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Effects of macrophyte removal on habitat use of brown trout *(Salmo trutta)*

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Preface

This thesis completes my master's degree in Environment and Natural Resources at the Norwegian University of Life Science (NMBU). It is a 60 credits thesis written in collaboration with the research project "MadMacs" to the Norwegian Institute for Water Research (NIVA). Working with the thesis has been an informative, interesting, and exiting process. And of course, a challenging process, especially with the covid-19 situation and unpredictable lockdowns. However, during the whole process I have had valuable help from several people which I would like to give a thank:

First, I would like to thank my main advisor professor Thrond Oddvar Haugen for supervision during the whole process. Your enthusiasm and knowledge for the field has been a source for inspiration. Also, thanks for indispensable help with the statistics and R.

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Ås, June 2021

Astrid Torske

Abstract

Aquatic macrophytes play an important role in freshwater ecosystems. They are primary producers, promote good water quality, and provide food and habitats for various organisms, including fish. When macrophytes have sufficient resources available in a combination with little stress and disturbances, they can grow to nuisance levels. Such extensive growth is often referred to as "mass development". Due to negative impacts of mass development on recreational value of the ecosystems and use of water for hydropower the macrophytes are often removed.

In this thesis, I investigated the consequences of mechanical removal of the macrophyte *Juncus bulbosus* (L.) (bulbosus rush) on habitat use of brown trout, *Salmo trutta*. An acoustic telemetry study was conducted in a section of the river Otra, Norway. Macrophytes were removed from an impact area but not a control area in June 2020 and brown trout movements were monitored before, during and after the removal period. A total of 93 brown trout were captured and tagged, their movements monitored between the 11th of March to the 8th of September 2020. From the data, home range size (both 50 % and 95 %), probability of area usage (impact/control) and average depth use were calculated.

There were no significant change in home range size after removal of *J. bulbosus*, although, the results indicated a tendency for increased home range size after the removal. Additionally, the results indicated a change in the probability of area usage. While trout used the control area significantly less after the removal, there was no significant difference in the impact area. The impact area was not used much during the whole study period. Moreover, the depth-use of the brown trout was influenced by the discharge levels, with positions in shallower parts of the water column after removal of *J. bulbosus*.

In conclusion, removal of *J. bulbosus* did not have much impact on the habitat use of brown trout in the study area. However, only small amounts of *J. bulbosus* were removed (approximately 2% of the entire biomass of *J. bulbosus* in the Rysstad basin). I therefore cannot exclude that removal of a larger part of the biomass of *J. bulbosus* in a larger area might have significant influence on trout habitat use. This thesis contributes to filling the knowledge gap about potential impacts caused by macrophyte removal on the habitat use of riverine salmonids in oligotrophic freshwater systems.

Sammendrag

Akvatiske makrofytter (vannplanter) har en viktig betydning i ferskvannsøkosystemer. De er primærprodusenter, er med på å sikre en god vannkvalitet, gir mattilførsel og habitat til flere organismer, inkludert fisk. Dersom makrofyttene har tilstrekkelig med ressurser til å vokse og drive fotosyntese, i tillegg blir lite utsatt for ytre påvirkninger som kan forårsake stress og degradering for makrofyttene, kan de vokse seg til store størrelser og mengder. Slik vekst er ofte uønsket og blir omtalt som «problemvekst». Problemvekst har ofte negative konsekvenser for menneskelig aktivitet knyttet til vannsystemene, derav blir makrofyttene ofte fjernet.

I denne masteroppgaven har jeg undersøkt konsekvensene mekanisk klipping av makrofytten *Juncus bulbosus* (L.) (krypsiv) kan ha for habitatbruk til brunørret, *Salmo trutta*, ved å utføre en akustisk telemetristudie i et område av elven Otra i Norge. I juni 2020 ble *J. bulbosus* klippet i et effektområde, i tillegg ble det valgt ut et kontrollområde uten klipping av *J. bulbosus*. Totalt 93 ørret ble fanget og merket, og forflytninger i studieområdet ble overvåket i tidsperioden 11. mars til 8. september 2020. Fra dataene ble størrelse på hjemmeområdet, sannsynlighet for bruk av effektområdet og kontrollområdet, og gjennomsnittlig dybdebruk beregnet.

Det var ingen signifikante effekter av klippingen av *J. bulbosus* på størrelsen av hjemmeområde størrelse, men resultatene kunne antyde en økt størrelse på hjemmeområdet etter klippingen. Resultatene indikerte en endring i sannsynlighet i områdebruk, hvor kontrollområdet ble brukt mindre etter klipping. Effektområdet var veldig lite brukt igjennom hele studieperioden. I tillegg, viste resultatene at dybdebruken var avhengig av vannføringen, hvor da ørreten stod grunnere etter klippingen av *J. bulbosus*.

For å konkludere, klipping av *J. bulbosus* hadde lite effekter på habitatbruken til ørreten i studieområdet. Uansett, var det bare et lite område med *J. bulbosus* som ble klippet (ca. 2 % av hele biomassen med *J. bulbosus* i Rysstadbassenget). Derfor kan jeg ikke utelukke at dersom et større område med *J. bulbosus* ble klippet kunne man potensielt se større effekter på habitatbruken til ørreten. Denne masteroppgaven bidrar med kunnskap om effekter av klipping og fjerning av makrofytter i oligotrofe ferskvannsystemer på habitatbruk hos ørret.

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1. Introduction

1.1 Macrophytes as ecosystem engineers

Aquatic macrophytes play an important role in freshwater ecosystems influencing physical, chemical, and biological characteristics of the ecosystem. They are therefore often considered as ecosystem engineers (Carpenter and Lodge, 1986, Thomaz and Cunha, 2010, Levi et al., 2015). Macrophytes contribute to the nutrient cycle in the aquatic environment by taking up nutrients, such as phosphate and nitrate, and incorporating them into their biomass (Malthus et al., 1990, Mohamed, 2017). They ensure good water quality (Verhofstad, 2017), by competing with cyanobacteria (Mohamed, 2017) and therefore ensuring a clear and stable water state (Scheffer, 1998).

Owing to the many roles and functions of aquatic macrophytes, densities of fish and macroinvertebrates inhabiting habitats with macrophytes can be dependent on macrophyte abundance and structure (Warfe and Barmuta, 2004). Higher macrophyte density and a more complex structure can provide a higher abundance and species richness of fish and macroinvertebrates as it provides a larger available surface for the colonization of microorganisms, increases available habitats and options for shelter (Warfe and Barmuta, 2004, McAbendroth et al., 2005, Thomaz and Cunha, 2010). However, it has also been shown that fish abundance is highest when the habitat has intermediate vegetation complexity (Grenouillet et al., 2002). Thus, macrophytes have a potential impact on positioning of riverine fish since they provide shelter and cover and are therefore bioenergetically favourable by minimizing energy expenditure (Jenkins et al., 2010, Lusardi et al., 2018, Heggenes et al., 1993). On the other hand, it has also been shown that fish would tend to avoid areas of highly dense macrophyte stands (Miranda et al., 2000, Lopes et al., 2015). This is because the dens macrophyte stands would cause an inhospitable environment for fish by having low oxygen concentration (Lopes et al., 2015).

1.2 Mass development of macrophytes

Mass development of aquatic macrophytes has been documented in water systems all over the world (Verhofstad et al., 2017, Kagami et al., 2018). What promotes plant growth into mass development is the availability of sufficient resources for utilization in growth and photosynthesis (e.g., light, temperature, nutrients) in a combination with little disturbances on the macrophytes (e.g., no ice scouring during winter and stable waterflow from hydropower plants). Additionally, an extra resource supply like discharge of sewage, runoff from agriculture, and liming can enhance plant growth. These point sources provide nutrients which can be used for growth, providing CO_2 and nutrients via enhanced decomposition of organic matter. Under such conditions, macrophytes can grow to be several meters, create huge surface mats, and cover substantial areas of the substrate.

Mass development has several impacts on the ecosystem, among others, it can suppress other macrophytes (Schultz and Dibble, 2011), alter flow velocities (Sand-Jensen and Pedersen, 1999), and influence the sedimentation rate of suspended particles (Madsen et al., 2001). When fine particles settle in, and around, the macrophytes it could reduce the availability of courser substrate which could be used for spawning and shelter for brown trout, *Salmo trutta*, and Atlantic salmon, *Salmo salar*, (Velle et al., 2014). On the other hand, it is also suggested that the mass development does not limit fish production as it also provides shelter and habitats for the fish and macroinvertebrates (Velle et al., 2021).

Mass development often impose problems for human activities associated with the water system, such as boating, swimming, angling, and can also affect the aesthetic impression when the macrophyte creates surface mats (Verhofstad, 2017). Additionally, it can clog water turbines in hydropower plants (Dugdale et al., 2013). Therefore, macrophyte removal is often implemented as a management strategy in water systems experiencing mass development and are often being removed partly or fully.

In Norway, mass development of the macrophyte *Juncus bulbosus* (L.) (Bulbosus rush) is reported in several lakes and rivers, with highest abundance in the south-west of the country (Johansen et al., 2001, Moe et al., 2013). One of the water systems in Norway experiencing, high densities of *J. bulbosus* is the river Otra and in particular the section of the river known as the "Rysstad basin" (Velle et al., 2019). Otra runs through Setesdalen in Southern Norway. It is oligotrophic/ultra-oligotrophic and slightly acidic and has good conditions for mass development of *J. bulbosus*. Nuisance levels of *J. bulbosus* were already reported during the 1970s-1980s (Rørslett, 1987). At this time, the reach from Brokke hydropower plant to Straume bridge (Rysstad basin, about 5 km), *J. bulbosus* covered 55 % of the riverbed (Rørslett, 1987). The nuisance growth of *J. bulbosus* in this area impair fishing, swimming, and boating, as the macrophytes would entangle the fishing lines, being touched when swimming, and motor on boats gets clogged in the macrophytes. Local authorities therefore remove the macrophytes regularly. Earlier, strategies such as the winter freezing and drawdown were tested but this had negative effects downstream, and the macrophytes returned to nuisance amounts within few years (Brandrud and Johansen, 1997, Danielsen et al., 2012). Today, *J. bulbosus* is removed every 2-3 years, from an about 50-60 m wide and 500 m long stipe along the shore, to enable recreational fishing. The removal is being done without fully understanding the consequences it has for the ecosystem in the river.

1.3 Macrophyte removal and effects on fish

Every year, a large amount of money is spent worldwide on the removal of macrophytes due to the negative consequences for human activities. Solutions to combat perceived nuisance growth of aquatic macrophytes worldwide include mechanical removal (dredging, cutting), chemical (herbicides) and biological control (biological control agents, shading) (Hussner et al., 2017).

Removal of macrophytes is a dramatic and sudden change in the aquatic environment and alters available habitats for the aquatic organisms. Previous studies conducted in rivers have shown that macrophyte removal affects fish communities by a reduction in abundance (Swales, 1982, Greer et al., 2012), both reduced and increased growth rate (Garner et al., 1996, Unmuth et al., 1999), and reduced survival (Mortensen, 1977). The consequences of macrophyte removal on salmonids have rarely been studied in oligotrophic riverine ecosystems (Thiemer et al., 2021). However, as trout is a habitat generalist, the selection of habitat would vary with changes in the surrounding environment (Ayllón et al., 2010).

Both horizontal and vertical movement, and habitat selection of trout in rivers are constrained by a balance between foraging strategy and risk avoidance from other predators to maximize net energy gain (Bachman, 1984, Fausch, 1984, Levy, 1990). Vertical movement in the water column is often related to the daily movement of the fish, seeking shelter towards the bottom during daytime and foraging closer to the water surface during dusk and dawn (Hoar, 1942). Horizontal area utilization is often territorial and dependent on the home range size. Burt (1940) defined the term home range (HR) as "the area, usually around a home site, over which the animal normally travels in search for food”. Studies on different vertebrates have shown that the size of HR is often smaller in environments with a constant food supply in comparison with environments where the food supply is sporadic (Wolf & Trillmich 2007, Kapfer et al.2012). The same tendency has been found for juvenile salmonids, where it is observed that the HR size decrease with increased food availability (Nicola et al., 2016).

Habitat selection and usage can be studied using acoustic telemetry, which is a frequent used method to monitor fish movement both in marine and freshwater ecosystems, as it is cost-effective and give detailed information about fish movement in their natural habitat without being disturbed (Crossin et al., 2017). This provides valuable information when investigating movement, habitat use, and behavioural responses of fish e.g., from anthropogenic disturbances in their living environment (Cooke et al., 2004). Additionally, by using acoustic telemetry fish movement can be monitored over large areas, for long and uninterrupted periods of time.

1.5 Research aims and hypothesis

Due to limited knowledge about impacts macrophyte removal has on freshwater ecosystems, the MadMacs-project (Mass Development of aquatic MACrophyteS) aims to investigate causes and consequences of mechanical macrophyte removal for ecosystem structure, function, and services. This thesis was done within the framework of MadMacs focusing on habitat use of brown trout in the Rysstad basin in the Otra, an oligotrophic river system with brown trout as the only fish species in the study site. The aim of this thesis was to investigate the impacts from removing *J. bulbosus* on the habitat use of brown trout, by conducting an acoustic telemetry study. To my knowledge such studies have never been done on brown trout before-, and I have formulated three hypotheses.

Because trout have been shown to respond to habitat modifications by increasing their home range, I expected:

i. Brown trout home range size increases after removal of *J. bulbosus*

Motivated by studies showing that trout tend to prefer habitats with opportunities for shelter from an intermediate vegetation complexity, I expected:

ii. Brown trout uses impact area less after removal of *J. bulbosus*
iii. Brown trout inhabit deeper parts of the water column after the removal of *J. bulbosus*

2. Materials and methods

2.1 Study area

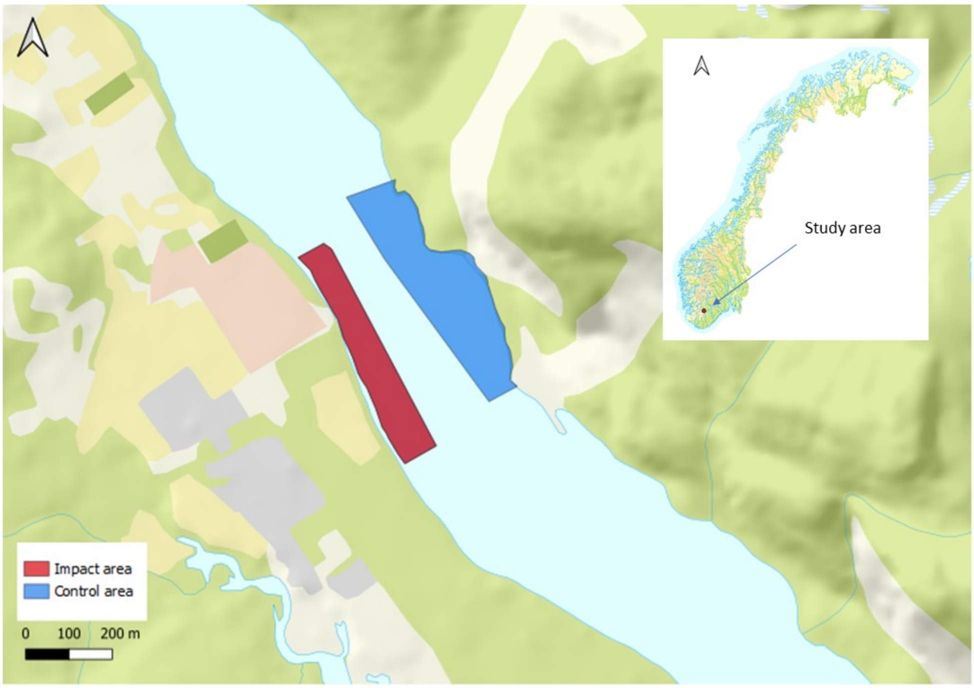

Figure 1 Map of the study site in the Rysstad basin and its location in Norway. The impact area is in red, and the control area is in blue

The river Otra runs through Agder county in the Southern parts of Norway (Figure 1). In total Otra is 245 km long. The discharge outlet is into Kristiansandsfjorden where the river has an average annual discharge of 150 m^3/s, despite that the discharge varies in the whole watercourse due to hydropower production. The total catchment area is 3752 km^2 (Norges vassdrag- og energidirektorat, 2020). It is dominated by birch forest and alpine uplands at higher altitudes, and deciduous forest and coniferous forest at lower altitudes. The whole water system of Otra consists of a lot of tributaries, and the main river also has several lakes, with the lake Byglandsfjord being the largest with a total length of about 35 km. The Otra has very clear water, and the river is classified as ultra-oligotrophic.

Brown trout can be found in the entire river system and is the most common fish species in Otra. Two types of Atlantic salmon can be found in the watershed; anadromous salmon in the anadromous reach from Kristiansand to Vigeland, and a unique relict freshwater resident stock of salmon called "Bleke" in Lake Bygelandsfjord. Other fish species in the water course are, among others, brook trout, *Salvelinus fontinalis*, and European perch, *Perca fluviatilis*, which both have been stocked into some of the tributaries. Additionally is the European minnow, *Phoxinus phoxinus*, spreading downstream in the Otra watershed after being introduced in an upstream lake (Hesthagen and Kleiven, 2012).

Like other watercourses in Southern Norway, Otra has been impacted by acid deposition since the 1960s (Aas et al., 2020). The acidification influenced the pH and the water quality in the river, which further had negative impacts on the biological life. The once renowned large-sized anadromous salmon got extinct (Kroglund et al., 2008), and the "Bleke" stock almost got extinct (Barlaup et al., 2009). Since 1990s, the water quality has improved due to, among others, less acid deposition and liming of the waters. This have had positive effects on the fish stocks (Kroglund et al., 2008, Barlaup et al., 2009). Fortunately, the acidification did not have as much negative impact on the brown trout stock in the river as brown trout tolerate acidic water better than salmon (Muniz, 1990)

Otra is highly regulated for the production of electricity. Already in the beginning of the 1900s, the lake Byglandsfjord was dammed. Since then, the whole water system has been extensively altered for the production of electricity. Installations of hydropower plants have influenced the whole water system by altering the water flow. Some reaches got increased water levels due to the discharge, and other reaches has no water at all. The altered water flow has consequences for the fish stocks. In addition, the dams would be a mitigation barrier for the fish. Installations of hydropower are also suggested to be one of the main reasons for the mass development of the macrophyte *J. bulbosus* in the river (Schneider and Demars, 2020).

The research area for this thesis is located where Otra passes the Rysstad village in Valle municipality (Figure 1). This part of Otra is also known as the "Rysstad basin" and has one of the highest extents of mass development of *J. bulbosus* in Norway (Velle et al., 2019). Despite the mass development of *J. bulbosus*, there are areas within the basin where the macrophyte is not present at all. The river substrate in Rysstad basin comprises mainly sand (Velle et al., 2019). Additionally, in this area is Otra wide and slow floating, and the water level is depending on the discharge from Brokke hydropower plant. Moreover, brown trout is the only fish species in the Rysstad basin.

2.2 Study species

2.2.1 *Salmo trutta*

Brown trout, *Salmo trutta* (L.), is a fish species within the family Salmonidae, hereafter referred to as trout. Trout is a native species in the northern hemisphere and Norway, however, the species is found in several places all over the world due to distribution and stocking by humans (Jonsson and Jonsson, 2011). Such wide distribution reflects that trout can be adaptive and flexible to different habitats and environments.

