

# Migration behaviour and loss rate of trout smolts in the transitional zone between freshwater and saltwater

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## ABSTRACT

Migration between freshwater nursery grounds and saltwater feeding areas is a critical event in sea trout life history. During their seaward migration, smolts encounter both natural and man-made obstructions as well as increased exposure to predators. This is particularly true in the transition zone between freshwater and saltwater where smolts enter a new environment, change their behaviour and encounter new predators. Over two years (2013-14), 81 trout smolts were trapped and acoustically tagged 17 km upstream of the tidal limit in the River Frome in Dorset, UK. Smolt migrations were then tracked by acoustic receivers deployed throughout the lower river and its estuary and the detected movements were used to estimate loss rate and migration behaviour. A Bayesian State Space model was applied to separate detection and transition probabilities. More than 90% of the in-river detections occurred at night whereas detections at the saline limit and throughout the estuary were spread evenly between day and night. Median migration speed in the river was 65-70 km day<sup>-1</sup> in both years, whereas the migration speed was slower through the estuary with median speeds of less than 10 km day<sup>-1</sup>. The loss rate was similar across the study zones (range 0.5-1.1 % km<sup>-1</sup>); hence there was no pronounced increase in mortality in any particular part of the transition zone as reported by a number of similar studies from other systems. Even though no individual study zone displayed a particularly elevated loss rate, the cumulative loss of tracked trout smolts through the 33 km section was 24%, demonstrating a significant cost in terms of loss associated with smolt migration.

**Keywords:** trout smolts; acoustic tags; loss rate; migration behaviour; transition zone; Bayesian state space model.

## INTRODUCTION

Many animal species undertake migration during their lifetime. Reasons for migration include seasonal changes in habitat and food resources, longer-term changes in habitat and/or dietary needs associated with the growth and development of the individual and for reproduction. Pursuing resources in space and time is among the most common reasons for migration, but individuals must reconcile the costs and benefits incurred, such as energy expenditure and increased mortality risk, with the decision to migrate.

Migration for some species is a fixed behaviour whereby environmental cues trigger synchronous migrations. A number of species, however, undertake partial migration whereby some individuals migrate and others do not. Partial migration occurs in a range of animal groups, such as mammals, birds, and fishes (e.g. pronghorn antelope, European robin, great white shark). A number of hypotheses have been proposed to explain why partial migration occurs and persists and among the most commonly cited, are ‘*dominance*’ and ‘*endurance*’. The dominance hypothesis states that when food resources are scarce, the larger and more dominant individuals can outcompete the smaller subdominant individuals so that it is beneficial for subdominant individuals to migrate to richer feeding grounds (Gauthreaux, 1982). The endurance hypothesis states that individuals of larger body size are better able to endure adverse conditions during periods with low food availability and reduced temperature so that smaller individuals are more likely to migrate to avoid hardship (Ketterson & Nolan, 1976).

Among salmonids, brown trout (*Salmo trutta*) exhibit one of the most polytypic life histories: with some individuals migrating to the marine environment before returning to spawn (anadromy), some staying in their freshwater natal stream all their life (residency), with others ‘doing something in between’ (Thorstad *et al.*, 2016). Anadromous trout encounter richer feeding grounds and attain greater final body size than their freshwater resident counterparts. Because fecundity is intrinsically linked to body size, particularly for females, anadromous individuals enjoy greater lifetime fecundity (Jonsson, 1985). However, migration is energetically costly, not only in terms of the actual energy expenditure during migration, but also during the physiological, morphological and behavioural transformation from parr to smolt (Sheridan *et al.*, 1983). Exposure to predation also increases during migration as the smolts move through the lower river, the estuary and into the marine environment (Mather, 1998; Klemetsen *et al.*, 2003).

The freshwater phase of migratory salmonid life history is well described. However, the marine phase is less well understood due largely to the technical issues involved in conducting studies at sea. A reduction in marine survival of Atlantic salmon (*Salmo salar*) over the last three decades, combined with technological advances, has led to increased interest and resulting improvement in our ability to collect migration data from the marine environment (ICES, 2015). Consequently, there has been a recent focus on the behaviour and loss of smolts in the near-shore environment to predators, such as European sea bass (*Dicentrarchus labrax*),

