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Should you catch them if you can? – Catch-and-release implications, migration and behaviour changes on *Salmo salar* in the Baltic Sea

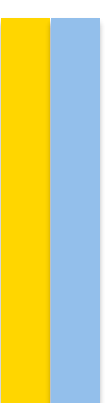
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**Should you catch them if you can? –
Catch-and-release implications, migration and behaviour
changes on *Salmo salar* in the Baltic Sea**

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A autora,

Barbara Ribeiro

Abstract

In a world where growing pressures on wildlife are pushing ecosystems to collapse, entire food webs are being fished down, even resilient apex predator species are at risk. Our study aimed to understand how Atlantic salmon was being affected by catch-and-release (C&R) especially after stricter fishing restrictions in the Baltic Sea were implemented to conserve vulnerable populations. To explore this, we tagged fourteen *Salmo salar* with Pop-up Satellite Archival (PSATs) tags and one individual with a Conductivity and Temperature Device (CTD) to follow the surviving fish's migrations and examine the different environments they experienced.

These devices provided crucial data on depth, temperature, light, and salinity allowing us to monitor survival rates and influences of abiotic factors on behaviour, more precisely vertical movement.

One salmon died immediately post-release, likely due to its small dimensions and prolonged fight time which resulted in a lethargic state and poor visual health when it was brought to the boat. This finding aligns with previous research indicating that C&R has certain effects on the species but the mortality rates are low (7%).

Our analysis revealed an influence of temperature on depth across all individuals: higher average temperatures were linked to shallower average depths. Most studied salmon favoured shallower above 15m waters, although irregular deeper dives (up to 60m) were observed.

The preferred temperature range was between 5°C and 9°C, though the fish swam in waters ranging from 1°C to 12°C.

In general, activity was similar between night and day periods, with some individuals exhibiting diel vertical migration (DVM), as would be expected for the species in the springtime.

The double-tagged fish, with the mini-PAT and CTD sensor, displayed an interesting pattern as a noticeable behaviour shift coincided with significantly different temperature and salinity measurements. Additionally, the increase in measured temperature while moving north contradicted typical Baltic Sea temperature gradients. We propose that the individual might have entered a river or stayed close to a freshwater influx in the time frame corresponding to the change, which was backed up by the pop-up location close to a river mouth and modelled data, offering a plausible explanation for this anomaly.

Key-words: Atlantic salmon; Fishing; Catch-and-release; Mortality; Migration; Behaviour; Biotelemetry; Abiotic conditions; Temperature; Salinity; Light; Depth

Resumo

Em um mundo onde as pressões crescentes sobre a vida selvagem estão a levar os ecossistemas ao colapso, teias alimentares inteiras estão a ser sobre exploradas e até espécies resilientes de predadores de topo estão em risco. O nosso estudo teve como objetivo compreender como o salmão do Atlântico está a ser afetado pela prática de catch-and-release, especialmente após a implementação medidas de regulamentação mais rigorosas à pesca no Mar Báltico para conservar populações vulneráveis. Para explorar esta questão, marcámos catorze exemplares de *Salmo salar* com tags Pop-up Satellite Archival (PSATs) e um indivíduo com um dispositivo de condutividade e temperatura (CTD) para analisar padrões migratórios e as condições ambientais a que estiveram expostos.

Estes dispositivos forneceram dados cruciais sobre profundidade, temperatura, luz e salinidade, permitindo-nos monitorizar as taxas de sobrevivência e a influência dos fatores abióticos no comportamento, mais precisamente nos movimentos verticais.

Um dos salmões morreu imediatamente após a reentrada no mar, provavelmente devido às suas pequenas dimensões e ao tempo prolongado de luta, o que resultou num estado de letargia e condição visualmente debilitada quando foi trazido para o barco. Estas observações estão em conformidade com pesquisas anteriores, que indicam que o catch-and-release tem alguns efeitos na espécie, mas que as taxas de mortalidade são baixas (7%).

A nossa análise revelou uma influência da temperatura na profundidade em todos os indivíduos: temperaturas médias mais altas estavam associadas a profundidades médias mais baixas. A maioria dos salmões estudados preferiu águas rasas acima dos 15 metros, embora tenham sido observados mergulhos mais profundos e irregulares (até 60 metros). A faixa de temperatura preferida encontra-se entre 5°C e 9°C, embora os peixes tenham nadado em águas com temperaturas variando entre 1°C e 12°C.

De forma geral, a atividade foi semelhante entre os períodos diurno e noturno, com alguns indivíduos a exibirem migração vertical (DVM), conforme seria esperado para a espécie durante a primavera.

