capture method was not, given that the method did not affect activity levels
166 or fate (i.e., capture method did not affect whether a fish died or disappeared). Furthermore, given
167 the collinear nature of mass and length, we used length only as a proxy for size for the analyses.

168 To investigate whether size and sex affected mean daily activity, we used a generalized linear
169 model (GLM). Whether fish exited the river or not was modeled as a binary outcome (GLM, logit
170 link) with size, sex and mean daily activity as model variables. The number of exits performed was
171 modeled as a Gaussian-distributed variable (GLM, log link) with size, sex and mean daily activity as
172 model variables. A final GLM was used to examine whether size, sex and mean daily activity affected
173 the final fate of the fish. All statistical analyses were performed in R version 1.1.383 (R Core Team,
174 2013) using the ggplot2 (Wickham, 2009), lattice (Deepayan, 2008) and MASS (Venables & Ripley,
175 2002) packages.

176

177 **Results**

178 Capture method did not affect mean daily activity and fate ($p > 0.05$). Out of 21 tagged individuals
179 tracked for one year, 15 travelled into the bay for one hour or more, but only 2 of these individuals
180 remained in the bay for more than 24 hours, and did so only once each.

181 Mean daily activity was not correlated to sex (GLM, $Z = -0.504$, $p > 0.05$) or length (GLM,
182 $Z = 1.03$, $p > 0.05$), though we note a trend for females being more active than males. Whether a fish
183 exited the river was positively correlated to mean daily activity (GLM, $Z = 1.89$, $p < 0.05$, **Figure 2**)
184 but negatively correlated to length (GLM, $Z = -2.05$, $p < 0.05$, **Figure 3**). The number of exits from
185 the river was not correlated to length, sex, or mean daily activity (GLM, $p > 0.05$).

186 Pike generally spent most of their time in the lower stretches of the river (**Figure 4**). Periods
187 when fish exited the river into the bay coincided with peaks in salinity in the river (between 6 and
188 10ppt, **Figure 5**). In fact, 14 of the 15 pike which exited the river did so either between 5 August to
189 8 August 2014 or 3 September to 6 September 2014.

190

191 **Discussion**

192 In this study, we show that in a population of Northern pike assumed-to-be brackish, individuals do
193 move into brackish water (15 out of 21, 71 %), but generally stay there less than 24 hours. We
194 found that of the individuals that did travel into brackish water, only 2 (13.3 %) stayed in the bay
195 for more than 24 hours, suggesting that in general, pike of this population do not utilize that
196 environment nearly as much as was previously thought. This finding also suggests that the high
197 growth rate observed in this population must be due to either high food availability within the river
198 itself, or large influxes in prey items coming in from the bay with strong currents. This hypothesis is
199 supported by the observation that smaller pike were more likely to exit into the bay and that pike
200 generally spent more time in the lower reaches of the river.

201 We found no sex-bias in activity levels. Sex bias in activity is not uncommon in fish during
202 the spawning season (cichlids, Taylor et al., 2003; salmonids, Bekkevold et al., 2004; Fraser et al.,
203 2004), but not always the case. It has been suggested that this behaviour may be to reduce the risk
204 of inbreeding; by having one sex move more than the other, the risks of inbreeding are greatly
205 reduced. In pike, an increased movement by females has been suggested to be a form of homing
206 behaviour in females to previously suitable spawning grounds (Koed et al., 2006). The females may
207 move more to regain that area and thus gain a competitive advantage over it. Females have also
208 been observed to move more than males regardless of the season (Jepsen et al., 2001), perhaps in an
209 attempt to forage more often and attain a larger size and greater reproductive potential (Casselman,
210 1978; Bregazzi and Kennedy, 1980; Casselman, 1996). While our approach does not allow us to
211 adequately distinguish activity levels over time (continuous manual tracking, as done in Koed et al.
212 2006 is more effective), our findings may suggest that in this river, adequate spawning and foraging
213 areas are plentiful and females do not need to move extensively to find them. The hypothesis that
214 food abundance is high and may not require active foraging is supported by the fact that size was
215 not related to mean daily activity, and females were larger than males. This may reflect different

216 behavioural tactics across individuals rather than sex- and size-driven differences (e.g., Thomaz et
217 al., 1997).