cod (*Gadus morhua*) and cormorants (*Phalacrocorax carbo*) (Dieperink *et al.*, 2002, Riley *et al.*, 2011, Thorstad *et al.*, 2012a). The transition zone, where the smolts migrate from the unidirectional flowing freshwater environment of the river into a saltwater environment affected by tides and waves, is thought to be a critical phase in their migration (Thorstad *et al.*, 2012b). Trout behaviour in this transition zone changes from being a benthic predator with a small territory to becoming a pelagic nomad actively exploring larger areas, as well as a complete change in diet. These physiological and behavioural changes in smolts in this zone may render them particularly vulnerable to other external stressors (Halfyard *et al.*, 2012). The transition zone of many rivers is heavily influenced by anthropogenic activity, such as dredging, netting, boat traffic and pollution; all with a potentially negative impact on smolt behaviour and survival. In summary, migrating smolts encounter new predators and physiological and anthropogenic stressors in the transition zone, and the combined effect of these stressors might be super-additive and greater than their individual effects (Brook *et al.*, 2008).

The decision whether to migrate or not is therefore a cost-benefit trade-off where the potential fecundity gain by migrating to sea is weighed against increased energy expenditure and mortality risk incurred by migration. Fecundity gain by returning anadromous individuals is relatively easy to estimate from the size of returning individuals. In this study we aim to quantify the more elusive risk associated with migration. In particular, we investigate migration behaviour and loss rate through individual zones of the lower river and the transition zone. We hypothesise that the highest loss rate occurs in the transition zone where smolts enter a new environment, change their behaviour and encounter new predators.

Fecundity gain is the obvious driver for migration. However, it is common for some anadromous individuals to return to their native river before their first winter in saltwater. These OSW individuals that return early from their marine migration have various local names in the British Isles (notably, finnock, whitling, herling and school peel). Why do some individuals that have incurred energetic costs and increased risk during migration return to the poorer feeding grounds of the river after such a short period at sea? Some of these anadromous individuals even return to the river in the middle of summer only a few weeks after their outward migration as post-smolts several months before their first potential spawning season. We hypothesise that individuals returning to the river before their first sea winter remain in the estuary so that they experience a lower energy cost in terms of migration and potentially avoid predation in the open sea.

## MATERIAL AND METHODS

### STUDY SITE

The river Frome in Dorset, Southern England, is a chalk stream receiving most of its discharge directly from the cretaceous chalk aquifer. It rises in Evershot and flows approximately 70 km

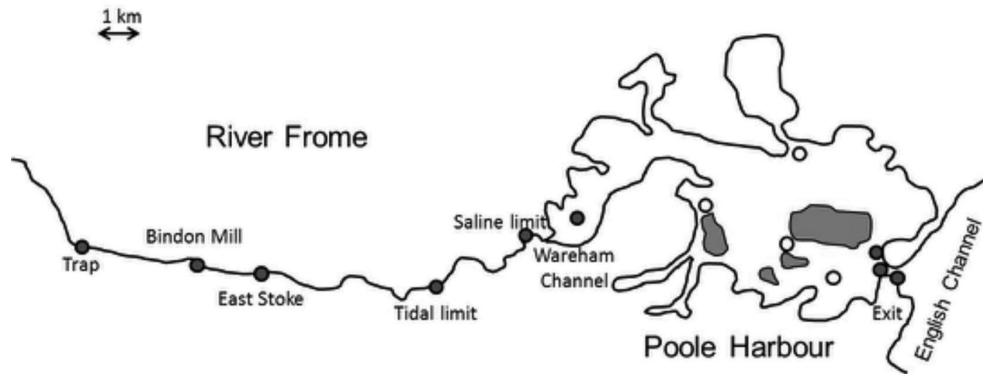
to the tidal limit near Wareham Bypass Bridge. Immediately downstream of Wareham the river enters Poole Harbour, a large natural estuary (36 km<sup>2</sup>) with a narrow exit (300 m wide) into the English Channel (Figure 1). This study took place in the lower part of the river Frome and its estuary, Poole Harbour.