Habitat use of trout is affected by complex interactions between both biotic and abiotic factors (Armstrong et al., 2003, Heggenes and Wollebæk, 2013). When investigating the habitat use of trout, it is important to distinguish between habitat use and habitat preferences (Beyer et al., 2010, Johnson, 1980). The preferred habitat may not be available due to local conditions, and therefore the trout individuals may use suboptimal habitats. It is shown that trout might be selective in habitat choice (Heggenes et al., 2000).

Rivers offer a variety of habitat opportunities for trout, like riffles, pools and streambanks, and often the habitat use vary in space and time (Heggenes et al., 1999). Positioning in lotic environments is often dependent on water velocities and food supply to maximize net energy gain in addition to minimize the risk of predation (Fausch, 1984). Foraging in rivers can be from drifting macroinvertebrates and macroinvertebrates on the bottom substrate (Chapman, 1966). The chosen positions in rivers and streams are also size- and age-dependent. Trout fry prefers coarse substrate due to opportunities for sheltering and low water velocities, and usually utilize areas closer to the riverbed (Heggenes, 1988). It is also shown that trout fry use submerged macrophytes as cover (Elköv and Greenberg, 1998). As the trout grows it chooses positions further from the riverbed where water velocities often are higher (Heggenes, 1996, Riley et al., 2006, Chapman and Bjornn, 1969). Moreover, larger trout tend to choose more slow-floating water velocities and deeper parts of the river (Armstrong et al., 2003, Ayllón et al., 2010) Generally, trout would prefer some kind of cover if available (Heggenes et al., 2000).

2.2.2 *Juncus bulbosus*

Juncus bulbosus L. (bulbosus rush) is a native plant species in Norway and belongs to the family Juncaceae. It is a grass-like, perennial, macrophyte with long, slim leaves, and creates bog rosettes. The growth strategy makes it well suited for growing in lotic environments. However, *J. bulbosus* has both terrestrial and aquatic growth form, but for this study, *J. bulbosus* is referred to as the aquatic macrophyte. *J. bulbosus* is highly tolerant to environmental changes and can even grow at temperatures as low as 4 °C (Svedäng, 1990). *J. bulbosus* utilize CO_2 from the water layer as a carbon source for photosynthetic activity (Hinneri, 1976). Which is one of the reasons why the macrophyte thrives in acidic waters and are often found in oligotrophic/ultra-oligotrophic water systems (Roelofs et al., 1984, Prockow, 2008).

J. bulbosus is usually a small plant, however, some areas can experience mass development of the macrophyte where it grows to be several of meters long and covers large areas of substrate (Johansen, 2006). In river systems with hydropower plants velocities is thought to be one of the reasons for development of nuisance growth patterns as it creates more stable environments and reduces flow velocities (Schneider and Demars, 2020).

2.3 Study design

In advance of the study period, an impact area and a control area were chosen in a section of the Rysstad basin. Both were limited to approximately 500 m x 60 m and were located separately at each side of the river (Figure 2). A network of 20 receivers (10 in each area) were installed in and placed in a formation that allowed for triangulation of the movement of the tagged trout. The position of the receivers was decided before placement in the river by using QGIS. Before placing out the receivers in the river they were attached to a rebar bow that was fastened to a cement block. At eight of these receivers synchronisation tags were mounted (Figure 2, Table 1, Figure A 6). When placing out the receivers it was necessary at some places to cut out a square in a *J. bulbosus* patch to facilitate transmission of sound.

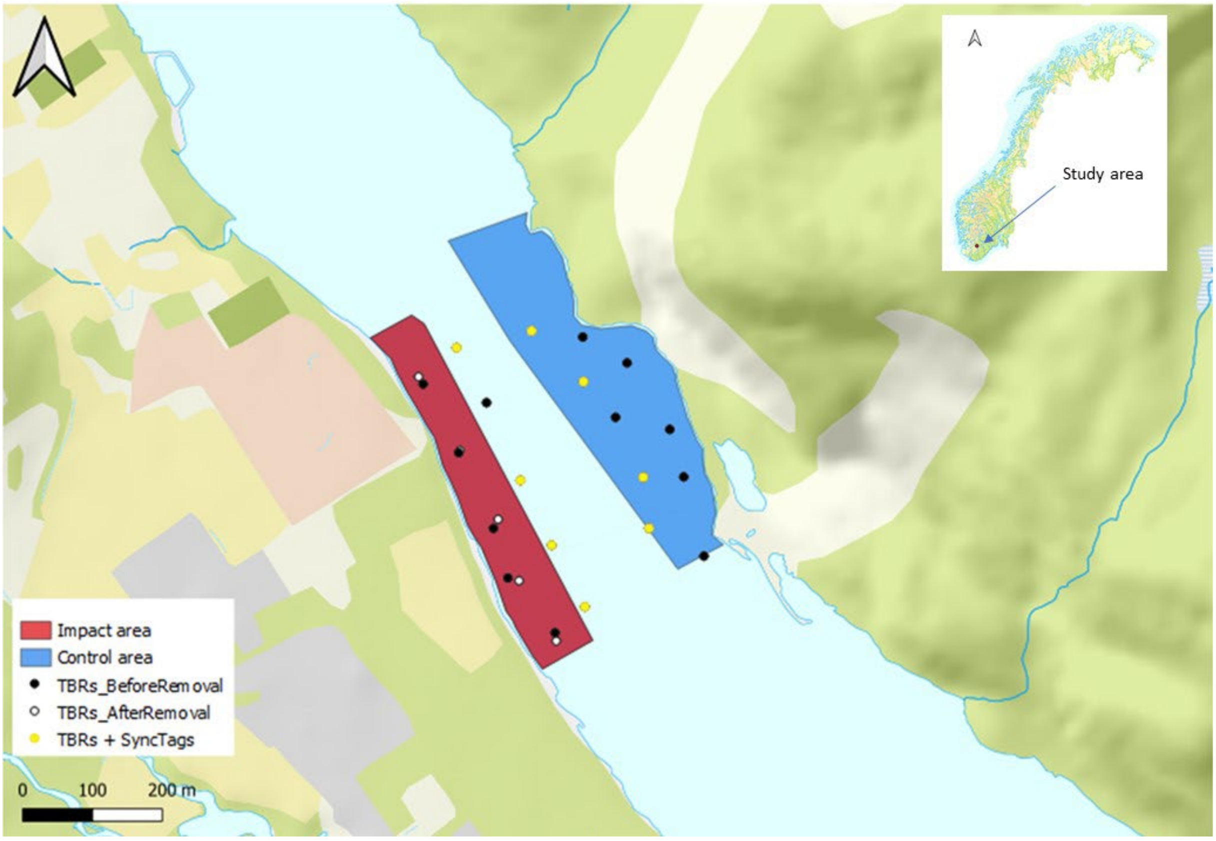

Figure 2 Placement of the receivers (dots, referred to as TBRs) in the impact area (red) and the control (blue). Yellow dots are where sync-tags also were mounted to the rebars, white dots are the new placement of the five TBRs taken out of the river during removal of J.bulbosus

The detection range of the receivers can vary among different sites and under different conditions (Reubens et al., 2018, Brownscombe et al., 2019). The Rysstad study site was expected to be challenging in terms of sound transmission as both macrophytes (in general) and powerplant-induced supersaturation of gasses are known to reduce transmission of sound energy (Gjelland and Hedger, 2013). From a range test done in the study area, a maximum detection range was found to be 120 meters. To be sure that we covered the study area it was chosen to place the receivers with approximately 100 meters between each.

The study period lasted from 11th of March to 8th of September 2020, i.e., receivers were launched in the river 11th of March, and final data was retrieved from the receivers 8th of September. Removal of *J. bulbosus* was undertaken from the 15th to the 23rd of June 2020. The removal was done using two special-designed boats for cutting most of the plant biomass, and afterwards, the sediment was harrowed by another special-designed boat to remove roots. However, *J. bulbosus* was not completely removed in the impact area (Figure 3). The average canopy height was reduced from 35 cm to 10 cm (Anonymous, 2021). Five of the receivers in the impact area were taken out of the river while *J. bulbosus* was removed. Hence, no available data from these receivers in this period (15th to 23rd). The receivers were put back in the river on the 24th of June, as close as possible to the original position (Figure 2).

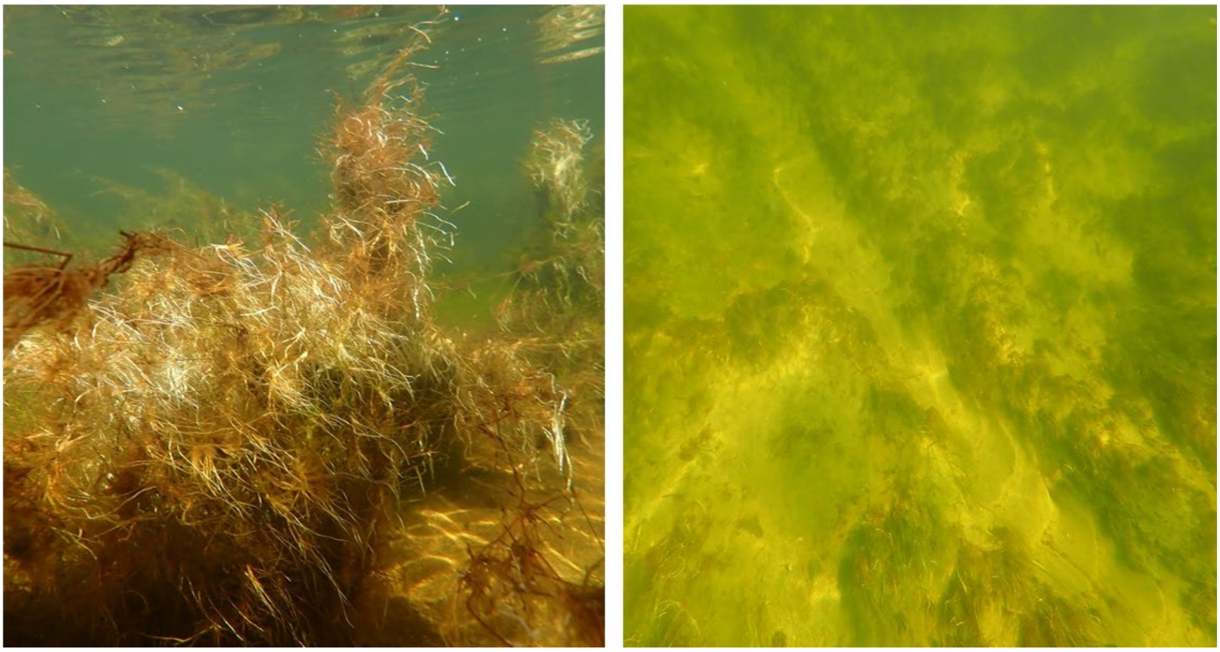

Figure 3 Example from the impact area before and after removal of J. bulbosus. *Before on the left side with dense growth of J. bulbosus, and after on the right side with still small stands of J. bulbosus (Photos: Kirstine Thiemer)*

2.3.1 Acoustic telemetry

In order to attain data on trout spatio-temporal habitat use, I conducted a telemetry study using acoustic transmitters in a triangulated receiver network. The principle of an acoustic telemetry study is to implant acoustic transmitters, hereafter called tag, in the chosen investigation object (here: trout). The tags transmit signals within a given interval which is received and stored in the receivers. By combining data from at least three receivers, it is possible to get approximate position data of the trout and reconstruct the movement (Figure 4).

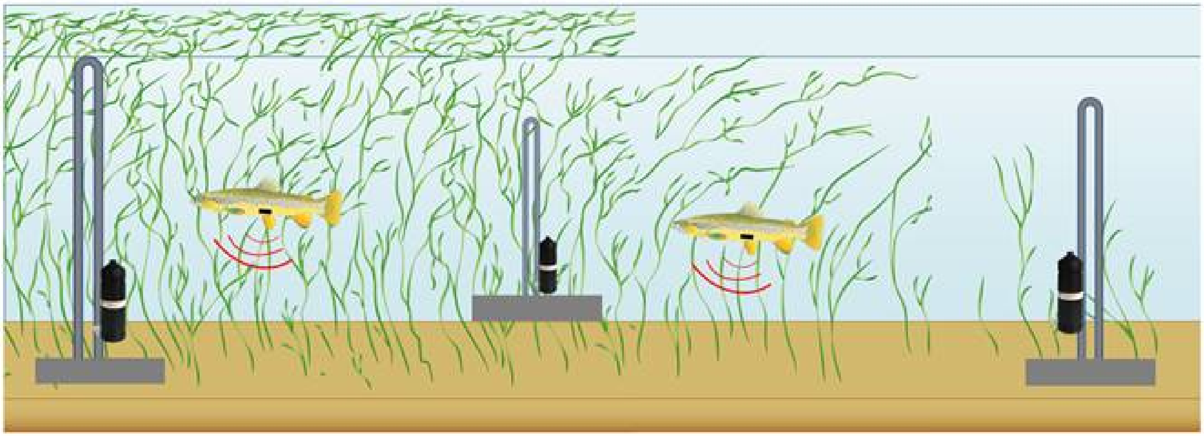

Figure 4 Principle of acoustic telemetry. Tagged trout swims within a receiver network, tags transmit signals which is received and stored by the receivers. By combining data from multiple (at least 3) receivers one can get positioning of the trout's movement. Here showing different densities of macrophyte stands (Figure produced by K. Thiemer)

2.3.2 Fish capture and tagging

In total, 93 trout were captured and tagged in March-May 2020. Beach seine and fyke nets were used for the capturing (Figure 5).

Figure 5 Left: Example from fish capturing by using a fyke net (Photo: K. Thiemer). Middle: Ongoing tagging of a trout. Left: Captured trout in a bucket before being anesthetized and tagged (Photo: K. Thiemer).

Tagging was done as soon as possible after capture by qualified people and with approval from the Norwegian Food Safety Authorities (FOTS id: 19476: Monitoring fish behaviour in a gas supersaturated river) (Figure 5). Thelma Biotel tags (Acoustic transmitter, Sensor Tag, D-2MP7; Thelma Biotel AS, Norway, www.thelmabiotel.com, Table 1) were used for tagging all the trout and were 9x32 mm and 3.7 g (mass in the air). A general "rule of thumb" indicates that internal tags should not be more than 2 % of the fishes' body weight and/or 8 % of body length (Jepsen et al., 2005), due to this fish < 90 g and < 200 mm were not tagged. The tags were set up to transmit coded acoustic signals randomly within every 60 to 120 seconds. This was done to avoid between-transmitter collisions of the signals. The transmitted signals get received and stored by receivers (here TBR-700, Thelma Biotel AS, Norway, www.thelmabiotel.com) that were mounted to cover the area of investigation. The transmitted signals gave information about fish ID, depth, and time. From the signal arrival times data (at millisecond level), a triangulation routine was done where each individual's average 3D-position at every 15 minute time slot (so-called PAV) were estimated using routine described in Simpfendorfer et al. (2012).

Table 1 Specs for the acoustic transmitters (D-2MP-7) and synchronization tags (ART-MP-13)

Tag specs	D-2MP7	ART-MP-13
Diameter	7 mm	12.7 mm
Length	32.9 mm	33.3 mm
Weight air	3.8 g	11.5 g
Weight water	2.4 g	7.5 g
Power output	141 dB re 1 µPa @ 1 m	153 dB re 1 µPa @ 1 m

The trout were anesthetized in a bucket with benzocaine (25 mL L^{-1}). The tagging was done when the fish showed no response when pressing the caudal peduncle (i.e., no spinal reflex). Under constant supply of ~ 50 % dose of the anaesthetic, a ~ 10 mm incision was made in the abdomen and a tag sterilised with chlorhexidine was inserted. The incision was closed back with two stitches of monofilament suture (Ethilon suture EH7144H 4-0 FS2 45 cm). Additionally, the total time of the surgery was registered for all individuals (less than 5 min), and while the fish was anaesthetized, fork length and weight of the fish were measured. Using tweezers, 1-7 scales were sampled from the area above the lateral line between the dorsal and adipose fin for age determination. Finally, a fin clip of the anal fin was taken for genetics analyses. The genetic analyses will not be further addressed in this thesis. After tagging, the fish was placed in a bucket with constant renewal of water from the river for recovery (6-10 hours). When the fishes were fully recovered, they were released back into the river.

The trout were released at three different sites. Either in the control or the impact area, or further downstream. 42 individuals were released in the impact and control area (21 in each site) and 53 were released further downstream (referred to as "Other" later in the analyses). The reason why some were released further downstream from the study area was because we were cooperating with another ongoing research project focusing on gas supersaturation in the river. Therefore, we used the same study population of trout. However, the trout released downstream from my study area is still of importance when analysing the data as the fish might migrate from downstream areas to my study area.

2.4 Scale readings

The scale samples were used for age determination and-, back-calculation of age-specific lengths that can be used for reconstruction of individual growth trajectories (Francis, 1990). Firstly, scales from each individual were inspected and the replacement scales were excluded as it is impossible to determine the first years on the scale (Figure 6). Intact scales were placed at a microscope glass with another microscope glass glued on top. For some individuals, there were only replacement scales from the samples, and these individuals were discarded for age determination and thus of the analysis of individual growth patterns.