218 Our findings on activity levels are not unlike a number of previous studies carried out on
219 pike inhabiting lakes and reservoirs which showed mostly sedentary behaviour during the non-
220 spawning season (e.g., Cook and Bergersen, 1988). While some individuals did exhibit high activity
221 levels, most exhibited sedentary behaviours with infrequent peaks in activity. However, individuals
222 with high activity levels were significantly more likely to make exits into the bay, perhaps
223 suggesting a more active foraging tactic. Lower activity levels may be associated with an ambush
224 predation tactic. These two contrasting behaviours are not unusual in *E. lucius*. Individuals of the
225 same populations have been observed to have widely different behavioural patterns. For example,
226 individuals from a western Baltic population living in transitional waters were found to either reside
227 in a lagoon year-round, or to spawn in the lagoon and migrate into freshwater during the non-
228 spawning period (Jacobsen et al., 2017). The authors found that these behaviours were consistent
229 within individuals over time, and may reflect individual variation in home ranges and resource
230 allocation/optimisation. Our findings support this idea, with active individuals undergoing short
231 journeys into the bay, and less active individuals remaining in freshwater. The observation that
232 smaller fish were more likely to exit into the bay may also support two behavioural tactics. For
233 example, it is possible that small individuals exit into the bay to acquire food actively if larger,
234 more dominant individuals are feeding in freshwater, and preventing smaller individuals from doing
235 so.

236 Exits into Køge Bay did not appear to be related to temperature or discharge, but coincided
237 with higher salinities. While 14 of the 15 individuals that travelled into the bay did so either
238 between 5 August to 8 August, or 3 September to 6 September, salinity was still high between the
239 two periods and peaked in early September (15ppt), but no pikes were detected leaving the river

240 during that time. This suggests that salinity itself is not a driver for migrations into brackish water.
241 Instead, it is more likely that strong winds which pushed saline water into the bay (Fischer and
242 Matthäus, 1996) during that period brought with them prey items which the pike could feed on. The
243 period between the two peak periods for exits into the bay may have been too saline for pike to
244 tolerate, and may explain why the pike migrated back into freshwater. The return of salinity to more
245 tolerable levels (8-10ppt) may have allowed active pike to return to the bay between 3 September to
246 6 September, where food items may have been more abundant than normal. Alternatively, it is also
247 possible that prey items actively swam into the outlet of the river during periods of high salinity,
248 and the pike subsequently followed them into the bay as they exited back under lower salinity
249 conditions. Regardless of the mechanism however, it appears smaller, more active individuals made
250 exits into the bay.

251 The commercial catches of pike in the Baltic Sea have been declining drastically in the
252 past decades, likely reflecting a decline in the population of Baltic pike despite their flexible nature
253 (Jacobsen et al., 2008; Lehtonen et al., 2009). While the specific causes for this decline remain
254 unknown, poor recruitment (Nilsson 2006) and anthropogenic activities (including overfishing and
255 habitat changes) are thought to be the main source (Jacobsen et al. 2008; Lehtonen et al., 2009). Our
256 study supports the idea that pike have flexible life histories, which may provide this species with an
257 advantage over other species with more strict life histories. Pike can utilize habitats with wide-
258 ranging salinities, exhibit both active and passive behaviours, and may be more adaptable to future
259 environmental changes caused by a human-dominated world, though current declines may suggest
260 otherwise. Future research should consider investigating the underlying mechanisms that lead
261 individuals in adopting one life history over another. Our findings do however suggest that long-
262 standing, widely-accepted descriptions of pike populations as anadromous or primarily brackish
263 may not be accurate.

264 **Acknowledgments**

265 We wish to dedicate this manuscript to Dr. Lene Jacobsen (author of this writing) who dedicated her
266 career life to science, but who left us too soon. We also wish to thank Hans-Jørn Aggerholm
267 Christensen, Jes Dolby, Michael Holm and Morten Carøe, as well as the volunteer anglers for their
268 help in the field. This study was funded by the Danish Fishing Licenses.

269

270 **Author Contributions**

271 Conceived and carried out field work: LBH, TK, LJ and KA. Contributed materials for field work:
272 KA and LJ. Data compilation and analyses: KBG and LBH. Wrote the manuscript: KBG.