## TRAPPING, TAGGING & TRACKING

Trout smolts were trapped on an eel rack at East Burton, some 16.8 km upstream of the tidal limit. The trap was built to catch emigrating silver eels (*Anguilla anguilla*) and consisted of inclining metal slats, situated downstream of undershot sluices in the river, that allowed the passage of water but retained fish and diverted them to a holding tank. Smolts were trapped at night in the spring of 2013 and 2014. In 2013, 30 trout smolts were trapped on the eel rack from 10<sup>th</sup> – 15<sup>th</sup> of April. Their average length was 182 mm (range 123–247 mm) with an average weight of 70 g (19–177 g). In 2014, 51 smolts were trapped from 28<sup>th</sup> March – 16<sup>th</sup> April. Their average length was 213 mm (163–273 mm) and their average weight was 105 g (44–199 g). The trapped smolts were anaesthetised in 2-phenoxy ethanol before surgically implanting a 16.5 x 6 mm, 180 KHz acoustic transmitter (V6, Vemco Ltd.) and a 12 x 2 mm passive integrated transponder (PIT) tag (Wyre Micro Design Ltd.) into the peritoneal cavity. The fish were allowed to recover fully after surgery before they were released immediately downstream of the trap. [All tagging was carried out in compliance with the UK Animal (Scientific Procedures) Act 1986 under Home Office licences PPL30/2732 and 70/7588.] The Vemco V6 transmitters were programmed to transmit with a nominal delay of 30 seconds and with a transmission rate varying randomly  $\pm 50\%$  of the nominal delay (the variation in delay avoided two tags transmitting in synchrony and causing a loss of data). In the second year (2014), the nominal delay was programmed to increase from 30 to 60 seconds two weeks after release to increase the battery life of the transmitters (>90% of the fish observed exiting the estuary in 2013 did so within two weeks). This increased the battery life of the transmitters from 43 to 105 days.

Vemco VR2W receivers were positioned at three locations in freshwater: namely at a) Bindon Mill, b) East Stoke and c) the tidal limit – at distances of 5.5, 8.3 and 16.8 km downstream of the trap respectively (Figure 1). Receivers were placed in the saltwater zone at a) the saline limit, b) in Wareham Channel and c) at the exit of the estuary – at distances of 21.1, 23.4 and 32.9 km from the trap respectively (Figure 1). At the mouth of the estuary (=Exit), three receivers were deployed with the first two covering the exit and the third receiver just outside the exit. When estimating the transition probability, the receiver outside the exit informed the model about the detection probability of the two receivers at the exit (*see* statistical methods below). In the second year (2014), a further four receivers were deployed in potential feeding areas of the estuary (Figure 1).

A low head Archimedes hydro-turbine was installed at Bindon Mill in 2012 and acoustic receivers were placed by the turbine during this study to detect smolt using this route (*see*



**Figure 1.** Map of the lower River Frome and its estuary at Poole Harbour. Grey circles indicate location of trap and acoustic receivers deployed in both 2013 & 2014. Open circles indicate estuary receivers deployed in 2014 only.

Moore *et al.*, 2017). Any smolts detected at the turbine were removed from the analysis because of the potentially adverse effect of passage through the turbine on their subsequent behaviour and survival.

An array of PIT-antennae covering the full width of the river at East Stoke detected the upstream and downstream migration of PIT-tagged fish (Welton *et al.*, 2002).

## DATA ANALYSIS

Migration speed through individual zones was calculated using the time difference between the first observation at one receiver station and the first observation at the next downstream receiver station. Variation in migration speed between zones and the effect of year and smolt size was analysed using an ANOVA with a Tukey's *post hoc* test of between-zone differences.

Telemetry data has the inherent problem that detection is imperfect; a passing tag is not always detected and so it is unknown if (a) the tag did not pass a receiver or (b) if it was not detected when it passed. This problem can, and should, be addressed statistically.

To estimate the risks to trout smolts associated with migrating through different zones, a Bayesian State Space models (BSSM) was applied. Other have used BSSM in this context: Gimenez *et al.* (2007) explain clearly the theory of BSSM for marked individuals and Holbrook *et al.* (2014) present an illustrative example of BSSM implementation for acoustically tagged lamprey (*Petromyzon marinus*). In essence, BSSM estimates jointly the probability that a tag is detected at a particular location and the probability that it completed the transition to that location successfully. Individuals may not complete the transition from one receiver to another for a variety of reasons including mortality, tag failure, taking up residence etc. Acoustic tracking alone cannot determine the underlying reason for an incomplete transition. To avoid invoking any particular reason for an incomplete transition, the term 'Stopped migration' was used.

In this study, it was assumed that all tagged smolts shared the same detection and transition

probabilities (i.e. that physical or behavioural differences between individuals were unimportant and that individuals travelled independently). Making these assumptions enabled the use of the simple (CJS) model (Cormack, 1964; Jolly, 1965; Seber, 1965) given by:

$$Y_t | X_t \sim \text{Binomial}(X_t - u_t, p_t)$$

$$X_{t+1} | X_t \sim \text{Binomial}(X_t, \phi_t) + u_{t+1}$$

Where:  $X_t$  is the total number of survivors from time  $t$ , including  $u_t$ , which is the number of newly marked individuals at time  $t$ ;  $Y_t$  is the total number of previously marked individuals encountered at time  $t$ ;  $p_t$  is the probability of detecting a tagged individual at time  $t$  ( $t=2, \dots, T$ ) and  $\phi_t$  is the probability that a tagged individual transitions to time  $t+1$  given that it is alive at time  $t$  ( $t=1, \dots, T-1$ ). This formulation separates the nuisance parameters (the detection probabilities,  $p_t$ ) from the parameters of interest (the transition probabilities,  $\phi_t$ ) because the latter are found only in the second or “state” equation.