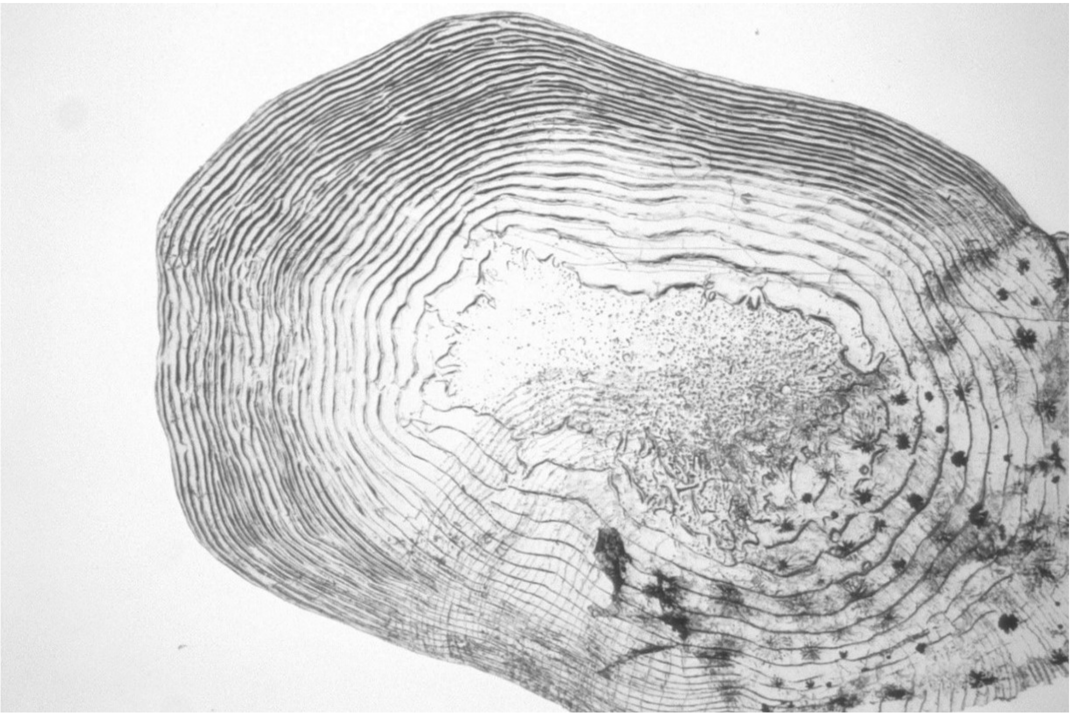

Figure 6 Example of replacement scale from one trout from Rysstad basin in Otra

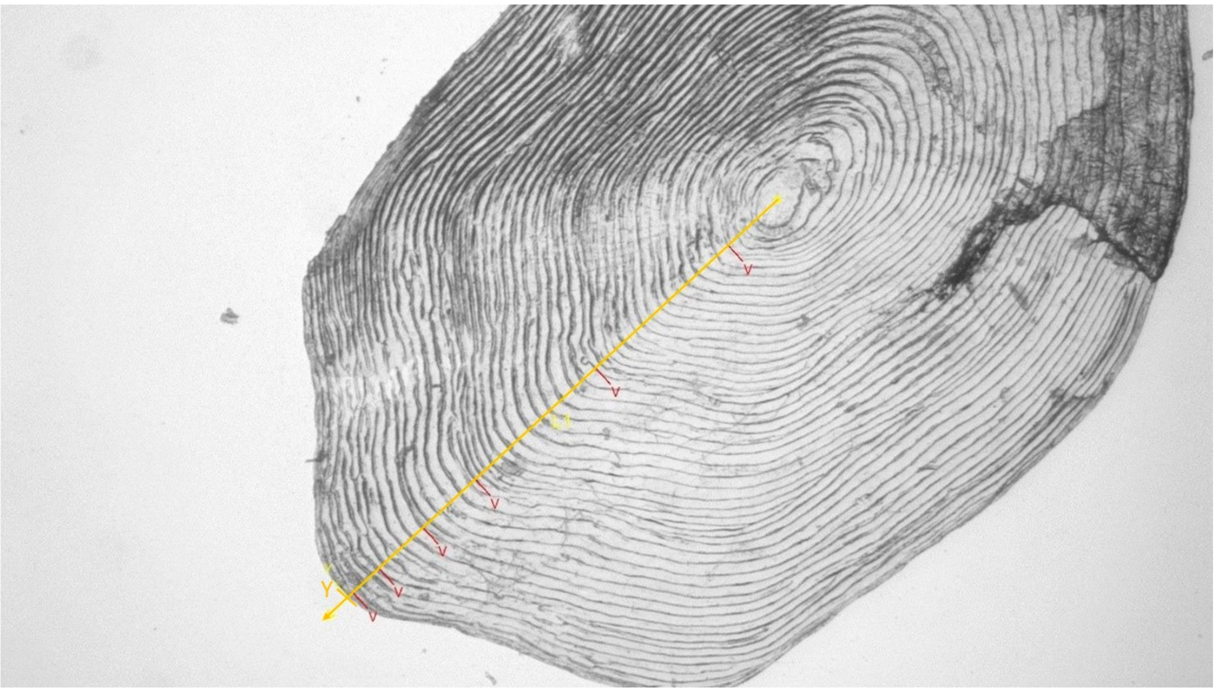

Figure 7 Example of scale reading for a six winter old trout from Rysstad basin in Otra. Yellow Y marks the end of the scale, and red V-'s mark the end of winter zones (annuli).

The scales that could be used for age determination were photographed using a LEICA DCF 425 CCD (Leica Microsystems GmbH) in a Leitz Aristoplan microscope (Ernst Leitz Wetzlar GmbH). Moreover, the photo files (.tiff) were exported to the software Image-Pro Express (Media Cybernetics Inc.) for digital marking of winter zones (annuli). Firstly, a line was drawn from the middle of the scale's central plate to the scales outer edge (Y, Figure 7), and next, the winter zones were marked at the respective transition areas between winter sclerites and summer sclerites (V, Figure 7). An Image-Pro Express macro was used to retrieve both the respective winter radii and the total radius of the scale and passed into an excel spreadsheet. The radii data were used to back-calculate the actual fish length at the different ages (i.e., at end of winter) by using the direct proportion method (Lea E., 1910, Dahl K., 1910):

$$L_f = L_t \frac{S_f}{S_t}$$

L_f = back-calculated fish length at annulus f,

L_t = fish length at capture,

S_f = scale length to annulus f, and

S_t = total scale length

In total, scales from 61 individuals were analysed. The number of scales from each individual varied from 1 to 7. For individuals with more than one analysed scale the average result for back-calculated length was used. Scales from the remaining 32 individuals were discarded as replacement scales.

2.5 Data processing and statistical analysis

Data from the receivers were downloaded on the 8th of September 2020.

Prior to analyses it was necessary to clean, and quality assure the data. Disturbances and ambient noise such as dense macrophyte stands, gas saturation, riverbed morphology could have influenced the signals. Additionally, it is possible to get collision between signals from several tagged fish that are in the same area. Pinging rates for each transmitter were set to vary between every 30 and 90 seconds to reduce this problem. However, when collisions occur, these disturbances could result in false detections and errors in the dataset, like detections of non-existing IDs, detections of trout at 20 meters depth (which is not possible as the study area had a maximum depth of about 4 meters). The false detections and errors were removed and not included in the analyses.

I investigated and analysed five main behavioural traits and how these potentially were affected by the removal of *J. bulbosus*. This was done in order to say something about how the trout use the *J. bulbosus* as a habitat and how the removal would impact the habitat use. The behavioural traits were divided into horizontal movements and vertical movements. The investigated horizontal movements were home range size, both where the trout uses 50 % of its time and 95 %, and the probability for the trout to use the impact area and the control area, analysed separately. The investigated vertical movement was depth use in the study area. By calculating these variables, it is possible to describe how the fish use *J. bulbosus* as habitat both before and after the removal.

The behaviour traits were analysed by estimating each individual's average 3D-position at every 15 minute time slot by using the position-algorithm (Simpfendorfer et al., 2012). This method provides an approximate average positioning of the trout in the 15 minutes time slot, so-called PAV. The average position was estimated by calculating the weighted mean X and Y position per time slot. Meaning, when the tagged trout move within the network of receivers the different receivers would receive different amount of transmitted signals, and one could assume that the receiver receiving the most signals was the one the trout was positioned closest to (Simpfendorfer et al., 2012). The calculation of weighted X and Y position require detections from at least three receivers.

The individual's utilization distribution over two days (UDs) was estimated based on the individual's PAVs. The UDs provides information about where each individual spent most of their time and was estimated for both for 50 % UDs and 95 % UDs. In order to estimate the individual UDs, the kernelUD function in the R-package adehabitatHR (Calenge, 2006) was used. The smoothing parameter h was found by running a selection of individuals, from which 200 utilization distributions were estimated, with h = "href". This setting uses an optimization algorithm that provide an optimal h-value given the data. This optimal h was estimated for each of the 200 distributions rendering an estimated average value of 15. Hence, h = 15 was used for all individuals.

For analysing the home range sizes, I differed between where the trout used 50 % of its time during the two days (HR50), and where it used 95 % of its time (HR95). The HR50 represent the core area for habitat usage and is most often used in studies. When investing HR95 it provides a wider picture of the area usage and territory (as their territory is often larger than the feeding area).

The probability of using the impact and the control area were estimated as the fraction of area overlap of HR50 with control and impact area, respectively. The R-package rgeos (Bivand and Rundel, 2019) and functions gIntersection and gArea was used for this purpose. Therefore, the probability estimates were also based on the detections combined of two days. The data indicated a binomial distribution. In order to simplify the further analysis, the probability of overlapping HR50 with impact area < 0.50 were set to be representing control area and > 0.50 impact area. Which means if less than 50 % of the time is spent in control area it equals 0.00, and if more that 50 % of the time it is impact area it equals 1.00, and contrary for control area.

In order to keep all spatial analyses on the same temporal scale, I used PAV-derived mean depth when analysing the depth use of the tagged fish (Simpfendorfer et al., 2012). This method does not provide exact position of the trout, but it provides estimates of the average position of the trout at a timescale of 15 minutes. For estimating the depth usage, PAV provides information about where the trout is in the water column related to the water surface.

Analyses of all the five behavioural traits followed the same procedure. Generalized linear mixed models (GLMM-models) was fitted using the R-package "lme4" (Bates et al., 2015) in order to investigate which effects were explaining the variations in the data. The tested fixed effects were "Treatment time" (Before, During and After removal of *J. bulbosus*), "Release site" (where the trout were released after tagging, "Impact", "Control" and "Other"), "Length" and "Condition factor (K-factor)". The k-factor tells us something about the condition of the fish at capturing/tagging, and was calculated by using the Fulton formula (Froese, 2006):

$$K = 100 \frac{W}{L^3}$$

K – condition factor

W – weight in gram

L – total length in cm

For the depth analysis, discharge and average water levels were tested as fixed effect in addition to the above-mentioned fixed effects. The discharge data was hourly measurements provided by Agder Energy/Otra kraft. For computing the average water levels, there were mounted pressure sensors both upstream and downstream for the study site. With data from these sensors it was possible to compute changes in water levels (z) by the following equations z = 0.48*Q - 0.48*85 (for pressure sensors upstream), and z = 67.6*exp(0.0027*Q) - 67.6*exp(0.0027*85) (for pressure sensors downstream). Q = discharge (m^3/s), and depth data were cross calibrated for a discharge of 85 m3/s, meaning at this discharge z = 0 (Figure A 7). To get the changes in water levels at my study site, the average values of upstream and downstream measurements were calculated. Moreover, gas saturation was intended to be tested as a fixed effect. But the datasets were not fully complete for the whole study period, which made it impossible to implement gas saturation in the model testing. However, a graph was made of gas saturation data from the 1st of May until the 8th of September (Figure A 8). Theses gas saturation data was provided by the other ongoing research project about gas supersaturation in the Otra.

All the tested fixed effects could be important indications of habitat use. Back-calculated length/ length at first year was not tested as a fixed effect since 32 of the individuals had scale samples determined as replacement scales. All models were tested with ID as a random effect. Further, the Akaike Information Criterion (AIC) was estimated by using the R-package "AICcmodavg" (Mazerolle, 2020). This gave a ranked list of the candidate models, where the model with the lowest AICc-value was first in the list and represent the model with the most support in the data. Models having ΔAICc > 2 were assumed to have little support in the data (Anderson, 2007). Prediction data was based on the model having the most support in the data. The prediction data contained the parameter estimates and the effect test (from an ANOVA variance analysis). Finally, a prediction plot was made using the R-package ggplot2 (Wickham, 2016).

Data handling, and all statistical analyses, of the data uploaded from the receivers, were done by using R version 4.0.5 (R Core Team, 2021) and scripting in the supporting program R Studio. All maps were produced by using QGIS (QGIS Development Team, 2021).

3. Results

The total study population comprised 93 trout, of which 61 had scale samples allowing for age determination and back-calculation of growth trajetories.

After combining two days for the HR analyses and for the analyses of the probability of using impact/control area, there were 132 PAVs for the trout released downstream from study area ("Other"), 103 PAVs for the trout released in the impact area, and 56 PAVs for the trout released in the control area. These PAVs were from 14 individuals in Other, 10 in the impact area, and 10 in the control area.

3.1 Age and size distributions

The tagged fish range from age 4 to age 11 where age groups 6 and 7 dominated (Figure 8).

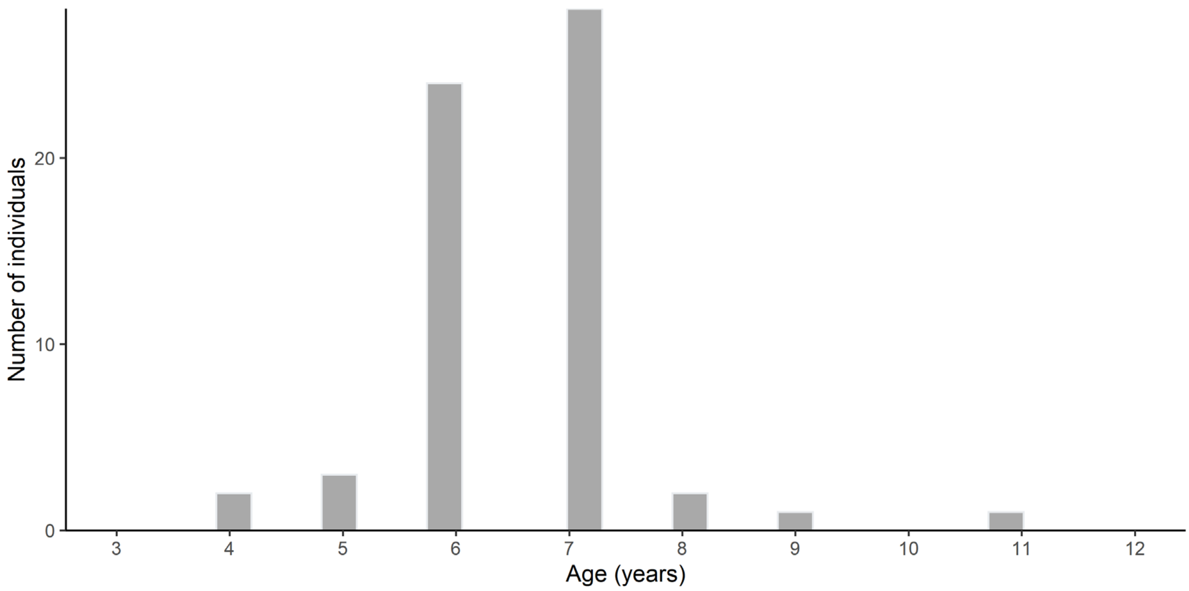

Figure 8 Age distribution of tagged trout in this study (n=61)

The individual lengths in the total study popluation ranged fram 204 mm to 323 mm, with a mean of 235 mm (Figure 9).

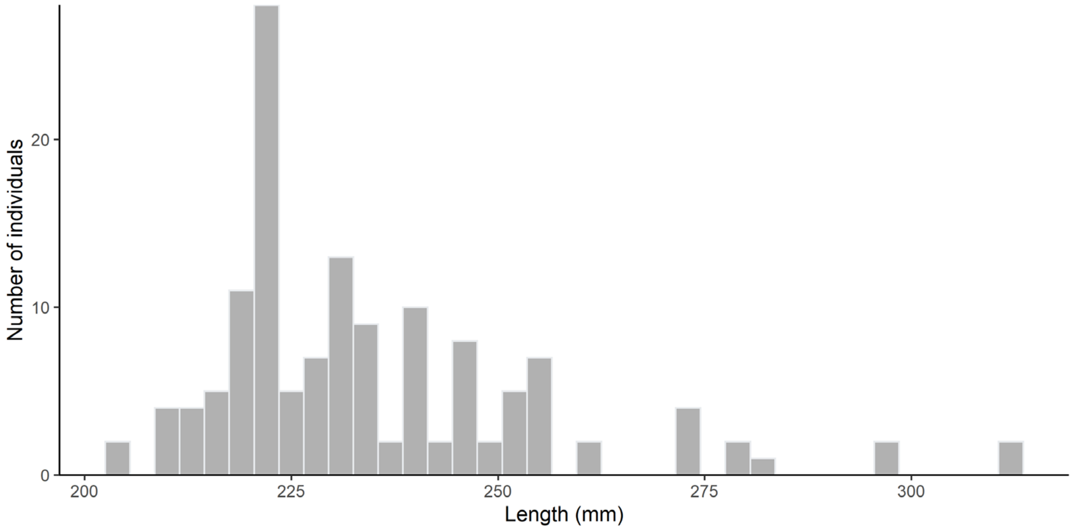

Figure 9 Length distribution (mm) of total study population (n=93)

There was large inter-individual variation in back-calculated growth trajetories where just a few individuals attained larger than 30 cm. Most old indiciduals in the data seemed to have a slow growing pattern (Figure 10). Back-calculated first-winter lengths varied between 17.6 and 62.9 (mean 39.8 ± sd 9.9) mm.

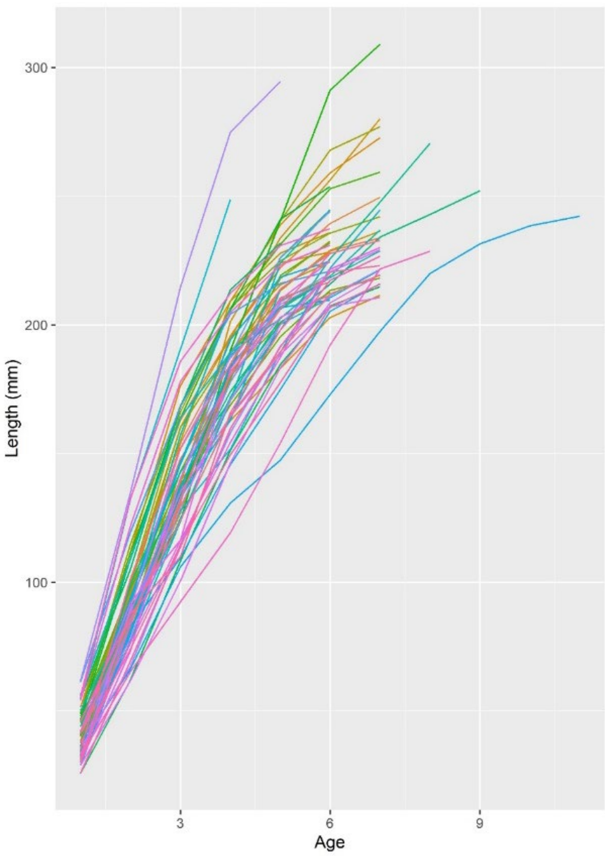

Figure 10 Individual growth trajectories of the tagged trout that were age determined (n=61)

3.2 Home range

3.2.2 Home range, 50%

HR50 varied between 0.11 and 1.73 (mean 0.31 ± sd. 0.19) hectares.

The HR50 distributions overlapped to a large extent through all three periods (before, during, and after) and variance was by far lowest during the "during" period compared (Figure 11).