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383 **Tables**

384 **Table 1.** Mean length and mass (\pm SEM) of tagged pike (*Esox lucius*) according to sex (range in
385 bracket).

	Females (19)	Males (11)
Length (cm)	87.3 \pm 3.6 (71.0 – 118.0)	76.2 \pm 1.3 (66.1 – 82.6)
Mass (kg)	6.02 \pm 0.8 (3.0 – 14.2)	3.4 \pm 0.2 (2.2 – 4.1)

386

387 **Table 2.** Position (m from river outlet), detection range (m) and detection efficiency (%) of receivers
388 upon range testing. Note: n/a indicates not applicable.

Receiver position (distance from outlet in m)	Detection range (downstream, upstream in m)	Detection efficiency (downstream, upstream in %)
12000	Not measured	Not measured
7800	Not measured	Not measured
5500	135, 60	100, 100
5400	70, 80	90, 90
2900	135, not measured	70, not measured
2800	130, 85	80, 70
150	85, 85	100, 100
80	70, 120	100, 100
30 in bay	200, n/a	100, n/a
100 in bay	200, n/a	100, n/a
560 in bay	100, n/a	100, n/a
800 in bay	100, n/a	100, n/a

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398 **Figures Captions**

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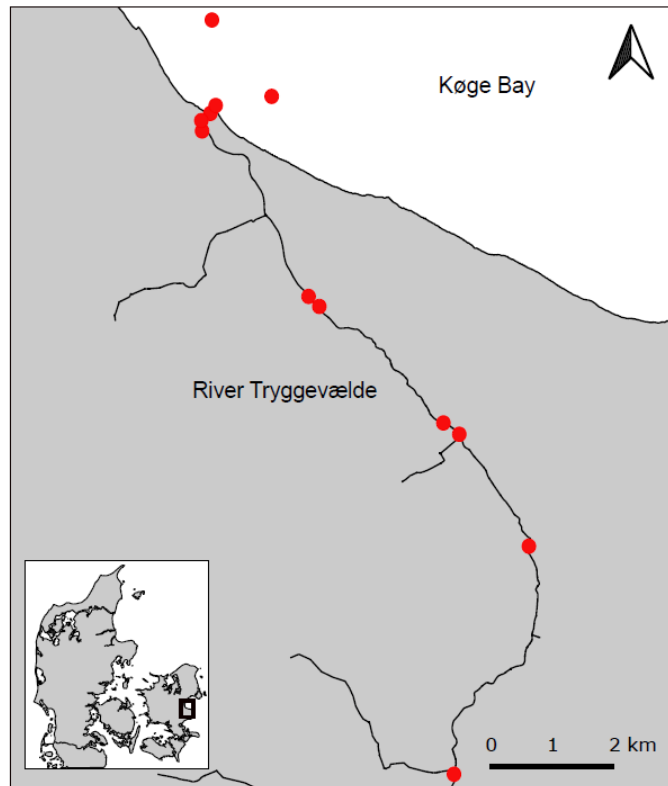
400 **Figure 1.** River Tryggevælde, Southern Sjælland, Denmark. The river runs for 45km before exiting
401 into Køge Bay. Red dots represent receiver placements.

402 **Figure 2.** Predicted probability (mean and 95% confidence intervals) that acoustically tagged pike
403 (*Esox lucius*) exited River Tryggevælde (March 2014 – June 2015) as a function of an individual's
404 mean daily activity (meters per day), assuming an average length of 85.0cm. Actual data are plotted
405 as filled circles. More active fish were more likely to exit into the bay.

406 **Figure 3.** Predicted probability (mean and 95% confidence intervals) that acoustically tagged pike
407 (*Esox lucius*) exited River Tryggevælde (March 2014 – June 2015) as a function of an individual's
408 length (cm), assuming an average daily activity of 242.9 meters per day. Actual data are plotted as
409 filled circles. Smaller fish were more likely to exit.