O salmão marcado com a mini-PAT e o sensor CTD apresentou um padrão comportamental interessante, uma vez que uma mudança notável no comportamento coincidiu com diferenças significativas nas medições de temperatura e salinidade. Além disso, o aumento da temperatura medido enquanto se movia para norte contradizia os gradientes de temperatura típicos do Mar Báltico. Propomos que o indivíduo possa ter entrado num rio ou permanecido perto de um influxo de água doce no período

correspondente à mudança. O que foi corroborado pela localização de pop-up da tag perto da foz de um rio e pelos dados modelados, oferecendo uma explicação plausível para esta anomalia.

Palavras-chave: Salmão do Atlântico; Pesca; Catch-and-release; Mortalidade; Migração; Comportamento; Biotelemetria; Condições abióticas; Temperatura; Salinidade; Luz; Profundidade.

List of abbreviations

C&R – Catch-and-release

CTD – Conductivity Temperature Depth sensor

FAO – Food and Agriculture Organization

HELCOM – The Baltic Marine Environment Protection Commission/Helsinki Commission

ICES – International Council for the Exploration of the Sea

ID – Identification Number

PIT - Passive Integrated Transponder

PSAT – Pop-up Satellite Archival Tag

TAC – Total Allowable Catches

TAD – Time at Depth

TAT – Time at Temperature

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Introduction

Are there plenty of fish in the sea?

Despite the undeniable economic and social value, that leads to high revenue and the harvest of an important source of protein (Hilborn et al., 2003), fisheries are pointed as the cause for a massive loss of marine resources and declines in fish stocks (Cooke & Cowx, 2006). It was in the 1950s that fisheries underwent a rapid expansion, the previous small-scale local fisheries had to compete for the same resources as the industrial trawlers fishing for local and international markets on a larger scale (Spijkers et al., 2023). The pressure on the ecosystems increased massively, as the fishing fleet grew twofold from 1950 to 2015, and the bycatch associated with the fish harvested for consumption depleted the underwater resources, from shallow tropical waters to the coasts surrounding developing countries (Rousseau et al., 2019). The Food and Agriculture Organization – FAO – was created and began gathering statistics worldwide. This overfishing in association with an El Nino event led to the first global collapse of the Peruvian anchoveta in the 1970s (Pauly & Palomares 1998). However the consequences were overlooked and the overexploitation continued which led to the rapid decline in catches in the North Pacific that continued throughout the 1980s and 1990s, and even the increase of fishing effort (Pauly & Zeller, 2016; Rousseau et al., 2019) could not balance the decrease in biodiversity as overfishing threatened marine ecosystems (Spijkers et al., 2023).

In a phenomenon known as fishing down the food web commercial fisheries move from large long-lasting apex predators that are becoming scarce to lower trophic levels depleting bottom fish until invertebrates are reached in an unsustainable manner (Pauly & Palomares, 1998). In fact, the first chain response of the marine ecosystem could be misleading, as the predation decreases the prey species seem to thrive resulting in rising catches. Nevertheless, since the food chains are interconnected in an inter-relating food web, where the predators become prey and help balance the dynamic ecosystems the result often is longstanding unpredictable consequences. The species that often prosper from this imbalance are frequently formerly suppressed ones with low commercial value (Pauly & Palomares, 1998). Therefore, the loss of fish species that influence key ecological functions could lead to a loss of ecosystem resilience, potentially causing a shift from one equilibrium state to another (Holling, 1986; Chapin et al., 1997; Grime, 1997; Tilman et al., 1997).

Marine life is threatened not only by this anthropogenic stressor but also by the changing climate and human activities that result in the introduction of exotic species, habitat destruction and loss, the spread of several types of pollutants, and eutrophication (Bruton, 1995; Cowx, 2002; Wolter & Arlinghaus, 2003; Lewin et al., 2006).

Fish populations provide numerous services that could be lost, including, the regulation of trophic webs that results in the stabilization of aquatic ecosystems. Moreover, their role as active and passive transporters is of great value as they transfer materials and energy both when migrating (Polis et al., 1997) and when energy is transferred through the food web as they get consumed by other organisms, connecting different types of ecosystems (i.e. aquatic and terrestrial) (Bilby et al., 1996; Larkin and Slaney, 1997; Holmlund & Hammer, 1999). Also to note is their importance in research, due to their dimensions and large populations, fish are easily sampled, making them excellent study subjects (Holmlund & Hammer, 1999). These animals are, in some cases, great monitors of water quality, reacting to a range of stressors such as possible water contaminants and pathogens (Harris 1995; Balk et al., 1997; Holmlund & Hammer, 1999). Additionally, due to their growth rates, body size, habitat preferences, and trophic positions, many species can bioaccumulate substances thus improving water conditions and acting as recordkeepers for future research (Schindler, 1990; Holmlund & Hammer, 1999). As shown, their value to humanity is immense through the many services they provide. Additionally, fish keep delivering an important protein source (Holmlund & Hammer, 1999), and fish-derived substances are utilized in pharmaceutical research, potentially playing a significant role in medicine development (Carte, 1996; Holmlund & Hammer, 1999).