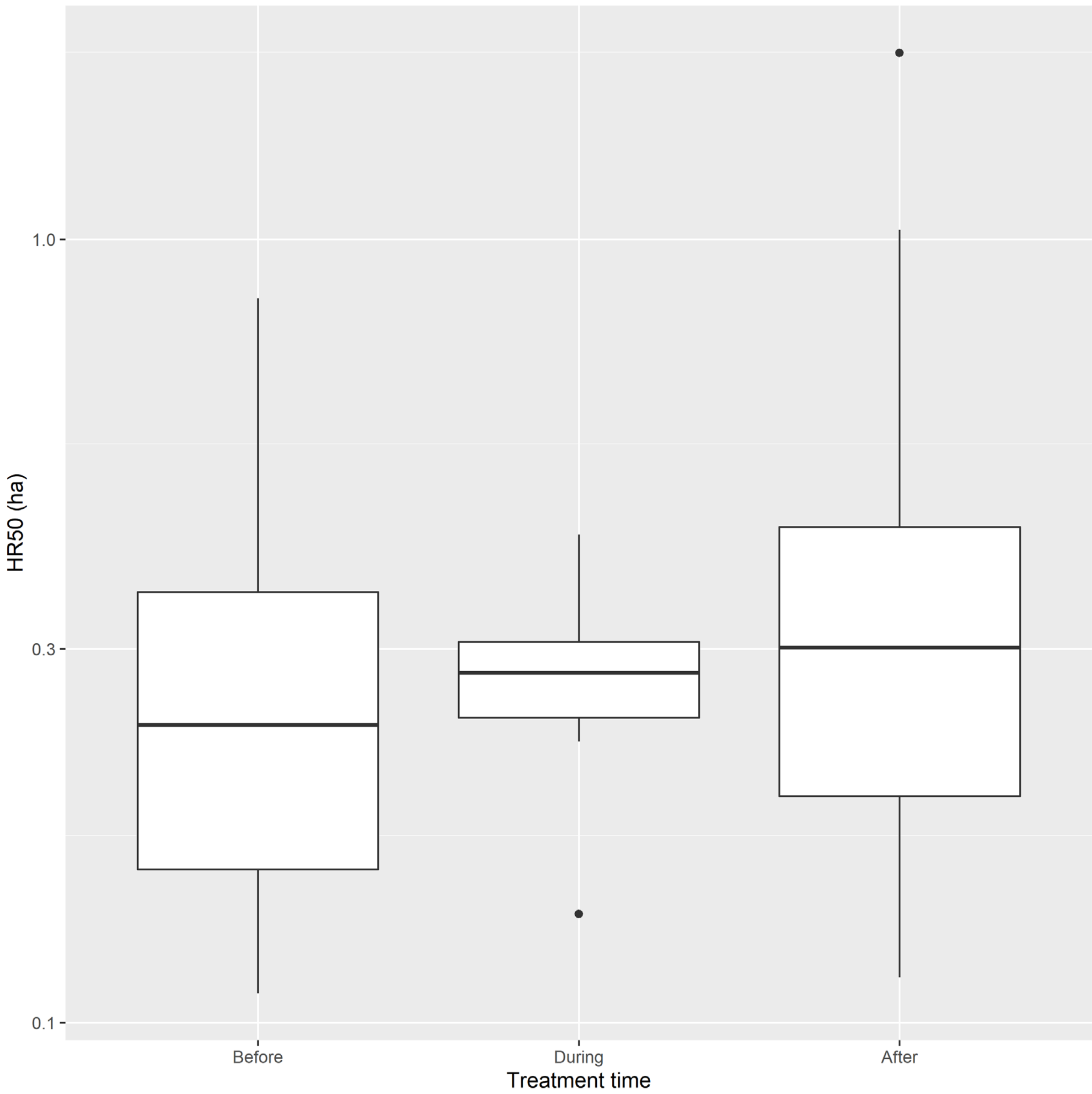

Figure 11 Boxplots of home range size in hectare, where trout used 50% of its time, before, during and after removal of J. bulbosus. *The boxes include 50 % of the observations and vertical lines 90 %. The thick horizontal line with boxes represents the median value*

An interaction model between release site (where the trout were released after tagging) and treatment time (before, during and after removal of *J. bulbosus*) was the candidate model with most support in the data (Table A 1, Table 2). This model got 100% of the AICc-weight.

Table 2 Parameter estimates and effect test for the model with the most support in the data in Table A 1. Im = impact area, Co = control area, RS = Release Site, TT = treatment time

		Parameter estimates			Effect test				
	Term	Estimate	SE	t value	Effect	F	Df	Df.res	p
Fixed	Intercept	-1.09	0.10	-9.90	RS	0.12	2	28.46	0.89
	RSIm	0.01	0.19	0.05	TT	9.78	2	269.24	<0.0001
	RSCo	0.38	0.21	1.78	RS:TT	9.34	3	272.40	<0.0001
	TTBefore	0.11	0.11	0.97					
	TTDuring	-0.08	0.18	-0.46					
	RSIm: TTBefore	-0.39	0.15	-2.66					
	RSCo: TTBefore	-0.82	0.17	-4.87					
	RSIm: TTDuring	0.40	0.28	1.43					
		Variance	Std.Dev						
Random	Among ID	0.11	0.33						
	Residual	0.16	0.40						

The interaction effect between release site and treatment time was highly significant ($p<0.0001$, Table 2). Therefore, the model predicted no parallel temporal developments among release-site groups over the course of the experiment (Figure 12). On average, the selected model estimated within-individual variation (variance=0.16, Table 2) in bi-daily HR50s to be slightly larger than the among-individual variation (variance=0.11, Table 2). Individual random effects were also fitted, showing detected individuals with increasing home range size (Figure A 1)

Predicted HR50 increased most for the trout released in control area (Figure 12). The trout released in impact area also had an increased predicted home range size after removal, but not as much as the ones released into control area. The predicted HR50 of trout released downstream from study area ("Other" in Figure 12) seemed to be little affected by the removal of *J. bulbosus,* with a small decrease in predicted HR50.

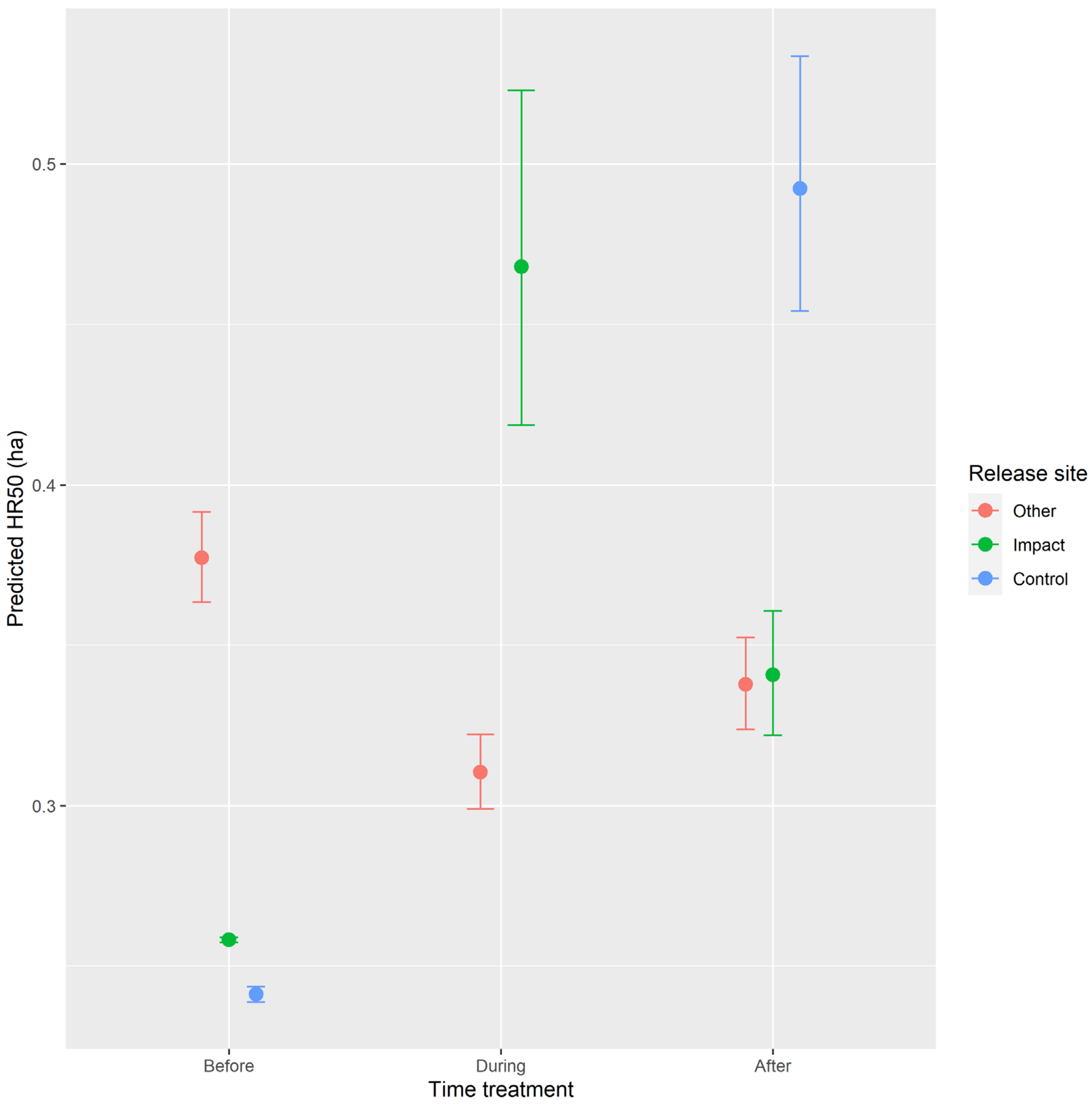

Figure 12 Predicted home range size (HR50) in hectare (ha) for where the trout uses 50% of its time before, during and after removal of J. bulbosus. *Release site = where the trout were released after being tagged ("Other" is further downstream from study area, additionally in impact and control area). Predictions were made from model reported in Table 2 and are only based on the fixed effects part of the model.*

3.2.3 Home range, 95%

HR95 varied between 0.56 and 5.87 (mean 1.5 ± sd. 0.78) hectares.

The HR95 distributions overlapped to a large extent through all three periods (before, during, and after) and variance was by far lowest during the "during" period compared (Figure 13).

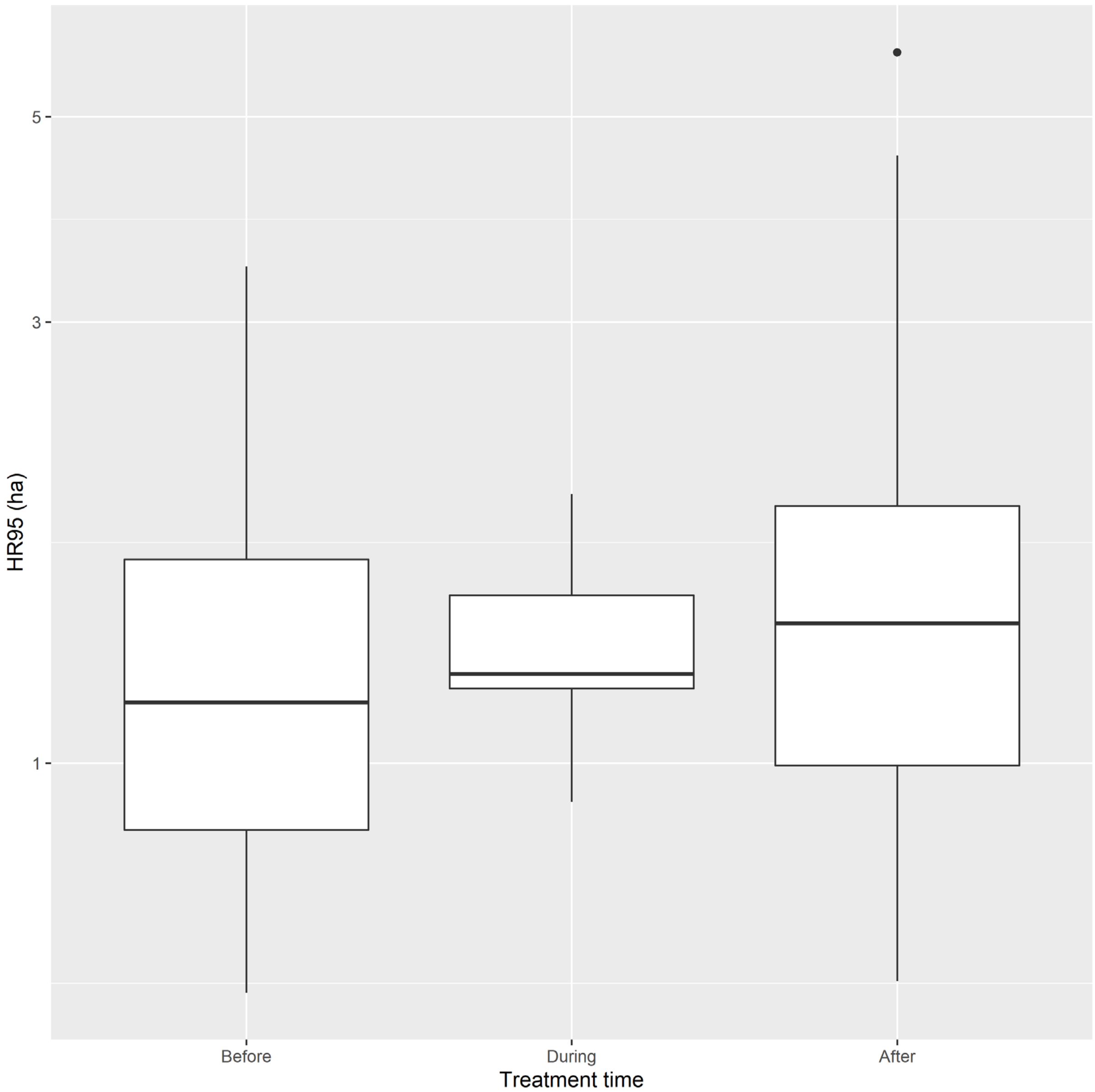

Figure 13 Home range size in hectare, where trout used 95% of its time, before, during and after removal of J. bulbosus*. The boxes include 50 % of the observations and vertical lines 90 %. The thick horizontal line with boxes represents the median value*

Just like the HR50, an interaction model between release site (where the trout were released after tagging) and treatment time (before, during and after removal of *J. bulbosus*) was the candidate model with the most support in the data (Table A 1, Table 3). The model got 100% of the AICc-weight.

Table 3 Parameter estimates and effect test for the model with the most support in the data in Table A 1. Im = impact area, Co = control area, RS = Release Site, TT = treatment time

		Parameter estimates			Effect test				
	Term	Estimate	SE	t value	Effect	F	Df	Df.res	p
Fixed	Intercept	0.42	0.10	4.35	RS	0.53	2	27.44	0.60
	RSIm	-0.10	0.10	-0.59	TT	6.36	2	241.93	<0.01
	RSCo	0.47	0.19	2.41	RS:TT	13.54	3	244.53	<0.0001
	TTBefore	0.20	0.10	1.93					
	TTDuring	0.07	0.19	0.36					
	RSIm: TTBefore	-0.38	0.14	-2.70					
	RSCo: TTBefore	-0.98	0.16	-6.20					
	RSIm: TTDuring	0.21	0.27	0.79					
		Variance	Std.Dev.						
Random	Among ID	0.08	0.29						
	Residual	0.13	0.36						

The interaction effect between release site and treatment time was highly significant ($p<0.0001$, Table 3). As a consequence, the model predicted no parallel temporal developments among release-site groups over the course of the experiment (Figure 14). On average, the selected model estimated within-individual variation (variance=0.13, Table 3) in bi-daily HR50s to be larger than the among-individual variation (variance=0.08, Table 3). Individual random effects were also fitted, showing detected individuals with increasing home range size appendix (Figure A 2).

Predicted HR95 increased most for the trout released in control area (Figure 14). The trout released in impact area also had an increased predicted home range size after removal, but not as much as the ones released into control area. The predicted HR95 for trout released downstream from study area ("Other" in Figure 14) seemed to be little affected by the removal of *J. bulbosus,* with a small decrease in predicted HR95.

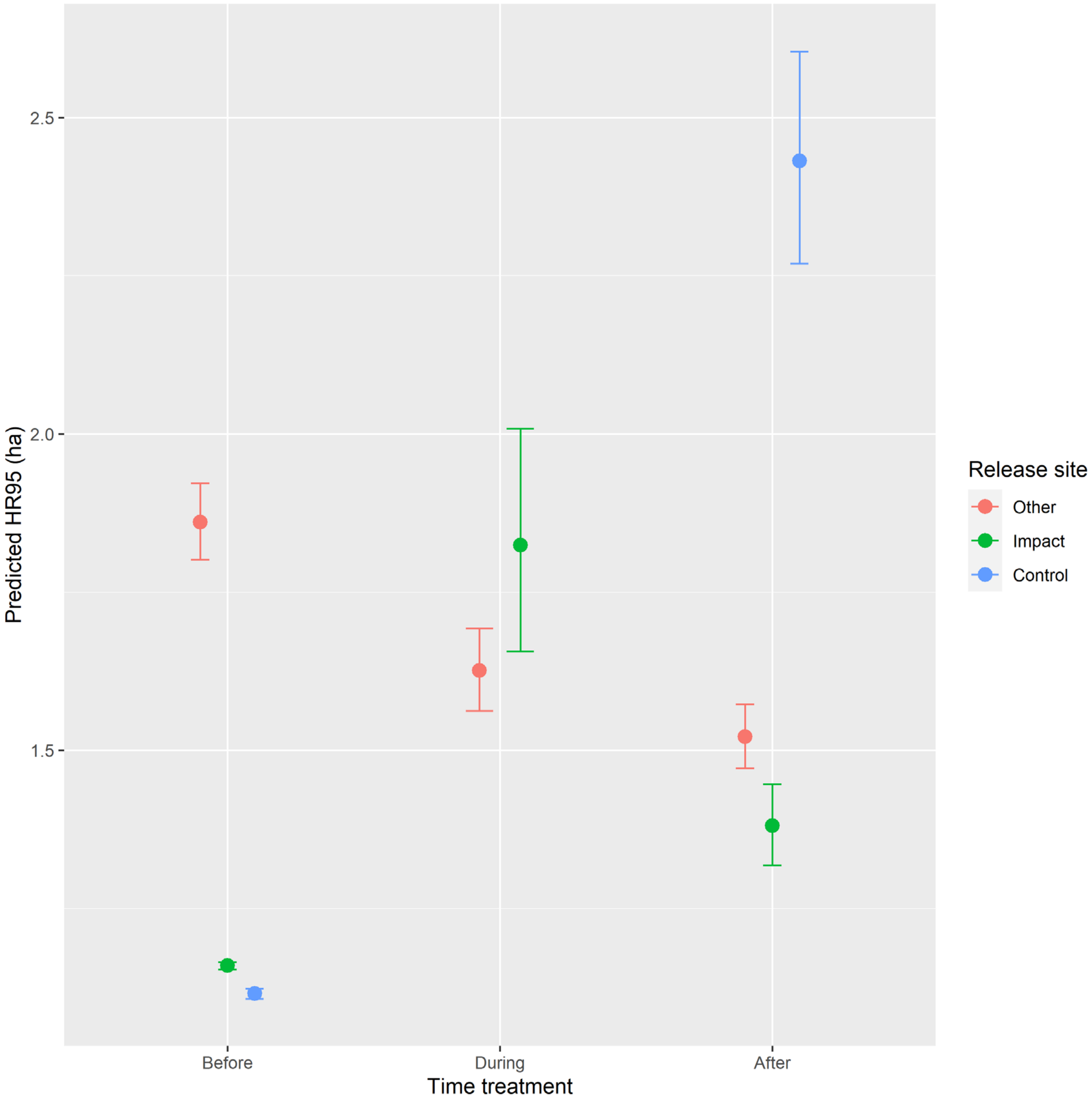

Figure 14 Predicted home range size (HR95) in hectare (ha) for where the trout uses 95% of its time before, during and after removal of J. bulbosus*. Release site is where the trout were released after being tagged (Other = further downstream from study area, additionally in impact and control area). Predictions were made from model reported in Table 3 and are only based on the fixed effects part of the model.*

3.3 Probability of using impact area

The probability for the trout using impact area was examined by looking at the chances for overlapping HR50 with the impact area. The impact area was not much used by the trout in this study as there were small chances of overlapping HR50 with impact area (Figure 15).