410 **Figure 4.** Movements of pike (*Esox lucius*) from least (A) to most (U) active, detected by the receiver
411 lines at approximately -580, -100, 3000, 5500, 8000 and 12000 meters from the river outlet. Red
412 traces represent females ($n = 16$) and blue traces represent males ($n = 5$). The horizontal line
413 represents the river outlet, with values ≥ 0 in the river, and values < 0 in the bay. Black dots represent
414 exits into the bay longer than 1 hour. Note: fish A spent long periods at the river outlet (though still
415 in freshwater).

416 **Figure 5.** Environmental variables. Number of pike (*Esox lucius*) which exited the river (black bars)
417 per day overlapped with temperature (top panel), salinity (middle panel) and discharge (lower panel)
418 between March 2014 and June 2015.



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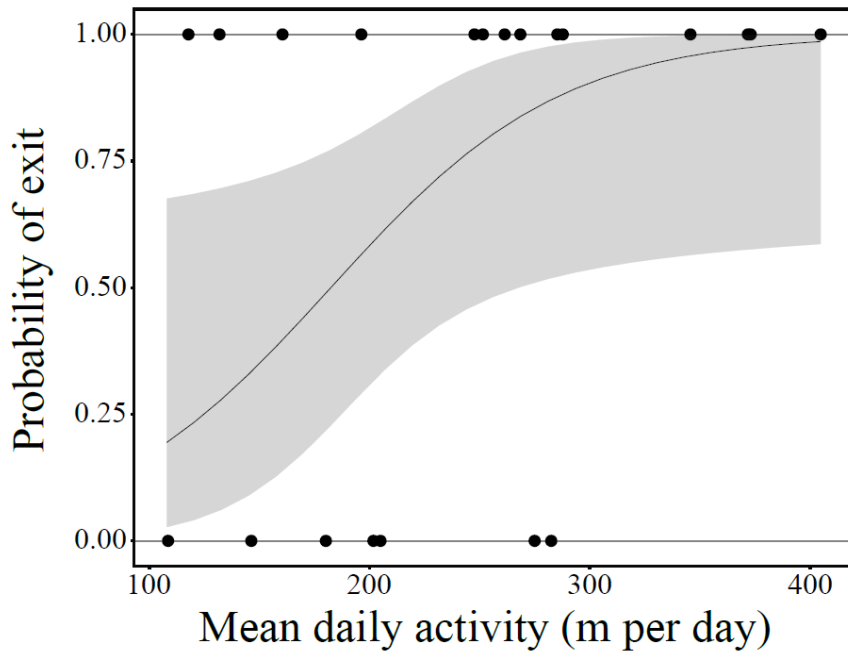
420 **Figure 1**

