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BRIEF COMMUNICATION

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Continuous outmigration and sequential encountering of environmental cues are important for successful homing of hatchery-reared, anadromous brown trout *Salmo trutta*

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Abstract

When rehabilitating and reintroducing trout *Salmo trutta* in rivers, it is a goal that as many as possible survive, home and form self-sustaining populations. Hatchery-reared, anadromous *S. trutta* have significant lower ability to return to the area where they were raised if (a) transported in a closed tank to sea and released 5 km from the River Imsa, relative to those that were (b) transported when swimming in a partly submerged tank with sea water run-through, while being slowly towed by a boat the same distance or (c) released at the outlet of the River Imsa. Thus, if deprived from environmental cues during part of the way, they lose their ability to home.

KEYWORDS

anadromous brown trout, homing, River Imsa, *Salmo trutta*, sequential imprinting

Philopatry, the tendency to return for breeding to the site where an animal was born, is a common trait for many migratory species, as it increases the probability of reproductive success (Wilson, 1975). Nonetheless, the homing ability is rarely perfect, and some individuals stray and reproduce in foreign sites (Bett *et al*., 2017; Jonsson *et al*., 2003). If the straying rate is low, this improves genetic resilience, demographic stability and colonization of novel habitats of populations (Keefer & Caudill, 2013). In managed populations, however, straying rates are often higher and can cause negative effects on the production and long-term viability of populations meant to be enhanced (McClure *et al*., 2008).

Anadromous salmonids are philopatric and home for spawning after months to years at sea (Putman *et al*., 2014). Possibly, the juveniles learn the migratory route during outmigration and reverse this in opposite sequence during the return migration (sequential imprinting, Harden Jones, 1968; Ueda, 2019). The navigation to the home river is rather precise for natural, undisturbed populations (Jonsson *et al*., 2003; McDowall, 2001), whereas this ability is often downgraded in hatchery-reared salmonids, especially if the released fish are transfers from a foreign river (Keefer & Caudill, 2013).

Predation pressure on outmigrating juveniles (smolts) in estuaries and near-shore oceans is often high (Thorstad *et al*., 2012), but this early mortality may be reduced if the fish are transferred offshore before released (Gunnerød *et al*., 1988). However, offshore transport can decrease the homing success as for example shown for coho salmon *Oncorhynchus kisutch* (Walbaum, 1792) (Solazzi *et al*., 1991) and Atlantic salmon *Salmo salar* L. 1759 (Hansen *et al*., 1993). Possibly, this is because the outmigrating juveniles are deprived of environmental cues needed for successful navigation to the home area (Harden Jones, 1968).

Natural populations of anadromous brown trout *Salmo trutta* L. 1759 tend to return to their river of origin, whereas the straying rate appears to be higher in translocated than local populations (Ferguson *et al*., 2019; Jonsson & Jonsson, 2014). For homing experiments, *S. trutta* is preferable over many other salmonids because many feed at sea only for a few months before they return to fresh water (Jonsson & Jonsson, 2009). In this study, the authors tested if juvenile, anadromous *S. trutta* of foreign origin, slowly towed by a boat from the mouth of the River Imsa and released offshore, had better homing ability than similar fish transported in a closed tank and released at the same location. They also tested if the survival measured as the number of recaptured *S. trutta* was higher for those towed by boat away from the river mouth than for conspecifics released at the river mouth. The fish were released between 14.00 and 16.00 hours on 8 May 1995. This is in the period of the year when the wild smolts left the river for feeding at sea (Jonsson & Jonsson, 2009).

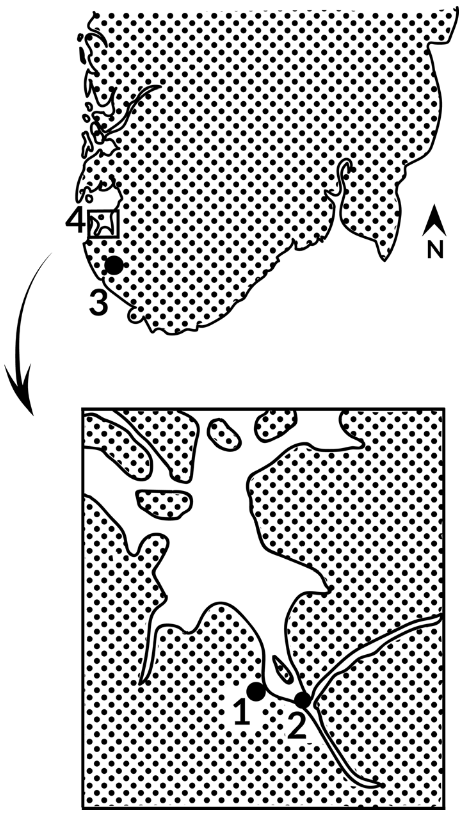

FIGURE 1 Anadromous brown trout *Salmo trutta* either released at the mouth of the River Imsa (1), transported in a closed tank and released in the sea at Lauvik (2) or swimming in a partly submerged glass fibre tank with sea water through-flow when slowly towed by boat from the River Imsa and released at Lauvik in the Høgsfjord estuary (4). The most distant recapture was from the River Figgjo (3)