Recreationally, the close interaction with nature provided by fishing is often cited as a major motivation for sport fishing (Schramm and Mudrak, 1994; Holmlund & Hammer, 1999). Therefore, this loss in fish stocks and biodiversity should be addressed as a global concern and measures should be taken (Lewin et al., 2006).

To balance the negative scale several management efforts are set in place such as: gear restrictions, total allowable catch decreases, total fishing effort reductions, closed areas, catch shares, fisheries certification, catch-and-release (C&R) impositions, and community management approaches. However, these managing strategies need to be reformed and employed in a more preventative approach as they are highly dependent on scientific analysis and data collection (Pikitch, 2012). This data collection is often low quality and misrepresents total catches, lacks precision in identifying species, and is clouded by poor recordkeeping (Camhi et al., 2008; Queiroz et al., 2016). Another main issue lies with the single-species approach that is used in a lot of management programs. Since it fails to consider the interaction between different species and their role in the trophic web, overlooking the ecosystems' dynamics (Pikitch et al. 2004). In fact, FAO, 2020 classified forty percent of fisheries as exploited to the maximum capacity and one-third of global fish stocks as unsustainably harvested. Additionally, the illegal fishing practices that decline to report the accurate number of catches sum up to a probable twenty percent of global catches, rushing up the overfishing decline (Agnew et al., 2009; Spijkers et al., 2023).

Nonetheless, despite the pressures endured on the ecosystems, the exploitation rates vary with some regions showing significant declines in these rates due to management actions. Thus, with the declining and collapsing examples, there are also stable and rebuilding success cases (Worm et al., 2009).

Broadly two types of fisheries exist, recreational and commercial fisheries. The latter term usually refers to the capture of aquatic animals/products for sale purposes (Smith, 2002) and is recognized as the core driver in the concerning decrease of fish stocks worldwide (Hilborn et al., 2003).

Recreational fisheries on the other hand describes the capture of fish by individuals for personal consumption, leisure, or sports (Pitcher and Hollingworth, 2002). These fisheries have several gear types such as trap, rod and reel, gillnet, and speargun (Arlinghaus & Cooke, 2009) however the main chosen method is rod and reel with hook and line (Cooke et al., 2019).

With most of the research focusing on the impacts on species and ecosystem dynamics resulting from commercial fishing, since extinction (Myers & Worm, 2004), massive population declines and ecosystem modifications (Jackson et al., 2001) have been connected to these practices. The true effects of recreational fishing were overlooked in the past. It was believed that the harvest resulting from commercial fishing was much higher when compared to recreational fisheries, yet in some cases, the former overexerts the latter (McPhee et al., 2002). Granting that one angler's effects on the stocks and ecosystem are not on the same scale as other mass captures, the cumulative consequences should not be overlooked (Lewin et al., 2006). The concerns linked to commercial fisheries such as collapse due to overfishing (Post et al., 2002), ecosystem changes, evolution, and degradation caused by fishing and bycatch (Cooke & Cowx, 2006) were all recorded in recreational fisheries (Cooke et al., 2019). From a public and political perspective, the impacts of recreational fishing seemed to be far less, and thus fewer measurements were required (Kearney 1999). Nevertheless, there has been a shift in this view with the limitation of these practices in many locations including the Baltic Sea (ICES, 2022). In addition, many consider this activity morally unacceptable as the pain caused to the sentient animals is viewed as pointless and unjustifiable. In a society where animal welfare is a growing concern, it is argued that it is a given fact that fish feel pain, and thus angling for leisure does not stand by these animal welfare pillars (Singer, 2015). In line with these some laws have been modified, the Swiss Animal Welfare Act of 2008 declares voluntary catch-and-release an offense as it causes unnecessary suffering (Arlinghaus et al., 2012).