Values of  $p_t$  and  $\phi_t$  were estimated from this model using the Monte Carlo Markov Chain (MCMC) method implemented in JAGS ([www.mcmc-jags.sourceforge.net](http://www.mcmc-jags.sourceforge.net)). JAGS uses Gibbs sampling to explore the joint probability distribution of  $p_t$  and  $\phi_t$ . Through an iterative process, weakly informative  $Beta(1,1)$  prior distributions on  $p_t$  and  $\phi_t$  were updated with increasingly credible values until, after sufficient iterations, the best stationary estimated values of  $p_t$  and  $\phi_t$  were taken to be the median of their posterior distributions.

JAGS was run from within R using functions from the package dclone ([www.cran.r-project.org/web/packages/dclone/index.html](http://www.cran.r-project.org/web/packages/dclone/index.html)). The MCMC chains were run for 30,000 iterations, of which the first 10,000 was discarded as burnin.

## RESULTS

### DETECTIONS

Tags were detected at all receiver stations and the detection efficiency was >80% at all stations, although no station was 100% efficient (Table 1). Receiver efficiency and transition probability was estimated using a Bayesian State Space model (*see methods*). It was discovered that some individuals at Bindon Mill migrated through a relief channel which was not covered by receivers (*see Moore et al., 2017*). Individuals that might have taken this unmonitored route were not available to be detected at Bindon Mill. Consequently, estimates of detection and transition probabilities for the section between the trap and Bindon Mill were subject to an unknown bias. To overcome this, we estimated detection and transition probabilities for the total section between the trap and East Stoke (i.e., encompassing Bindon Mill and the relief channel).

More than 80% of the first detections of individual smolts at any receiver station in the

freshwater zone occurred in the hours of darkness (Table 1). There was no such nocturnal detection pattern at the saltwater stations, but 70% of the first detections at the saline limit were made during ebbing tides.

**Table 1** Number of tags observed and time of day of first observation at the receiver stations. A Bayesian approach was used to estimate the detection probability at each station. CI used here denotes credible interval which is similar to, but not identical to, confidence interval. \* In both 2013 and 2014, two tags were detected at the turbine at Bindon Mill: these four fish were removed from the analysis and are not included in the count of tags.

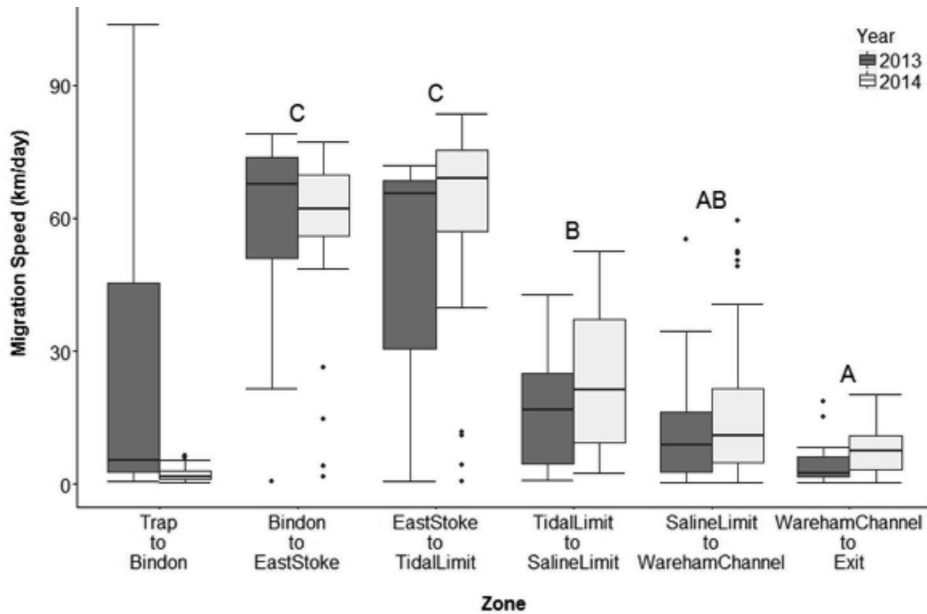
Station	Distance from trap (km)	Year	No. Tags detected *	Detection probability (95% CI)	Day time obs.	Night time obs.
Bindon Mill	5.4	2013	20	N/A	0%	100%
		2014	36	N/A	14%	86%
East Stoke	8.2	2013	25	0.93 (0.86-0.95)	0%	100%
		2014	42		10%	90%
Tidal Limit	16.7	2013	24	0.99 (0.95-1.00)	8%	92%
		2014	45		18%	82%
Saline Limit	21.1	2013	21	0.96 (0.90-0.99)	43%	57%
		2014	42		48%	52%
Wareham Channel	23.4	2013	20	0.81 (0.70-0.84)	40%	60%
		2014	37		62%	38%
Exit	32.9	2013	22	0.84 (0.72-0.87)	68%	32%
		2014	36		56%	44%