1 | ETHICAL STATEMENT

The care and use of experimental animals complied with the Norwegian animal welfare laws, guidelines and policies as approved by the Norwegian government at the time when the experiment was performed.

The experimental fish were reared at the NINA research station, Ims (58° 50′ N, 6° E), south-western Norway. They were individually tagged with numbered Carlin tags after being anaesthetized with chlorobutanol. To test the homing ability of a foreign stock, 2-year-old smolts of anadromous *S. trutta* of the River Emån were used. The River Emån *S. trutta* are from eastern Sweden, belonging to the Baltic lineage (McKeown *et al.*, 2010). The fish were reared from eggs in River Imsa water until smolting, as described by Fleming *et al.* (1994). The smolts were released into sea water, either (a) outside the mouth of the river (*n* = 517), or (b) towed by a boat from the outlet of the River Imsa at a speed of *c.* 1 $km \cdot h^{-1}$. The towed fish were swimming in a cylindrical glass fibre tank (1.7 × 7 m), closed by nets (5 mm bar mesh) at both ends so that water was passing through and kept with ropes alongside the boat while towing. The cylinder was partly submerged and towed a distance of 5 km to outside Lauvik (Figure 1), where the smolts were released into the sea (*n* = 491). A third group was transported in River Imsa water, in a closed tank on the deck of the boat, and released into the sea at Lauvik (*n* = 388). The fish were recaptured by fishermen at sea, in other rivers than the River Imsa by fishermen and anglers, or in the fish trap of the River Imsa on their return from the sea. In the River Imsa, all upstream moving fish are monitored in a box trap situated at the top of a three-step fish ladder, *c.* 150 m above the river mouth (Jonsson & Jonsson, 2011). The trap was emptied of fish twice a day all year-round, when possible life-history data and tag numbers were recorded. The number recaptured was used as an index of survival (Jonsson & Jonsson, 2009). An earlier experiment with River Emån *S. trutta* released in the River Imsa indicated that *c.* 5% of the released smolts were recaptured, which is similar to the recapture of wild *S. trutta* smolts of the River Imsa (Jonsson & Jonsson, 2014). The data were analysed using SPSS. The distributions were tested by Fisher's exact test and χ^2-test.

Mean total lengths and wet masses of the smolts released at the River Imsa (L_T = 30.2 ± 2.4 cm; W = 332 ± 91 g), towed by boat to Lauvik (L_T = 30.2 ± 2.6 cm; W = 340 ± 93 g) or transported in a closed tank and released at Lauvik (L_T = 30.0 ± 2.5 cm; W = 329 ± 86 g) were similar. Furthermore, mean reported recapture was 4.9% and number of *S. trutta* recaptured from the various release groups did not differ significantly (χ^2 = 0.71, 2 *df*, *P* = 0.8) (Table 1). Nonetheless, the

TABLE 1 Number and percentage of anadromous *Salmo trutta* captured in the River Imsa, other rivers and at sea when either released at the mouth of the River Imsa (*n*= 517), towed by boat from the Imsa and released at Lauvik 5 km from the mouth of the River Imsa (*n* = 491), or transported in a closed tank from Ims and released at Lauvik (*n* = 388)

	Imsa		Towed		Tank		Total	
Captured	Captured	%	Captured	%	Captured	%	Captured	%
Imsa	5	1.0	10	2.0	0	0	15	1.1
Other rivers	9	1.7	5	1.0	6	1.6	20	1.4
Sea	9	1.7	12	2.4	12	3.1	33	2.4
Total	23	4.5	27	5.5	18	4.6	68	4.9

distribution of recaptures among groups differed significantly (Fisher's exact test, $P = 0.02$). More fish returned to the River Imsa, if towed by boat when swimming in sea water and released at Lauvik, than those which were transported in a closed tank and released in the same place or released at the outlet of the River Imsa. Reported recaptures at sea or straying to other rivers were similar among groups ($P > 0.05$). Thus, the best method for recapturing adult *S. trutta* in the River Imsa was towing by boat to sea from the mouth of the River Imsa. All recaptures in other rivers, except one (Figgjo), were from watercourses emptying into the Høgsfjord estuary (Figure 1).