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426 *Figure 2*

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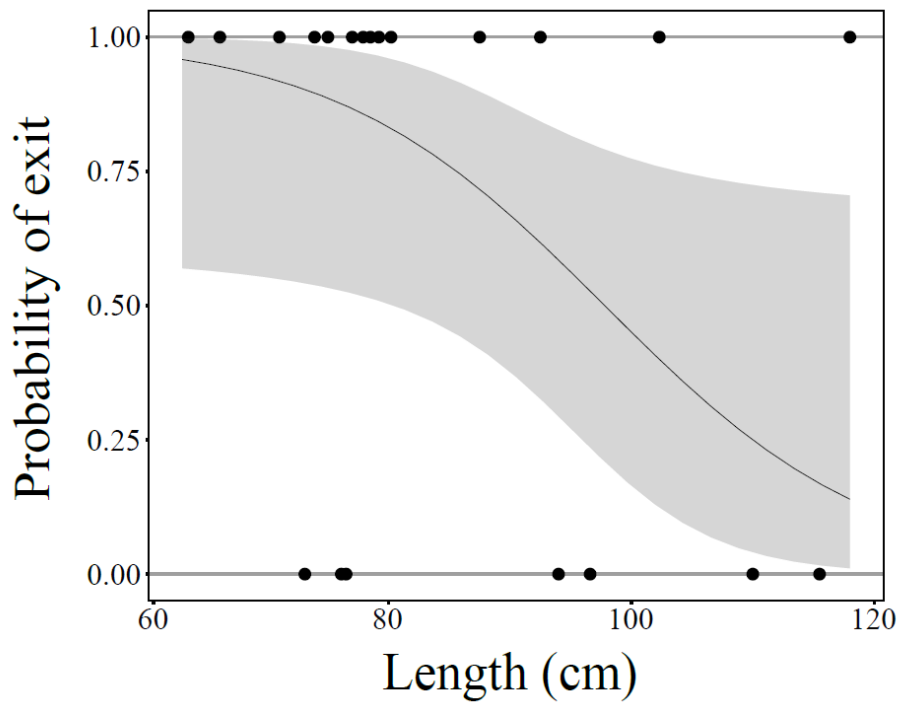
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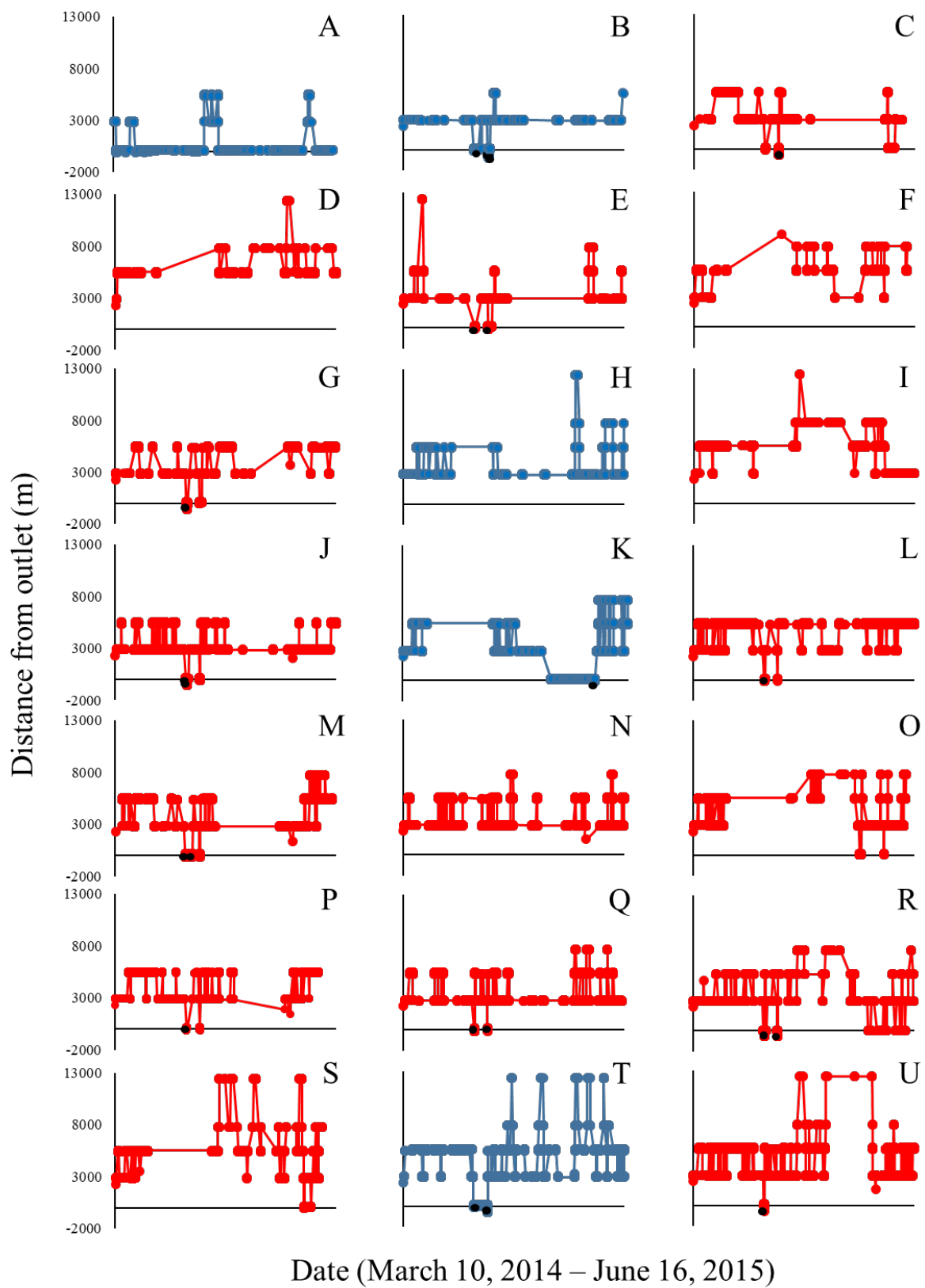