## MIGRATION SPEED

With one exception, variation in migration speed between the two years was negligible within zones (Figure 2). Initial analysis showed a highly significant interaction between zone and year that was driven purely by differences between years in the Trap – Bindon Mill zone. When this zone was removed from the analysis, the zone x year interaction was no longer significant and while there was a significant effect of zone ( $F_{5,194} = 111$ ,  $P < 0.001$ ) there was no effect of year. The migration speed of the smolts was highest in the middle and lower river sections where the median speed varied from 62.2 km day<sup>-1</sup> in the middle river (Bindon Mill – East Stoke) to 69.1 km day<sup>-1</sup> in the lower river (East Stoke – Tidal limit), both in 2014 (Figure 2). The lowest migration speed was in the upper river (Trap – Bindon Mill) where the median speed was 5.2 and 1.7 km day<sup>-1</sup> in 2013 and 2014 respectively. Migration speed in the tidal section of the river and within the estuary was considerably slower than in the middle and lower river. Results of the Tukey's *post hoc*



test of between-zone differences are given in Figure 2. There was a significant effect of size ( $F_{1,194} = 5.4$ ,  $P = 0.02$ ) indicating that migration speed increases slightly with smolt size.



**Figure 2.** Migration speed in the six different zones in 2013 (grey boxes) and 2014 (open boxes). Migration speed in those zones that share the same letter are not significantly different ( $F_{5,194}$ , Tukey's;  $P > 0.05$ ).

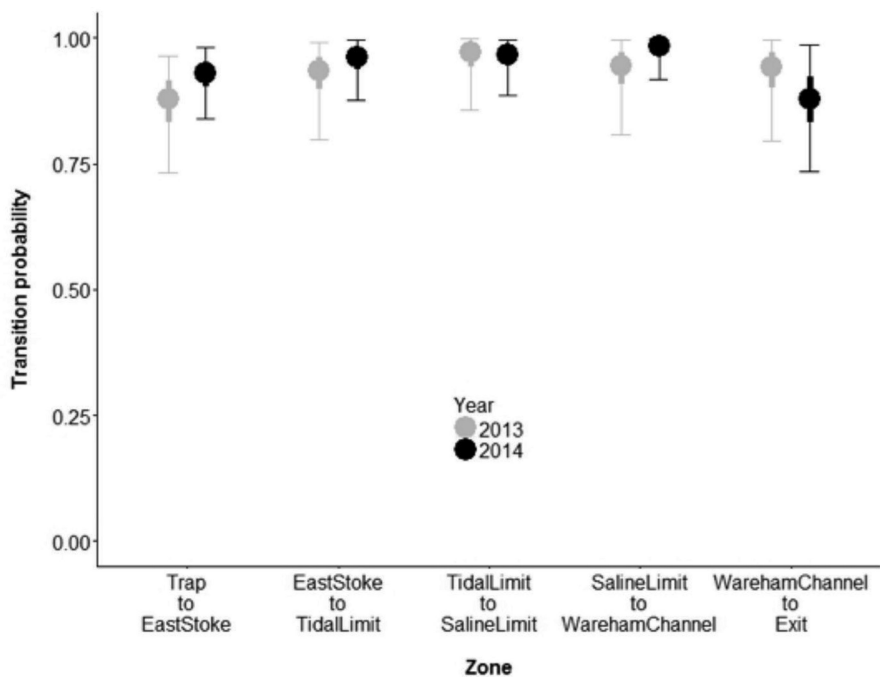
## STOPPED MIGRATION

The transition probability within individual zones was practically identical between years (Figure 3) allowing data from the two years to be combined and the estimation of a single transition probability for each individual zone. The zone with the lowest transition probability and, therefore, the highest probability of stopped migration (10%) was observed in the outer part of the estuary from Wareham Channel to the exit of the estuary, whereas the lowest probability of stopped migration (1.5%) was observed in the zone from the tidal limit to the saline limit (Figure 4). After considering zone length, the highest probability of stopped migration was observed in outer estuary at  $1.1\% \text{ km}^{-1}$  followed by the zone from the trap to East Stoke at  $1.0\% \text{ km}^{-1}$ , whereas the probability of stopped migration was  $0.5\text{--}0.7\% \text{ km}^{-1}$  in all other zones (Figure 5). The cumulative stopped migration rate from the trap to the exit of the estuary was 24%.