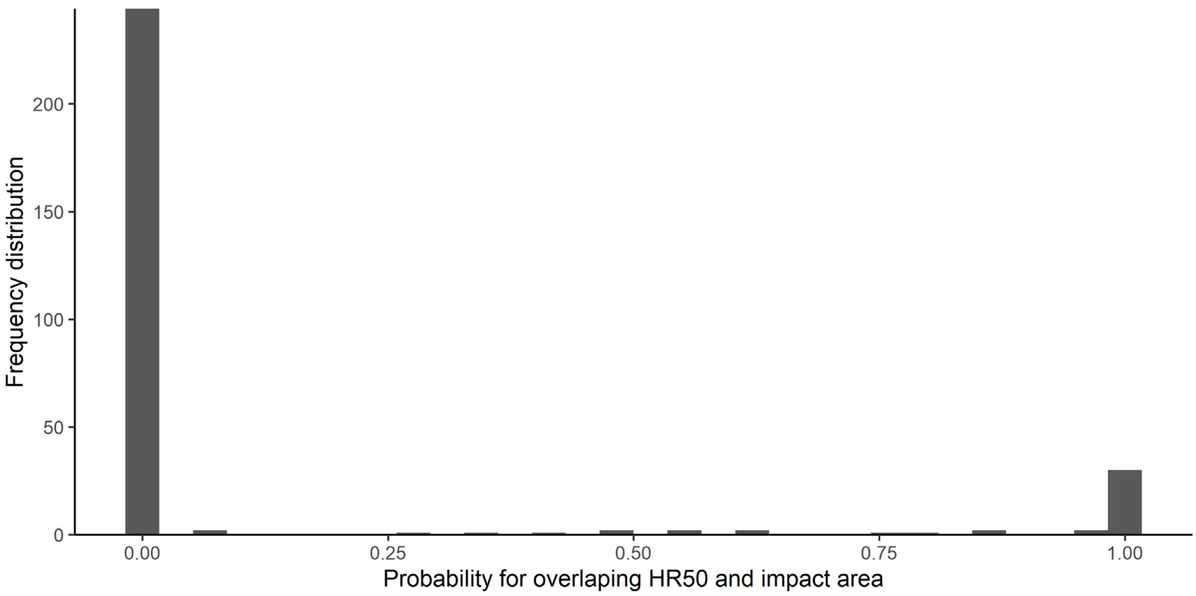

Figure 15 Frequency distribution of ration of the HR50s that were overlapping with the impact area over the course of the experiment. 1.00 on x-axis represents full time use of the impact area

Treatment time alone had most AICc-support in the data as a predictor for probability of HR50 to overlap with impact area (about 51% of the AIC weight, Table A 1). The model selection also revealed that an interaction between treatment time and length of the fish influences the probability of using the impact area, attaining about 20% of the AIC weight.

The treatment time did not have a significant effect on the probability of using impact area, (Table 4). Standard error of during the removal of *J. bulbosus* was very high, SE=2.12e+07 (Table 4, Figure 16). During removal of *J. bulbosus* there were few detections, and therefore a large uncertainty of the probability of using impact area. Individual random effects indicate which individuals having the largest probability of using impact area (Figure A 3).

Table 4 Parameter estimates for the model with the most support in the data in Table A 1. TT = treatment time

		Parameter estimates				Effect test			
	Term	Estimate	SE	z value	Pr (>|z|)	Effect	Chisq	Df	Pr (>Chisq)
Fixed	Intercept	-8.91	4.97	-1.80	0.07	TT	3.16	2	0.21
	TTBefore	-7.42	4.18	-1.78	0.08				
	TTDuring	-5.14e+02	2.12e+07	0.00	1.00				
		Variance	Std.Dev						
Random	Among ID	253.90	15.93						

The probability of using impact area was very small, almost zero, during the whole study period (Figure 16) and few individuals were detected in the impact area during the study period (Figure A 3). However, the confidence interval impact area increases after removal of *J. bulbosus*, which indicates a higher probability to use the impact area after removal.

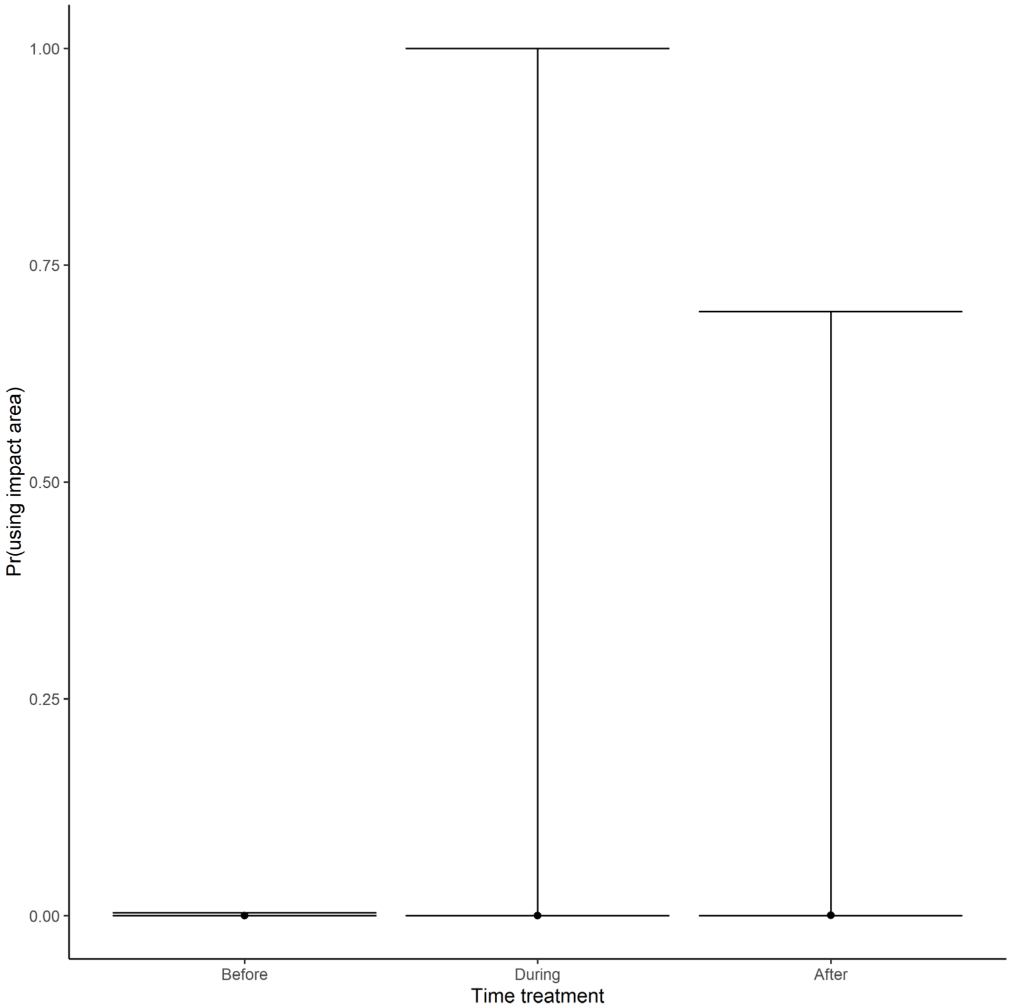

Figure 16 Predicted use of impact area before, during, and after removal of J. bulbosus. The dots represent the predicted usage (ranging from 0 to 1, where 0 equals almost no usage), the vertical lines are the confidence intervall indicating the uncertainties related to the predicted usage. Predictions were made from model reported in Table 4

3.4 Probability of using control area

The probability for the trout using control area was examined by looking at the probability for overlapping HR50 with control area. Figure 17 shows that there was high probability of overlapping HR50 with control area, which indicates that the control area is being used by the trout in this study.

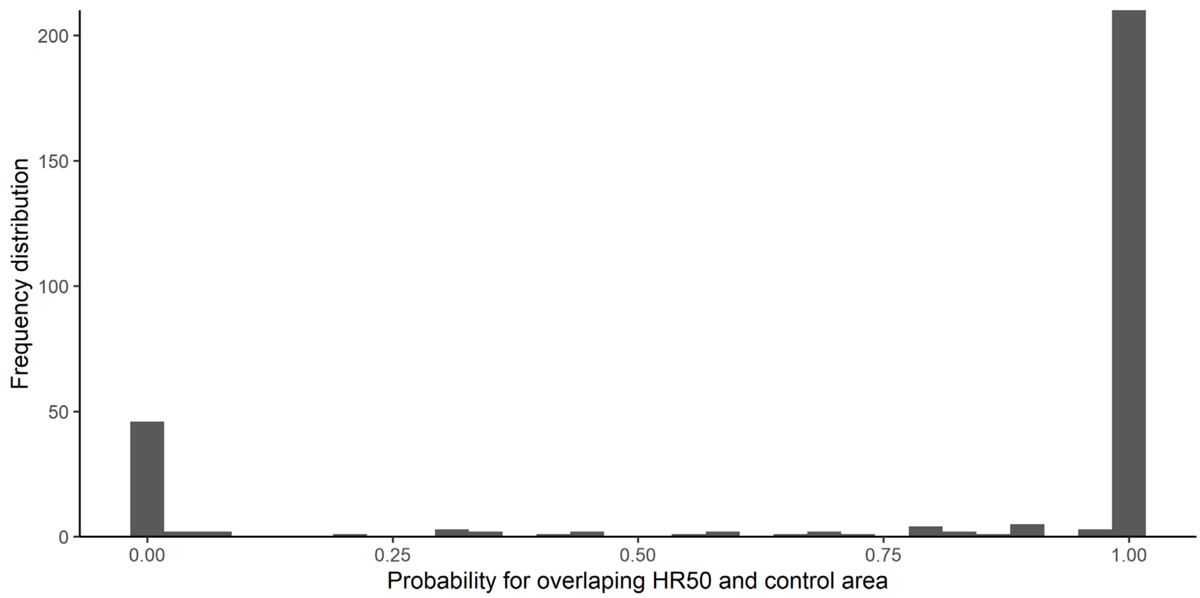

Figure 17 Frequency distribution of ration of the HR50s that were overlapping with the control area over the course of the experiment. 1.00 on the x-axis represents full time use of the control area

Treatment time alone had most AICc-support in the data as a predictor for probability of HR50 to overlap with control area, attaining about 40 % of the AICc weight (Table A 1). The model selection also revealed that an interaction between treatment time and release site, and between treatment time and condition factor, correlated with the probability of using the impact area. These interaction models attained about 20% of the AICc weight for each.

Treatment time had a significant effect on the probability of using control area, ($p<0.0001$, Table 5). Standard error of during the removal of *J. bulbosus* was very high, SE=92288 (Table 5, Figure 18). During removal of *J. bulbosus* there was few detections, and therefore a large uncertainty of the probability of using impact area. Individual random effects indicate which individuals having the largest probability of using impact area (Figure A 4).

Table 5 Parameter estimates for the model with most AICc-support in the data in Table A 1. TT = treatment time

		Parameter estimates				Effect test			
	Term	Estimate	SE	z value	Pr(>|z|)	Effect	Chisq	Df	Pr(>Chisq)
Fixed	Intercept	-0.11	1.15	-0.09	0.93	TT	12.85	2	1.62e-3
	TTBefore	5.05	1.41	3.59	3.37e-4				
	TTDuring	23.72	92288	0.00	1.0				
		Variance	Std.Dev						
Random	Among ID	23	4.80						

The results showed a high probability of using control area before removal of *J. bulbosus* and a lower probability of using control area after the removal (Figure 18). However, larger uncertainties related to the probability of using control area after the removal. The individual random effects related to probability of using control area can be seen in (Figure A 4).

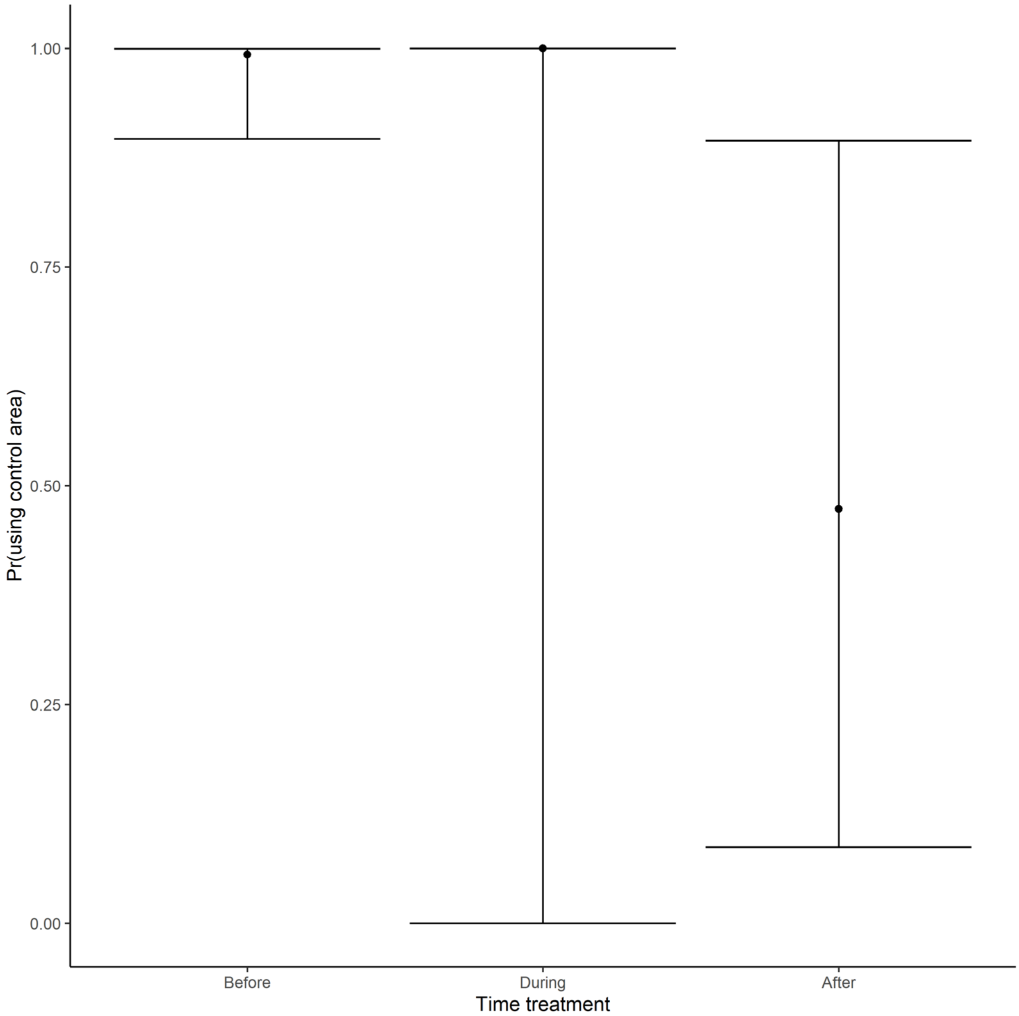

Figure 18 Predicted use of control area before, during, and after removal of J. bulbosus. The dots represent the predicted usage (ranging from 0 to 1, where 1 equals high probability of usage), the vertical lines indicate the uncertainties related to the predicted usage. Predictions were made from model reported in Table 5

3.5 Depth use

Depth use varied between 0.1 and 3.9 (mean 1.3 ± sd. 0.49) meters.

The average depth distributions before the removal overlapped with "During" and "After" (Figure 19). The average depth distributions during and after the removal differed more. The figure indicates a slight tendency of shallower depth use after the removal of *J. bulbosus*.

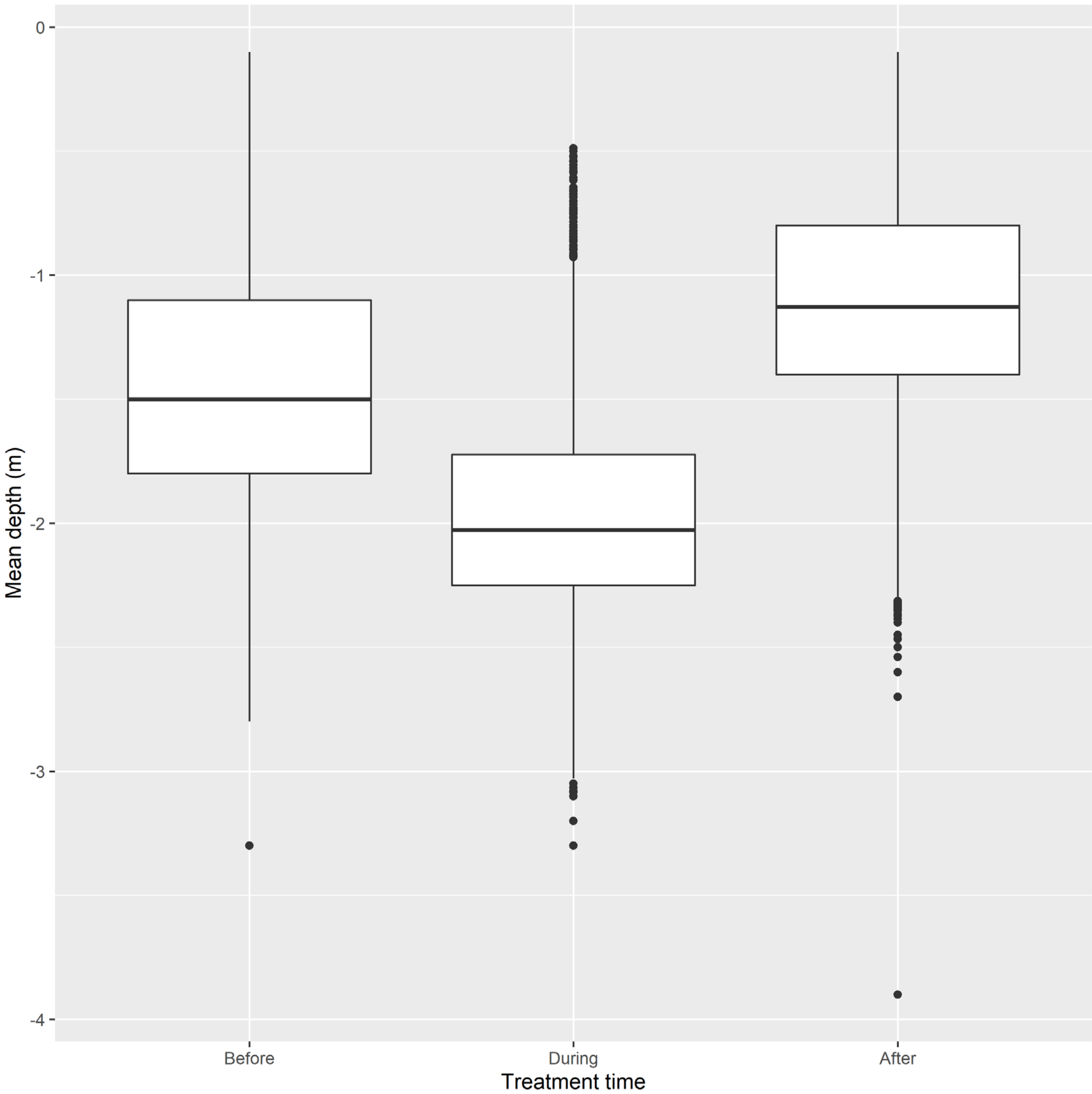

Figure 19 Boxplot of average depth use in meter below the water surface before, during and after removal of J. bulbosus*. The boxes include 50 % of the observations and vertical lines 90 %. The thick horizontal line with boxes represents the median value.*

The depth-use model selection yielded that an interaction model between discharge and time treatment had most support in the data. Hence, this model was most parsimoniously explaining the variations within the data with an AICc weight of 100 % (Table A 1, Table 6). The discharge levels fluctuated during the whole study period, ranging between 49.4 m^3/s and 312.5 m^3/s, with a mean of 115 m^3/s (Figure A 9).

Table 6 Parameter estimates and effect test for the model with the most support in the data in Table A 1. Im = impact area, Co = control area, D= discharge, TT = treatment time

		Parameter estimates			Effect test			
	Term	Estimate	SE	t value	Effect	Chisq	Df	Pr (>Chisq)
Fixed	Intersept	-0.59	3.1e-02	-19.28	TT	7951.99	2	<0.001
	TTBefore	0.45	2.0e-02	23.00	D	11133.18	1	<0.001
	TTduring	0.48	1.7e-02	28.84	TT:D	164.79	2	<0.001
	D	4.2e-03	4.3e-05	96.31				
	TTBefore: D	-4.1e-04	1.6e-04	-2.52				
	TTduring: D	-1.2e-03	9.1e-05	-12.21				
		Variance	Std.Dev.					
Random	Among ID	0.05	0.22					
	Residual	0.11	0.36					

The interaction effect between discharge and treatment time, was highly significant (Table 6). In the interaction, the additive effects of the involved effects were of little interest by themselves. Their unique effect was not of importance, however, when estimating the effects, one cannot predict the effect (e.g., before) without considering the discharge. Individual random effects were also fitted, showing detected individuals with increasing depth usage (Figure A 5).