The best recapture rate from any of the release groups was 5.5%. This was the group towed by boat and released at Lauvik. This figure is similar to the recaptures found for similar-sized, 2-year-old River Emån *S. trutta* smolts released downstream of the fish trap in the River Imsa (Jonsson & Jonsson, 2014), and better than the group released outside the river mouth. Thus, towing of hatchery-reared smolts out to sea is a suitable method for smolt releases in systems with high predation rate in the river estuary. The advantage of smolt releases in rivers is that the fish can decide when to move to sea, whereas those released directly into sea water must be fully smolted to perform adequately in sea water (McCormick *et al*., 1998). Smolting is a gradual process, and all fish in a group may not be ready for sea life on the same day. Predation from fish, such as saith *Pollachius virens* (L. 1959) and cod *Gadus morhua* L. 1759, outside the river mouth may be high (Jepsen *et al*., 2006; Lennox *et al*., 2019), and *S. trutta* that are not smolted may be particularly vulnerable. Furthermore, on the return as adults, *S. tuttta* released in a river may more readily enter that river as found for *S. salar* (Jonsson *et al*., 1994). These authors showed that smolts of *S. salar* released at the river mouth entered the fish trap *c*. 2 weeks later on their return than those released 900 m farther upstream. The present trout had no prior experience from the river, but was raised in River Imsa water, in tanks close by the river. If individuals stay in the estuary long instead of readily entering the home river, mortality may increase as predation is assumed to be higher in estuaries than in rivers (Nevoux *et al*., 2019).

The straying rate was high, on average 57%. Least straying occurred in the group towed by boat that had a straying rate of 33% (*cf*. Table 1). The straying of the fish released at the mouth of River Imsa (64%) was high, but not much higher than that found in earlier releases of this stock released in the river (Jonsson & Jonsson, 2014). Hatchery practice tends to increase the straying tendency, and transplanted fish stray more than local conspecifics (Jonsson *et al*., 2003; Quinn, 1993). Nonetheless, towed by boat where the fish swam naturally reduced the straying rate over the other methods tested.

It is hypothesized that salmonids learn their migration route on the outmigration and use the knowledge obtained when returning to the home river for spawning (Hansen *et al*., 1993; Harden Jones, 1968). In the partly submerged cylinder, the fish swam freely and could pick up navigational cues that they could use on the return. Possibly, they use a navigational system in which magnetic cues guide fish through the open sea (Lohmann & Lohmann, 2019; Neave, 1964). Whether this navigation system is important in a fjord is unknown. According to Ueda *et al*. (2007), visual, but not magnetic cues were critical for the homing of sockeye salmon (kokanee) *Oncorhynchus nerka* (Walbaum 1792) in Lake Toya, Japan. Anadromous *S. trutta* seldom migrate far out into the ocean (Jonsson & Jonsson, 2011), and almost all the present recaptures were from the Høgsfjord estuary and rivers entering into this fjord. Thus, the navigational system of fjord-feeding *S. trutta* may be similar to that of *O. nerka* in a lake. One recapture was from outside the fjord, and this was a stray found in the River Figgjo. The mouth of River Figgjo is *c*. 60 km along the coast from the River Imsa. Jonsson and Jonsson (2014) reported that *S. trutta* of the Emån strain has been recaptured up to 450 km from the release site in the River Imsa. Thus, this fish may move long distances, but most move less than 250 km from the river mouth where visual cues may be vital for the homing success.

When rehabilitating streams and reintroduce *S. trutta*, it is a goal that as many as possible of the released fish survive, home and form self-sustaining populations. Transporting smolts in tanks reduces possible predation that may be high near the river outlet (Aarestrup *et al*., 2014; Lennox *et al*., 2019). Nonetheless, tank transport on board the boat seems to disrupt the learning of the migratory route in the fjord. From the closed tank, the *S. trutta* cannot pick up any visual or olfactory cues other than from the River Imsa water in which they were transported, and on board a boat, magnetic signals may also be interrupted. Furthermore, transportation instead of swimming may add to the reduced homing success (Chapman *et al*., 1997; Hansen *et al*., 1993; Keefer & Caudill, 2013). In addition, tank transportation may be stressful, and the abrupt transfer to sea water with no prior acclimatization before release may reduce the success of tank transported fish (Hansen & Jonsson, 1986). Thus, active swimming and the possibility to pick up natural cues along the migratory route appear essential for successful homing. In a tank with water through-flow while transported offshore, the fish were protected while moving to sea and could pick up essential navigational cues from the environments.

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