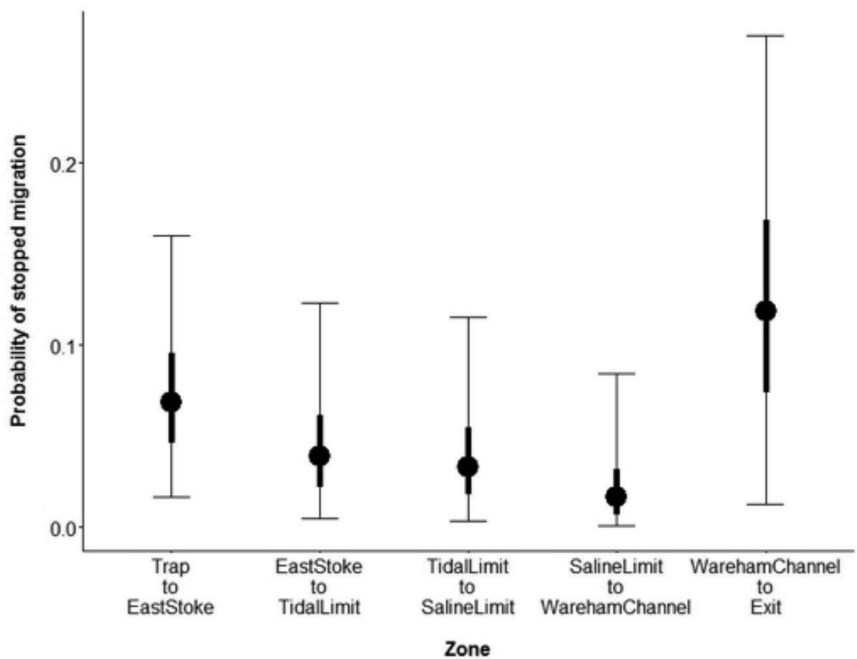
## LOSS RATE BY SIZE

There was no difference between years ( $P > 0.05$ ) in the probability of recording the smolts at



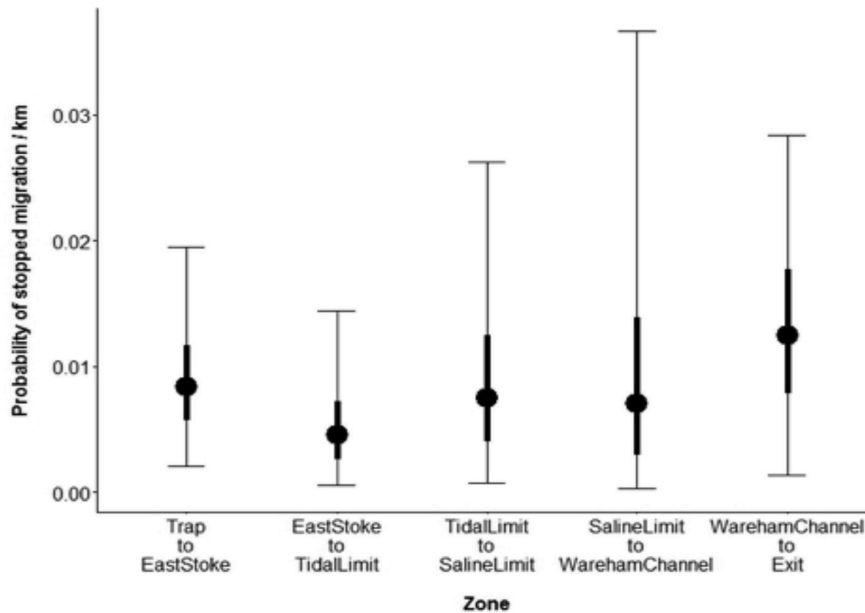


**Figure 3.** Transition probability by zone and year with 95% credible intervals. Credible intervals are similar to confidence intervals but not the same.