The predicted average depth use decreased with higher discharge levels (Figure 20). The interaction with discharge and treatment time indicates deepest average positioning before the removal of *J. bulbosus,* compared to both during and after the removal. Figure 20 also shows an overlap between the confidence intervals between “Before” and “During”.

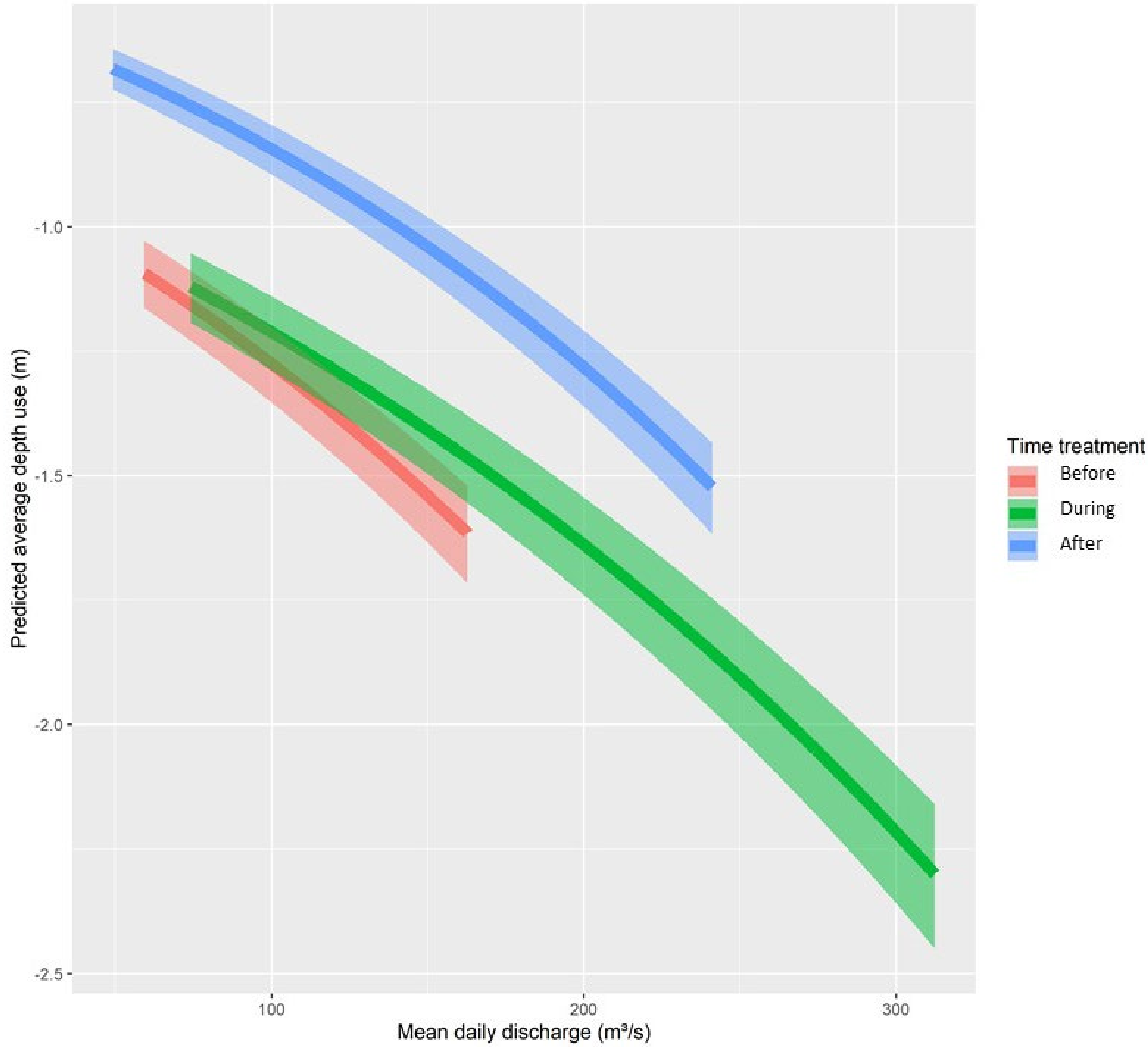

Figure 20 Predicted average bi-daily depth use changes with an increased mean daily discharge before, during, and after removal of J. bulbosus*. The thick lines are the predicted average depth, the coloured area is the confidence interval. Predictions were made from model reported in Table 6 and are limited to discharge levels that were registered during corresponding treatment periods (to avoid extrapolations).*

4. Discussion

The aim of this study was to evaluate effects of removal of *J. bulbosus* on habitat use of trout in the oligotrophic river Otra, Norway. Overall, my results indicate that the removal did not have strong effects on the habitat use.

4.1 Effects of removal of *J.bulbosus* on home range size

I hypothesised that the home range size of trout would increase after removal of *J. bulbosus*. In contrast, the results showed that macrophyte removal did not have an overall effect on the home range size of trout in the Rysstad basin. However, an interaction between release site and treatment time indicated an effect from removal on the different release site groups. As effects of macrophyte removal on home range size in oligotrophic environments have not been extensively studied before (Thiemer et al., 2021), it is difficult to conclude with a reason why there was no overall effect from removing *J. bulbosus* on the home range size of trout. Most likely, several factors were influencing the outcome of the analysis, which has previously been studied and is known to influence fish distribution and movement in rivers. Previous research found that trout tend to establish the home range size during their first years and it is not much change after the establishment (Bachman, 1984). This could be related to my results with no overall effect on the home range size after removal.

The predicted increase in the home range size after the removal for trout released in the impact area and the control area could be explained by changed food availability. Nicola et al. (2016) found that if an area has high productivity, and there is sufficient food supply, the home range size would be small. Additionally, Romaniszyn et al. (2007) found a higher amount of terrestrial invertebrates and drifting aquatic larvae in spring and early summer. Applied to my results, both these studies indicate sufficient food supply for the trout in the impact area before the removal, hence a smaller predicted home range size before the removal than after. When macrophytes are being removed it also removes macroinvertebrates feeding/attached to the macrophytes. A recent study conducted in the same study area found fewer EPT taxa (Ephemeroptera=mayflies, Placoptera=stoneflies, Tricoptera=caddisflies) in the impact area after *J. bulbosus* were removed (Aasland, 2021). This could indicate that macroinvertebrates were removed with the macrophytes, and/or trout foraged on the macroinvertebrates as the macroinvertebrates also lose their shelter opportunities. Many macroinvertebrates are an important food source for fish. If the macroinvertebrates were removed with *J. bulbosus* the trout were most likely to feed on other not so preferable macroinvertebrates or move larger distances to find a sufficient food supply. Consequently, a predicted increase in home range size after removal for trout released in the impact area and the control area in the search for new habitats with enough food resources.

The smaller predicted home range size before the removal of *J. bulbosus* than after the removal could also be explained by external environmental factors, like water temperature and the seasonal variation during the study period. The “before”-period was from March to June, a period it is expected that the trout are likely to be little active due to low water temperatures decreasing the activity and the swimming performance (Rimmer et al., 1985). The decreased activity patterns during spring with low water temperatures is a behavioural response in order to minimize energy expenditure (Heggenes et al., 1993). The water temperature in the Rysstad basin was below 8 °C from the beginning of the study period until about mid-June (unpublished data). In accordance to Rimmer et al. (1985) that suggested at water temperatures below 8 °C, Atlantic salmon would have a markedly change in activity, which is most likely the case for trout as well since they are in the same family. Hence, a smaller predicted home range size before the removal of *J. bulbosus* than after the removal. However, one could argue for that if water temperature and seasonal variation influenced the home range size, the control and the impact area should have reacted the same way. As my results on home range size does not differ between usage of the impact area and the control area, there were only effects from the macrophyte removal depending on where the trout was released after the tagging.

During the removal of *J. bulbosus,* trout released in the impact area had their largest home range size, which indicates much movement during the period *J. bulbosus* were undertaken. This is consistent with Swales (1982) who suggested that macrophyte removal could cause stress for the fish and therefore the fish would move from the area where the removal is being undertaken. However, there were few detections registered during the removal of *J. bulbosus,* since five of the receivers were taken out of the river and the removal period lasted only for about a week. Results from during the macrophyte removal should therefore be interpreted with caution.

As there were no overall effect of the removal of *J. bulbosus* on the home range size of the trout, there were most likely other factors that were not statistically tested influencing the home range size. Previous studies have shown, both for vertebrates and fish, that interspecies competition, resource abundance and other biotic factors generally have an impact on the home range size (Hansen and Closs, 2005, van Beest et al., 2011, Nash et al., 2015). Home range size is shown to be related to the dominance of trout, whereas dominant trout tend to have a larger home range and additionally move longer e.g., for spawning (Höjesjö et al., 2007). It is also dependent on the site fidelity, whereas the home range size decrease with increasing site fidelity, particularly in areas with high densities of trout (Slavík and Horký, 2019). This is in accordance to studies done on other vertebrates where it is shown that home range size would decrease with increased population density (McNab, 1963). Body mass can also be positively related to the home range size. However, individual variations exist, and large trout may have small home ranges (Slavík and Horký, 2019). From the above-mentioned studies investigating potential effects influencing the home range size, only the length of trout was used in my analysis in relation to the treatment time. Still, the tested length model did not have the most support in the data. Such behavioural responses in the aquatic environment could compensate for potential effects from the removal.

The observed effect from the removal on where the trout were released could also be explained by individual variation within the study population (Figure A 1, Figure A 2) and size of the different release site groups. From the different release site groups, the estimated PAVs were from 14 from "Other", 10 from impact area and 10 from control area. Additionally, when doing the analysis, some individuals had considerably more detections than others. This unbalance may influence the result of the analysis, as some individuals could have considerably more detections. The estimated home range size (HR50) for trout release site in impact and control area was about ± 0.25 ha before and had an estimated increase to 0.59 ha and 0.34 ha, respectively. Surprisingly, trout released downstream for the study area had a slight decrease after removal from being 0.37 ha before and 0.34 ha after. The trout released downstream from the study area had already migrated quite some distance, and therefore one might think the home range size would also be large.

Overall, the impact of macrophyte removal on home range sizes of trout could be explained by trout being habitat generalists. Trout could therefore be capable of adapting to changes in the available habitat as well as occupy new environments (Ayllón et al., 2010). Even though we are creating new habitat with less macrophytes after the removal, it has little effect for the home range size of the trout as it could adapt quickly to the new habitat.

4.2 Effects of removal of *J.bulbosus* on the usage of impact and control area

I hypothesized that the trout would use the impact area less after the removal of *J. bulbosus* compared to before. In agreement to my hypothesis, the results indicated that there were small changes in probability for using after the removal. Surprisingly, the chances for using the impact area before the removal were also small. However, there was a greater uncertainty related to the usage of the impact area after the removal of *J. bulbosus*. The increased uncertainty indicates that there was a higher chance for the trout to use the impact area after the removal, even though the probability for usage was still small. The uncertainties can be related to the individual random variation for using the impact area (Figure A 3), of which indicates few individuals using the impact area. Overall, this means that the impact area was not much used during the whole study period, but the chance for the trout to use it increased after the removal of *J. bulbosus.* In addition, the results indicated that the trout used either the impact area (even though the probability was small) or the control area, and the midchannel areas were to some extent avoided. This was not surprising, as trout tend to choose positions in rivers near streambanks as it usually provides cover (Shuler et al., 1994). Individuals with the highest probability of using impact area seem to have the least probability of using the control area. It might also indicate that the study population of trout were quite sedentary and did not move between the impact and the control area (Figure A 3, Figure A 4).

The small probability for trout to use the impact area before the macrophyte removal could also be related to the river morphology. Before the removal of *J. bulbosus* the impact area consisted mainly of dense macrophyte stands. The small probability for trout to use the impact area before the removal was surprising as it is shown that macrophytes of high complexity would provide shelter and habitats with a higher abundance of fish (Warfe and Barmuta, 2004, McAbendroth et al., 2005, Thomaz and Cunha, 2010). Velle et al. (2021) also indicated that *J. bulbosus* does not limit fish and invertebrates as there were higher densities of both juvenile fish and invertebrates in areas with *J. bulbous* compared with areas consisting of gravel. Lusardi et al. (2018) also found a higher density of invertebrates in areas with macrophytes compared to gravel-beds, which would provide foraging possibilities for fish. This is also supported by other studies showing that patches with macrophytes are preferred habitat by trout (O'Connor and Rahel, 2009, Ayllón et al., 2010). Based on this, I expected the impact area to be used more before the removal of *J. bulbosus* than it turned out to be. However, Lopes et al. (2015) found that several fish species tend to avoid areas densely occupied by macrophytes as it could create harsh environment. Although Lopes' study was conducted in a floodplain lake it could be related to my results since it shows a fairly small change to use the impact area before the removal. The dense biomass of *J. bulbosus* in the impact area could prevent the horizontal distribution of the trout using the impact area and by making it difficult for the trout to move within the densest macrophyte stands. Moreover, the small chances for trout to use the impact area could be related to human activities and disturbances. On the impact side the riverbank is influenced by human disturbances such as a residential area, a camping site, and farmland. These factors could scare the trout away from the impact area and rather choose to use other parts of the river with less disturbances. Also, the riverbank at the impact area had larger areas with sparse side vegetation. The riverbank at the control area on the other hand, were less impacted by human disturbances and had more side vegetation. These factors could indicate that the control area was a more suitable site for the trout compared with the impact area as the trout had a high probability to use the control area before the removal. However, the probability of using the control area decreased after removal. This decrease can be related to the observed increase in the home range size after the removal. As the home range size increased after the removal, the trout used a larger area which was not included in the defined control area and therefore not included in the probability estimations.

The increased uncertainty for the trout to use the impact area after removing *J. bulbosus* could be related to water velocities and food availability. The combination of these factors is shown to be of great importance for the positioning for riverine salmonids (Fausch, 1984). Within the study area, the water velocities varied with slightly higher velocities in the impact area compared to the control area. After the removal of *J. bulbosus* the water velocities in the impact area increased (Aasland, 2021), not surprisingly as it is shown that generally macrophytes slows down water velocities (Madsen et al., 2001). However, in this case the increased water velocities could also be related to a higher discharge in the period after the removal (Figure A 8). Since trout tend to prefer higher water velocities as they grow (Heggenes, 1996), the increased water velocities from removing *J. bulbosus* might indicate that the removal established a new habitat with more preferable water velocities for the larger and older trout. Beckett et al. (1992) found that macrophyte removal increased the change for macroinvertebrates to be predated by fish, as the macroinvertebrates' shelter and refuge disappear with the removed macrophytes. Hence, the impact area in my study had a higher chance for being used by the trout after removal due to possible higher food availability. In contrast, Garner et al. (1996) found that the increased water velocities from macrophyte removal might cause a decrease in food availability (washout). Which could also be the case in the impact area in this study since Aasland (2021) found fewer EPT taxa macroinvertebrates in the impact area after the removal. On the other hand, fewer EPT taxa could also indicate that they were foraged by the trout, which supports my results indicating a higher chance to use the impact area after the removal. This indicate that the removal of *J. bulbosus* provided a higher food availability, and therefore the impact area after could be a more attractive area for the trout to use.

My results indicate that there is probably not one factor alone influencing the probability for trout using the impact area and the control area. Several factors like river substrate, macrophyte densities and patches, riverbed conditions, water velocities and food availability, do all have certain impacts when investigating the habitat use of trout in the Rysstad basin. However, it is important to be aware that some individuals have considerably more detections than other individuals and may therefore influence the result of the analyses.

4.3 Effects of removal of *J.bulbosus* on the depth use

I hypothesised that the trout would inhabit deeper parts of the water column after the removal of *J. bulbosus.* Contrary to what I hypothesised, were there a tendency for the trout to be positioned in shallower parts of the water column on an average after the removal.

The depth use was, not surprisingly, influenced by the discharge levels at the study site. This explained by that the predicted depth use was estimated according to the water surface (water surface equals 0). Therefore, higher discharge levels would increase the water levels, and by this the trout had the possibility to be positioned deeper. From the beginning of the study period (11^{th} of March) the discharge were ranging between a minimum of 59.3 m^3/s to a maximum of 162.8 m^3/s (Figure A 7,Figure A 9). After the removal of *J. bulbosus* (from 23^{rd} of June until 8^{th} of September), the discharge had a larger range (min. 49.8 m^3/s, max. 241.2 m^3/s) than before the removal. This corresponds to the results indicating shallower positioning after the removal compared to before. However, the largest range in discharge was in the “during”-period with a min. of 74.1 m^3/s and max. of 312.5 m^3/s. Even so, in this period the trout was positioning shallower that before the removal. Overall, trout positioned deeper with increasing discharge.

Even though my data overall were explained by the discharge levels, there is still other abiotic factors that could possible influence the depth use at the study site. Deep positioning in the water column could be explained by the events of gas supersaturation. During the study period there were several events of gas supersaturation at the study site, and generally the vales were above 100 % saturation (Figure A 6). The highest reported value of gas saturation was at 130 %, registered on the 15^{th} of June which was the start of the macrophyte removal. As the gas saturation decreases with about 10 % each meter down in the water column (Henry, 1803), the fish often compensate for the harmful gas saturation by moving deeper in the water column (Beeman and Maule, 2006). During these events, the trout were likely to be positioned deeper in the water column. Even so, trout were observed leaping at insects despite the gas supersaturation. Another factor that could likely influence the depth positioning of the trout in the river was the seasonal variation. Chapman and Bjornn (1969) found that during winter trout tend to hide in gravel substrate and therefore stay closer to river substrate. This in consistency of my results as the trout tend to use deeper parts of the water column before the removal of *J. bulbosus,* as the "before" period was early in the year with low temperatures. Additionally, with increasing water temperatures trout becomes more active (Rimmer et al., 1985), and change diet to feed more on drifting organisms from terrestrial areas/terrestrial matter rather than benthic organisms (Romaniszyn et al., 2007). This also cause a shallower average positioning in rivers. However, in contrast, Heggenes et al. (1993) trout to be active over the substrate during winter. Anyhow, my depth-use results are most likely explained by the discharge levels and the fact that the trout mostly stays close to the riverbed.

4.4 Evaluation of data reliability

When analysing and interpreting the data, several external factors were likely to influence the outcome of the results.

The trout were caught in the period March – May 2020 when the water temperature in Otra was still relatively cold (below 8 °C). Trout generally have a low activity in spring when the water temperature is cold, and therefore it was difficult to catch them. The trout caught and tagged in March would possibly have more detections than the trout caught and tagged in May, however, only five individuals were tagged in May. The sampling gear used, influenced variation of the individuals within the total sample and the total sample may therefore not be representative for the whole stock of trout. Beach seine generally has a low selectivity; however, large and active individuals avoid the streambanks and could easily swim away. The various fish traps that were used, were more selective as the fish must move to get caught, therefore the more active individuals are more likely to get caught, in addition to the fact that larger individuals often use larger areas. However, sufficient number of trout were caught for doing the analyses.