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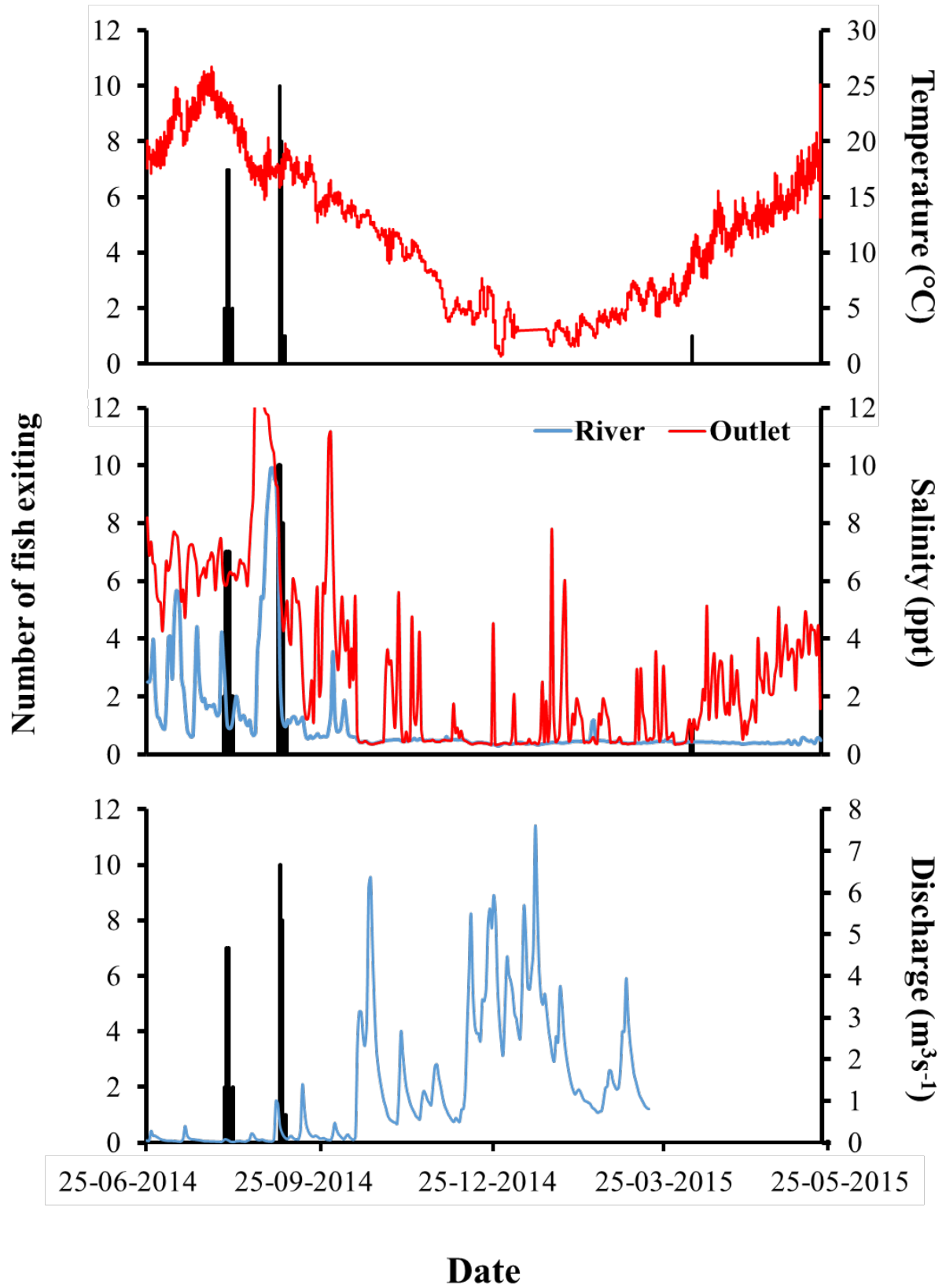
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434 *Figure 3*



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436 *Figure 4*



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438 *Figure 5*