**Figure 4.** Probability of stopped migration within individual zones years combined with 95% credible intervals.

the exit of the estuary, but there was a small effect of size on the probability of being recorded at the exit (Logistic regression, odds multiplier  $e^{0.02}$ ,  $Z = 2.1$ ,  $P = 0.03$ ).



**Figure 5.** Probability of stopped migration within individual zones divided by the length of the zone (km) years combined with 95% credible intervals.

## SUMMER OBSERVATIONS AND RETURNING ADULTS

In 2013, 4 of 22 smolts observed leaving the estuary were detected migrating into and out of the estuary exit several times between first leaving the estuary and the end of the battery life of the acoustic tags (battery life = 43 days). In 2014, when the battery life of the acoustic tags was extended to 105 days, the last observation in the estuary was made on the 15<sup>th</sup> May. No further tags were detected until the 22<sup>nd</sup> July when the first individual was detected re-entering the estuary. A further 4 individuals were detected re-entering the estuary between July 22<sup>nd</sup> and the end of the lifespan of the batteries (= August). All 5 individuals were observed entering the freshwater zone of the river within 20 hours of being observed at the mouth of the estuary. A further 6 individuals were observed returning to the river by the PIT-tag system at East Stoke. The first observed returns to the river of the 11 returning adults were made as 0SW finnock for 5 fish, a further 5 fish returned after 1SW and 1 fish was recorded as a 2SW fish.

## DISCUSSION

The hypothesised increase in the loss rates of smolts in the transition zone was not observed

as the loss rate of the fish tracked through the lower river and estuary in this investigation was evenly spread. A number of studies have reported very high loss rates in the transition zone for sea trout and salmon smolts (Hvidsten & Lund, 1988; Dieperink *et al.*, 2001; Dieperink, 2002). However, other studies have reported loss rates in the transition zone similar to the 0.7 – 1.1% km<sup>-1</sup> observed here: Thorstad *et al.* (2007) reported 1.8% km<sup>-1</sup> and Aarestrup *et al.* (2014) reported 0.6 – 0.9% km<sup>-1</sup> for wild sea trout smolts in the transition zone. High loss rates in the transition zone are therefore not inherent and it appears that the wild smolts tagged in this study were fully adapted for the physiological and behavioural changes experienced in the transition zone. Studies reporting high loss rates were linked to very high predation rates that will be highly variable depending on the predator populations in different estuaries.

Larger trout were more likely to make the transition from the trapping location to the exit of the estuary. This size-dependent transition probability may be linked to the observed positive correlation between size and swimming speed because the predator avoidance potential increases with both speed and size: an observation also made in a number of other studies (Dieperink *et al.*, 2001; Finstad *et al.*, 2005).

The cumulative loss of sea trout smolts through the 33 km section where the smolts were tracked in the lower river Frome and its estuary was 24%. Similar loss rates have been reported for wild trout smolts from Scandinavia. Thorstad *et al.* (2007) reported a 35% loss over 37 km of the transition zone of a Norwegian river and Aarestrup *et al.* (2014) reported a 23% loss over 46 km of combined river and estuary from a Danish river. This indicates that there is a significant cost associated with the seaward migration of smolts in terms of loss. However, because all these studies were conducted with acoustic tags, these losses effectively represent stopped migration. Stopped migration could be caused by fish mortality, but there are other possible explanations, such as tag failure or the fish taking up residence between receivers, as observed by del Villar-Guerra *et al.* (2014).

The in-river median migration speed was >60 km day<sup>-1</sup> in the zones between East Stoke and the tidal limit. This is higher than the 36.8 km day<sup>-1</sup> migration speed reported for wild trout smolts by Aarestrup *et al.* (2014). The high migration speed indicates an active migration; however, as the vast majority of the observations in this zone were made at night, the smolts must have held station during the day, indicating an in-river ‘start-and-stop’ pattern of migration behaviour. Similar nocturnal freshwater migration patterns have been observed elsewhere and it has been suggested that nocturnal migration is an adaptive behaviour to avoid visual predators (Solomon, 1978; Moore & Potter, 1994; Moore *et al.*, 1995).