There were risks that some of the trout died during the study period. All the tagged fish in this study were 220 mm or longer. At these lengths there is a low risk for fish predation, however, higher risk for e.g., bird predation or being caught by humans. Grey heron, *Ardea cinerea*, individuals were observed in the area, and angling is a common recreational activity in Otra. Death could also be caused by the gas supersaturation events during the study period (Figure A 6). It is shown that gas saturation values over 110-120 % can be acute mortal for fish

(Heggberget, 1984). Several dead trout were observed both trapped in *J. bulbosus* patches, in the water column, and at the riverbanks (especially in June).

There was spatial variation in sync-tag detections indicating that the detection range was most likely to vary within the receiver network at the study site (Figure A 6). The conditions in the Rysstad basin made it difficult to work with acoustic telemetry, as several environmental factors were degrading the quality and transmission efficiency of acoustic signals. It is also likely that gas saturation had a certain effect on the detection range as it is shown that air bubbles often absorb and scatter the signals (Gjelland and Hedger, 2013). *J. bulbosus* could also affect the transmission of the signals (Gjelland and Hedger, 2013). An ongoing research project is currently investigating the details about how different densities of macrophytes influence transmission signals and detection range, indicating that the dense macrophyte biomass significantly reduced the detection probability of transmitters (i.e., trout) positioned closed to the water surface and close to the sediment. Therefore, trout positions may have been biased in this study (Thiemer et al. *in prep*). However, an increased discharge and increased water levels above the macrophyte stands could possibly favour transmission of sound from the tags as the signals have more free water masses to travel in. Although there was variation in the detection probability, there were enough detections from the trout to estimate reliable PAVs.

As this study was conducted as a real-world experiment it was difficult to tell whether it was the macrophyte removal itself causing the observed changes in habitat use, or if it was other abiotic and biotic variables present at the study site and during the study period. Results of this study indicates that the removal of *J. bulbosus* has a certain impact on the spatial habitat use of trout, but there were several environmental factors with equal importance affecting the habitat use during the study period. Also, the levels of *J. bulbosus* biomass removed in the impact area was small compared to the total of the total biomass in the Rysstad basin (approximately 2 %).

Although there are several biotic and abiotic factors influencing the reliability of the data used in this thesis, it is still valuable information about how trout can be affected my macrophyte removal in an oligotrophic river system. Also, it indicates the difficulties about conducting an acoustic telemetry in such environment. However, for future work I would suggest making improvements in the study design in order to get a more robust telemetry study. For instance, one could consider to use radio transmitters rather than acoustic transmitters, as radio transmitters is shown to be more suitable for conducting telemetry studies in freshwater ecosystems < 8 m water depth (Brownscombe et al., 2019). Additionally, I would recommend using stronger sync-tags and having sync-tags attached to every receiver. These improvements would ensure a good synchronisation of the receivers. Such improvements would likely ensure more robust data and give more detections and positions. With this, one could use YAPS for the analyses (Baktoft et al., 2017), which would provide more detailed and exact information about fish movement and habitat use in the river.

5. Conclusion

My finding suggests that partly removal of macrophytes does not affect trout to a large degree. The changes in home range size after the removal of *J. bulbosus* appear to be related to individual variation. This because home range size had most effect depending on where the trout were released after the tagging. The trout released in the control and the impact area had an increase in the home range size after. Further, only a few individuals used the impact area during the study period, and they had an increased chance to use the impact area after the removal. Additionally, the results showed that the trout poisoned in shallower parts of the water column after removal of *J. bulbosus* depending on the discharge levels.

The conditions in the Rysstad basin with both dense macrophyte stands and gas supersaturation made it difficult to conduct a robust acoustic telemetry study, as both of those factors influenced the detection range and probability. For future work, I would recommend conducting a more robust telemetry study in a similar environment by using sync tags at all receivers with a higher output power. In addition, one could use a combo with radiotelemetry might also provide more data as radio waves travel easier through vegetation. These improvements would provide more detailed information about the habitat use of trout.

This thesis contributes to filling the knowledge gap about potential impacts caused by macrophyte removal on the habitat use of riverine salmonids in oligotrophic freshwater systems. Despite my results indicate little impact on the habitat use of trout, removal of macrophytes most likely cause stress and disturbances during the removal as well as afterwards. This due to a complete change of the ecosystem and available habitat in the area where the macrophyte removal is undertaken. Although, other studies show that macrophyte removal indeed can have negative effects, I would conclude that that the management strategy which is used in the Rysstad basin may be a nice balance: some removal to prevent fishing lines to get entangled, but the trout still thrives as it can move to preferred areas.

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Appendix

Candidate models

Table A 1 Model selection for estimating home range (50% and 95%), probability of using impact area, probability of using control area, and estimated average depth use, of the tagged trout in the study area, according to Akaike's Information Criterion (AICc). Every model has ID as random effect (1|ID)

Model structure[a]	K[b]	AICc	ΔAICc[c]	AICcwt[d]	Cum.wt	LL[e]
Home range, 50%						
Release.site*time.treatment	10	351.19	0.00	1	1	-165.20
time.treatment*k_factor	8	363.04	11.85	0	1	-173.26
time.treatment*Length	8	365.07	13.88	0	1	-174.28
time.treatment+k_factor	6	367.56	16.37	0	1	-177.63
time.treatment+Length	6	367.87	16.68	0	1	-177.79
time.treatment	5	368.30	17.11	0	1	-179.04
Release.site+time.treatment	7	372.19	21.00	0	1	-178.90
1	3	383.04	31.85	0	1	-188.48
Home range, 95%						
Release.site*time.treatment	10	265.65	0.00	1	1	-122.38
time.treatment*Length	8	286.60	20.96	0	1	-135.01
time.treatment*k_factor	8	292.52	26.87	0	1	-137.97
time.treatment+Length	6	294.82	29.17	0	1	-141.24
time.treatment	5	294.95	29.31	0	1	-142.36
time.treatment+k_factor	6	295.10	29.45	0	1	-141.38
Release.site+time.treatment	7	297.83	32.19	0	1	-141.69
1	3	303.37	37.72	0	1	-148.64
Probability of using impact area						
time.treatment	4	121.13	0.00	0.51	0.51	-56.49
time.treatment+Length	5	123.08	1.95	0.19	0.70	-56.43
time.treatment+k_factor	5	123.20	2.07	0.18	0.88	-56.49
Release_site+time.treatment	6	125.03	3.90	0.07	0.95	-56.37
time.treatment*k_factor	7	127.09	5.96	0.03	0.98	-56.34
Release_site*time.treatment	9	128.08	6.95	0.02	1.00	-54.71
Release_site*time.treatment+Length	10	131.01	9.88	0.00	1.00	-55.11
1	2	141.32	20.19	0.00	1.00	-68.64
Probability of using control area						
time.treatment	4	186.68	0.00	0.39	0.39	-89.27
Release.site+time.treatment	6	187.92	1.24	0.21	0.60	-87.81
time.treatment+k_factor	5	188.20	1.52	0.18	0.79	-88.99
time.treatment+Length	5	188.74	2.06	0.14	0.93	-89.27

Release.site*time.treatment	9	191.40	4.72	0.04	0.96	-86.38
time.treatment*k_factor	7	192.39	5.71	0.02	0.99	-88.99
Release.site*time.treatment+Length	10	193.53	6.85	0.01	1.00	-86.37
1	2	223.43	36.75	0.00	1.00	-109.69
Depth use						
time.treatment*avg.dis	8	31255.20	0.00	1	1	-15619.60
time.treatment*avg.water.level	8	31357.44	102.23	0	1	-15670.72
time.treatment+avg.dis	6	31415.69	160.49	0	1	-15701.84
time.treatment+avg.water.level	6	31612.97	357.77	0	1	-15800.48
avg.dis	4	38739.19	7483.99	0	1	-19365.59
avg.water.level	4	39021.23	7766.03	0	1	-19506.62
Release.site*time.treatment	11	40984.39	9729.19	0	1	-20481.19
time.treatment*k_factor	8	41006.98	9751.78	0	1	-20495.49
time.treatment*Length	8	41072.76	9817.55	0	1	-20528.38
time.treatment	5	41382.46	10127.25	0	1	-20686.23
Release.site+time.treatment	7	41383.64	10128.44	0	1	-20684.82
time.treatment+Length	6	41384.38	10129.18	0	1	-20686.19
time.treatment+k_factor	6	41384.43	10129.23	0	1	-20686.21
1	3	52380.84	21125.64	0	1	-26187.42

[a] Relative contributors which the model estimates. Release.site = where the fish were released after tagging (Impact area, control area, downstream from study area), time.treatment = when *J.bulbosus* was removed (Before, during, after), k_factor = condition factor (weight/length ^3 * 1000000), Length = total length of trout individuals, dis = discharge

[b] Number of estimated parameters

[c] The difference between one models AICc and the model with the lowest AICc

[d] AICcwt = Relative AICc-support to the models (AICc weighted)

[e] Log Likelihood

Individual random effects

Home range, 50%

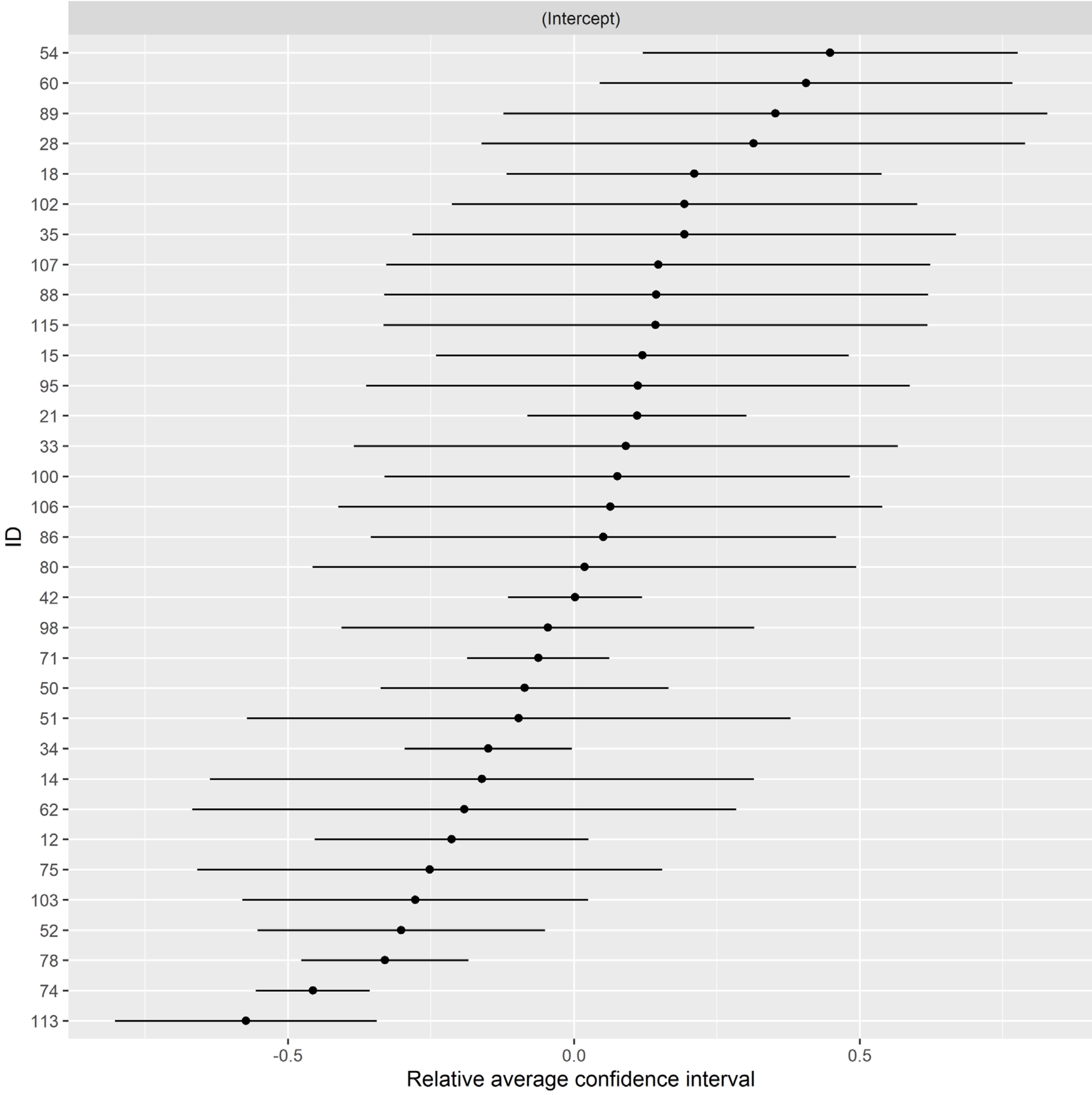

Figure A 1 Individual random effects for HR50 (home range size, where trout uses 50% of its time). Individuals with largest HR50 at the top. Vertical lines represent individual confidence interval

Home range, 95%

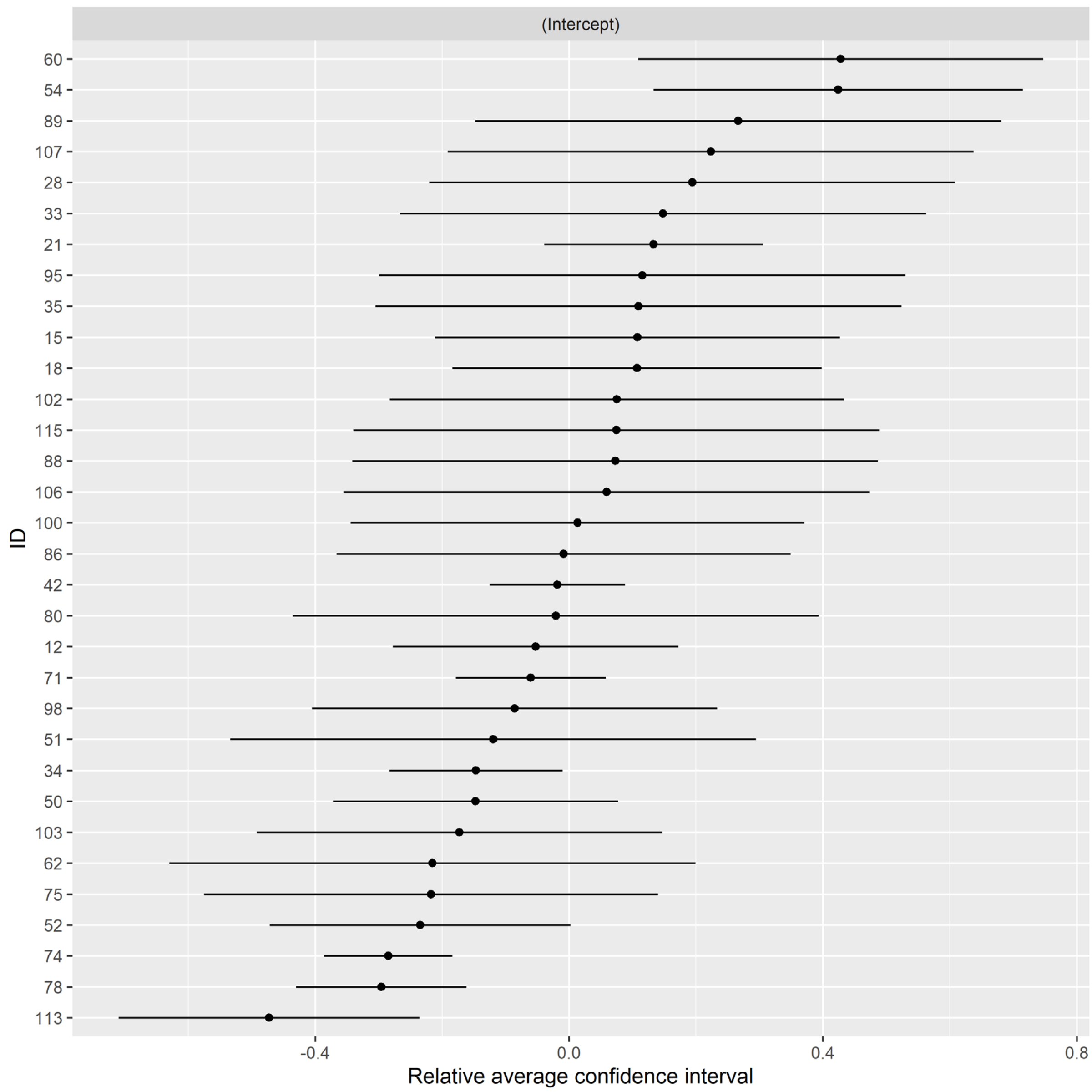

Figure A 2 Individual random effects for HR95 (home range size, where trout uses 95% of its time). Individuals with largest HR96 at the top. Vertical lines represent individual confidence interval

Probability of using impact area

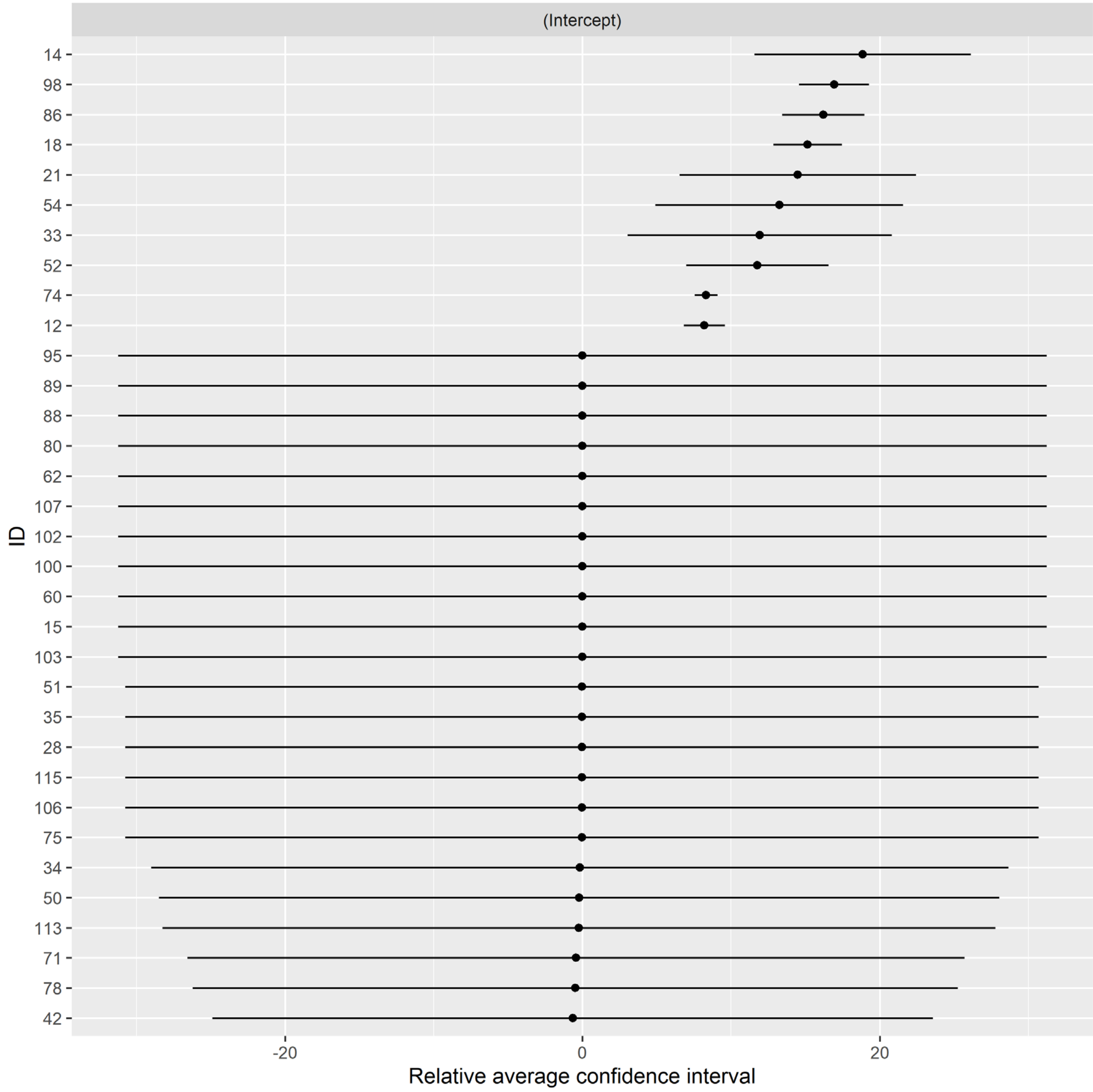

Figure A 3 Individual random effects for the probability of using impact area. Individuals with highest chance to use impact area on the top. Vertical lines represent individual confidence interval