Entry into the saline zone was associated with ebbing tides, thus saving energy while progressing through the transition to saltwater by following the freshwater plume into the transition zone; a behaviour reported in a number of previous studies (Moore *et al.*, 1995; Lacroix *et al.*, 2004). Once in the estuary, there was no diel pattern in migration behaviour and the migration speed of the smolts was significantly lower than in freshwater. The migration speed was particularly low from Wareham Channel to the exit of the estuary (2.5–7.3 km day<sup>-1</sup>). While this is considerably slower than the in-river migration, the water velocity in this section

was much slower than in the river and it is unlikely that the smolts followed the shortest route through estuaries (Thorstad *et al.*, 2004). The observed migration speed through the estuary was similar to the 3.2 km day<sup>-1</sup> reported by Aarestrup *et al.* (2014), but was significantly slower than the 31.9-42.2 km day<sup>-1</sup> reported for the outer zone of a Norwegian fjord by Finstad *et al.* (2005).

No fish were detected foraging in the estuary during the summer of the second study year (2014) when the battery life of the acoustic tags had been extended and extra receivers were placed in the estuary. Furthermore, of the 11 adults observed returning to the river, all but one were recorded by the acoustic receivers at the exit of the estuary as smolts and the first in-river observation of the individual not recorded by the exit was as a 1SW fish. It appears that the anadromous individuals of river Frome all leave the estuary and seek inshore or offshore feeding areas in the English Channel. There was no support for the hypothesis that the individuals returning to the river before their first winter at sea remained in the estuary to reduce energy expenditure and exposure to predators. The marine migration distances undertaken by these individuals before returning to the river is not clear, but all anadromous individuals migrated >12 km (furthest receiver) from the river mouth. This contrasts findings by Berg & Berg (1987) from a Norwegian river where 53% of tagged fish were recaptured within 3 km of the river mouth but it concurs with generally longer migration distances observed for sea trout from the UK (Pratten & Shearer, 1983).

Handling fish during capture and tagging induces stress. Lower *et al.* (2005) showed this by measuring excretion of the well-established stress indicator, cortisol, from roach and carp undergoing different treatments. They showed that tagged fish excreted significantly higher levels of cortisol than control fish although the cortisol levels returned to pre-stress levels within 24 hours after tagging. Therefore, the impact of capture and handling on the behaviour of smolts is most likely to occur in the first day or two after tagging. Increased post-tagging stress may explain the large variation in migration speed observed in the zone immediately downstream of the trap (Figure 2). Reduced migration speed in the zone immediately downstream of tagging has been observed in a number of other smolt tagging studies (Finstad *et al.*, 2005; Aarestrup *et al.*, 2014). Alternatively, individuals merely drifting downstream in the early, slower, passive stage of smolt migration prior to active migration may also have been trapped and these would be likely to exhibit slow migration speeds immediately after tagging. Both scenarios highlight the importance of experimental design when planning studies that involve handling fish because the tagged fish will need time and space to recover before it may be assumed that normal behaviour is being observed. Even though the main effect of tagging is likely to occur within the first couple of days of handling, the vulnerability of tagged fish to delayed physiological stress and predation may continue for longer so that the estimates of loss rate may be greater among tracked smolts. Eleven of the 81 tagged fish (14%) were observed returning to the river as adults. This return rate is similar to the 20% reported for wild untagged trout from River Bresle, a French chalk stream (Euzanat *et al.*, 2004), the 21% reported from Burrishoole in the west of Ireland (Poole *et al.*, 2006) and the 19% reported for River Tamar

in the southwest of England (Simon Toms, *pers. comm.*), but it is considerably lower than the 37% reported from a Norwegian river (Berg & Jonsson, 1990). There is currently no measure of the return rate of untagged sea trout from the Frome but it seems likely that any impact that tagging and handling on the survival of tagged smolts in this study fish was small so that the reported loss rates in the lower river and estuary were probably close to the natural mortality.

We established a significant cost-penalty in terms of the cumulative loss associated with the outward migration of smolts through the lower river and the transition zone. Although this study does not indicate if this mortality rate is outweighed by benefits in growth and fecundity, it contributes to our understanding of near-shore mortality in relation to the cost-benefit analysis that must underpin the life-history strategy choices of sea trout.

## CONCLUSIONS

This study demonstrated a significant cost in terms of cumulative loss associated with smolt migration through the lower river and the transition zone. However, as none of the sections within the transition zone of this study displayed a particularly elevated loss rate, there was no pronounced increase in mortality during migration through the transition zone specifically as reported by similar studies elsewhere.

The reduced migration speed in the zone immediately below the trap emphasised the importance of handling and tagging early enough in space and time so that the tagged individuals then behave “normally” when they enter the section of interest for a given study.

The trout smolts migrated quickly through the freshwater zone primarily at night but no such nocturnal movement pattern was observed in the saline zone.

Individuals returning to the river before their first winter at sea did not take up residence within the estuary so that there was no evidence to suggest that this life-history strategy was associated with a shorter marine migration.

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