Probability of using control area

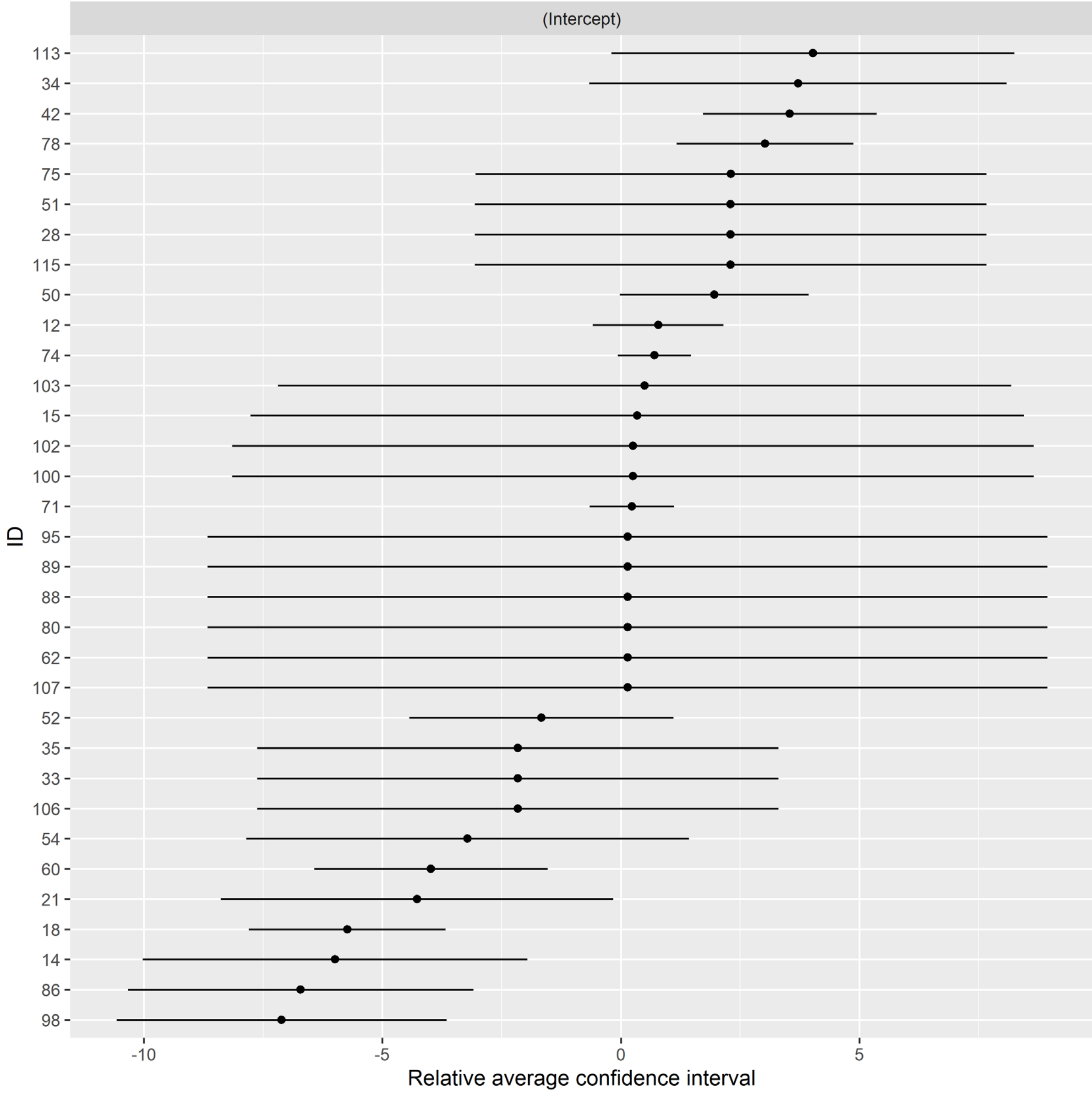

Figure A 4 Individual random effects for the probability of using control area. Individuals with the highest change to use the control area on the top. Vertical lines represent individual confidence interval

Depth use

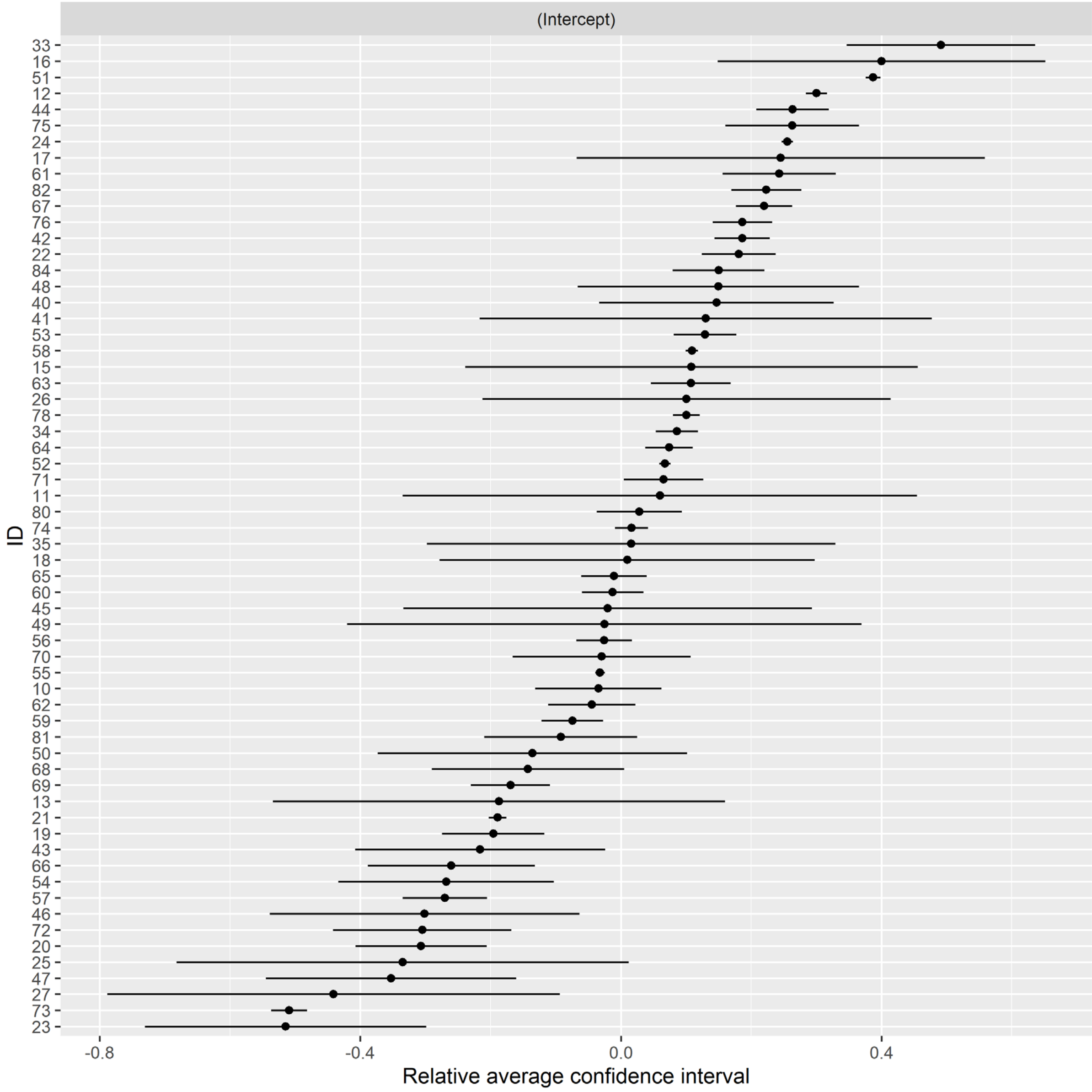

Figure A 5 Individual random effects for depth use. Individuals with the deepest positioning on the top. Vertical lines represent individual confidence interval

Sync-tag detection

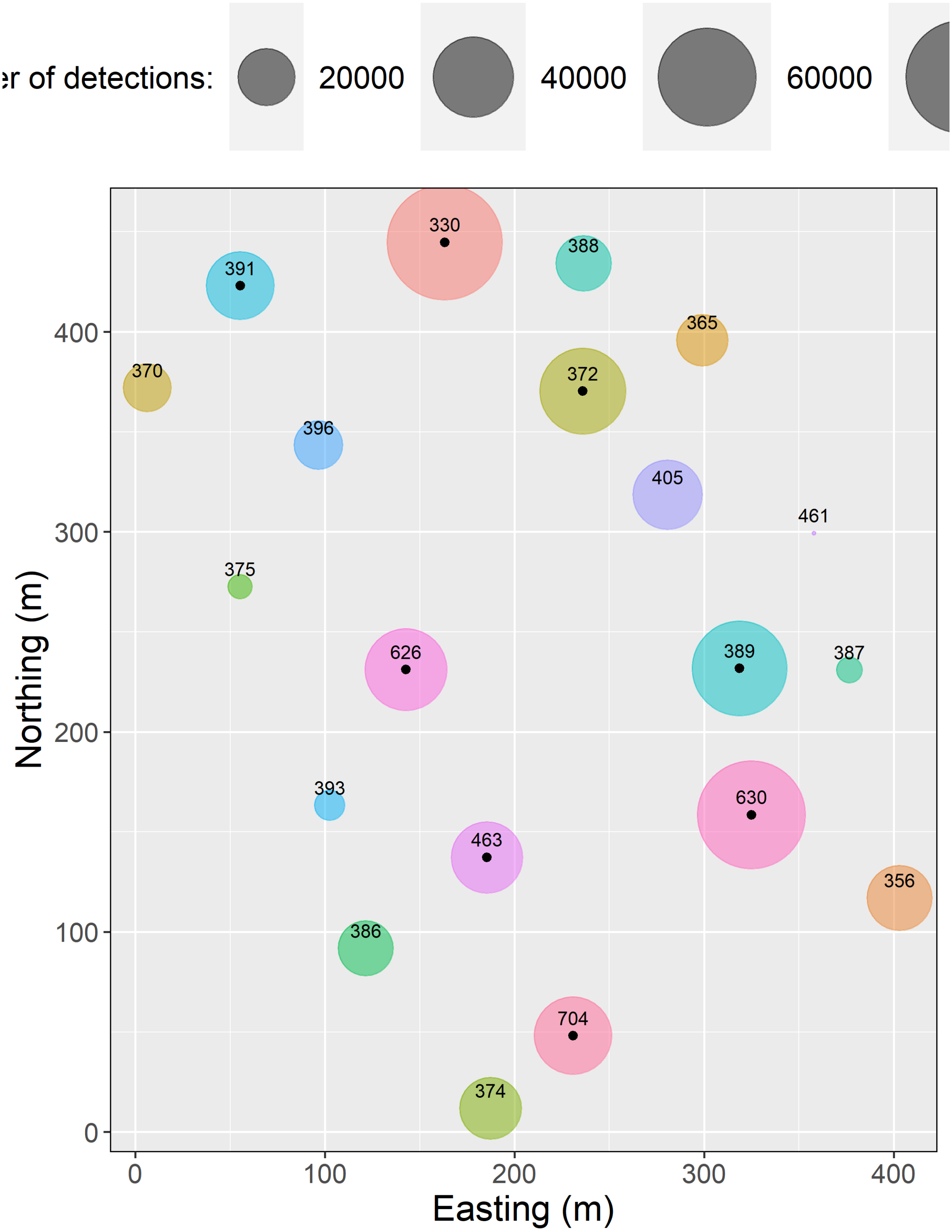

Figure A 6 Bubble-plot showing showing sync-tag pings received by each receiver in the receiver network within the study area. Numbers representing the different receivers, size of bubble indicate how many sync-tag pings each receiver has detected. Northing and easting is the coordinates transformed into meters.

Relative water level

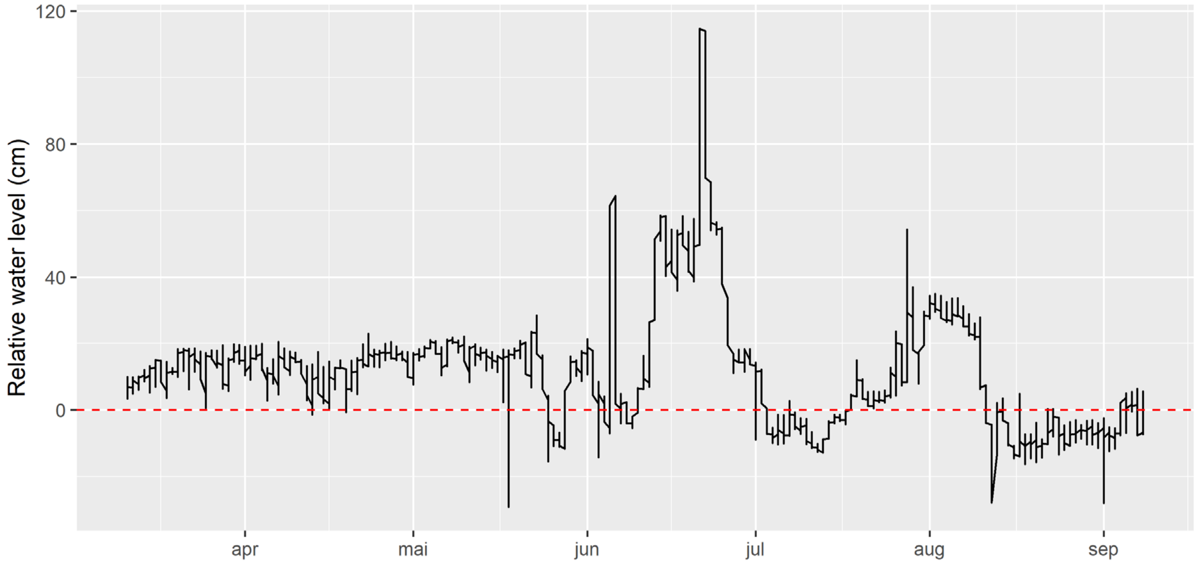

Figure A 7 Relative water level during the study period. The relative water levels were calibrated for a discharge of 85 m^3/s, implying the red dashed line at y = 0 represent a discharge of 85 m^3/s.

Gas saturation

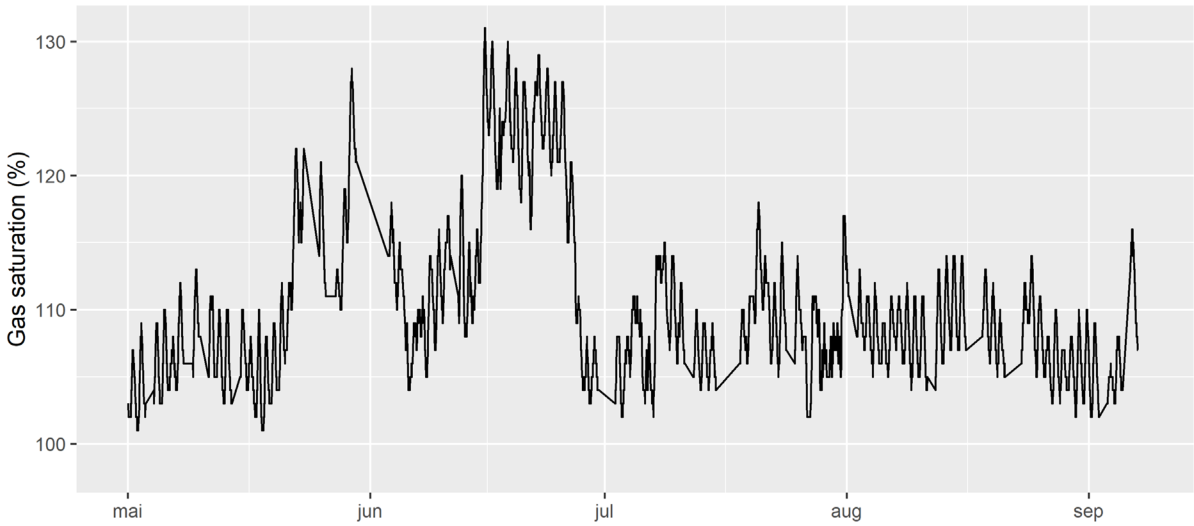

Figure A 8 Gas saturation (%) in study area in the period 1st of May until end of study period at 8th of September

Discharge

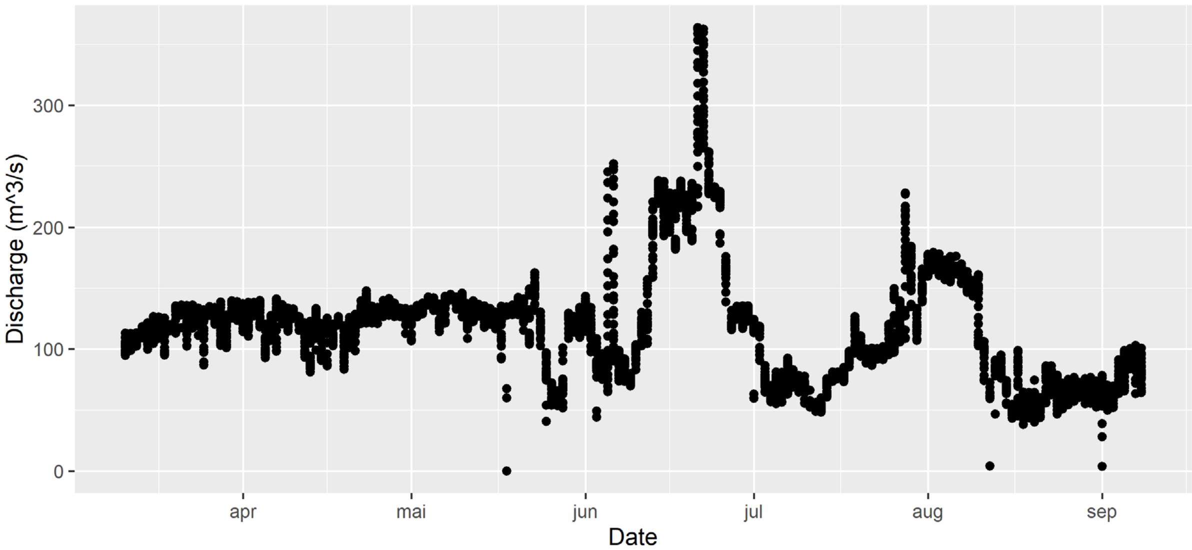

Figure A 9 Discharge (m^3/s) in study area during the whole study period

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