In a world with growing pressures on the many forms of life, fishing is a major one. Both morally condemned and a drain to the habitats, fishing can be painted in a heavily black tone. Regardless, there is a silver line as fishing comes with many anthropogenic benefits,

and it is not realistic to assume that such activity will cease to exist in the near future. As a source of immense income (Ditton et al., 2011), a leisure activity (Pitcher & Hollingworth, 2002), an important protein resource, and a significant tourism activity in many areas including developing ones (Smith et al., 2005) recreational fishing increased in the 21st century since the newer disposable income allowed novel leisure activities (Arlinghaus et al., 2002). The International Council for the Exploration of the Sea (ICES) estimates that 35,000 - 40,000 salmon are caught (and released) by trolling in the Baltic Sea annually, i.e. almost half of the total allowable catch (TAC) for 2017, and up to 10,000 of these are caught by Swedish anglers. With 80% of the salmon caught in the 1970s and 1980s in the Baltic Sea through offshore fishing, the trend began to change in the 1980s with an expansion of coastal and river fishing. However up until the 2000s 66% of the catch was offshore (Romakkaniemi et al., 2003). The fish reaching the main basin of this sea come from different rivers and are of mixed origins, in the 1990s ICES determined that some of these river stocks were very unhealthy. It was in 2022 that ICES recommended unprecedentedly the ceasing of all salmon catches in this area, encompassing commercial and recreational fisheries as some salmon populations are vulnerable. Globally, the International Union for Conservation of Nature Red List places Atlantic salmon as near threatened with some populations vulnerable (Darwall, 2023). In the Åland Sea and Gulf of Bothnia coastal targeted fishing should still be allowed (ICES subdivisions 29, 30 and 31, 2022). Following such advice, the European Council ended salmon fishery with the exclusion of scientific fisheries, determining total allowable catches for inevitable by-catches. C&R was also banned and anglers have a daily limit of one adipose fin-clipped salmon - hatchery fish. The farmed fish have their fin clipped before release so that the distinction can be made. According to ICES, 60-90% of caught fish are of wild origin (ices.dk). In the EU regulation 2022/109 articles 9 and 10 these measurements for sea trout and salmon fishing regulations and management and conservation are clearly stated and should be followed by the Member countries. For 2024 the zero-catch in the main basin guidance remains, now with targeted fishery in coastal areas during the summer migration months only allowed in the Bothnia Bay and with lower TACs than ever before with a decrease of 15% (ICES subdivision 31) for all Member States (ICES, 2023; <https://www.havochvatten.se>). For sea trout the bycatch limited is established at 3% and fishing is prohibited if done more than 4 nautical miles of coast. These measurements should help in the reduction of the misreporting of catches for both species (<https://eur-lex.europa.eu>).

As for Sweden, the fish stocks were severely affected in the 1920s when trolling began permitting fishing to move further from the coast (Eero et al., 2007; Ojaveer et al., 2010). Nowadays, commercial fishing of salmon is heavily regulated with the lowest quota ever set

in place, decreasing 15% in 2024 in line with the European law (<https://eur-lex.europa.eu>). Fishing in the open ocean is banned, and the allowed fishing practices have been directed towards the coast to be more stock-specific. Nowadays, Baltic salmon are mainly exploited by commercial and recreational coastal and river fisheries (ICES, 2018). These fisheries target returning adults on their spawning migration from their feeding grounds towards and within their natal rivers. Thus, river fisheries are population-specific while the coastal fisheries still target salmon from a mix of populations but become increasingly more population-specific the closer to the river mouth that the fishing is conducted (Whitlock et al., 2018; Jacobson 2019). In 1994 the Helsinki Commission (HELCOM), a commission formed to protect the Baltic Sea area, established marine and coastal protected areas intending to protect the whole ecosystem instead of targeted species or habitats. Initially, 62 sites were denominated (Ojaveer et al., 2010).

Anglers share some characteristics with researchers as they are advocates for conservation, many with deep knowledge of the species participate in the collection of data and subsidizing research (Bate, 2001; Granek et al., 2008; Florisson et al., 2018; Cooke et al., 2019). It is important to balance fishing practices with the ecosystem's viability long term. The route to sustainable fishing is not linear and implies the combined action of decision-makers, companies, anglers, and citizens all contributors to the web of actions affecting the system. FAO, 2012 defends that the permission to fish comes hand in hand with the accountability to do so in a responsible manner, aiming for a sustainable future. In the past, a narrow vision of conservation only accounted for maximum sustainable yield (MSY), meaning the maximum catch that could be harvested without leading to compromised impending catches. This fails to consider the web of interaction between different species and the cascade consequences the depletion of a single species leads to (Hilborn et al., 2003, 2015). Perhaps population dynamics should make way for ecosystem dynamics and the carrying capacity (K) concept (Lotka, 1925), long used in management ecology should be broader and englobe the interactions, populations, and habitat as a whole (Chapman & Byron, 2018). So, measurements should be made according to the habitat in question as a dynamic web of relations with future prospects outweighing immediate benefits. This might be through TACs limitation, restoration of habitats for instance by investing in hatchery stocks (Cooke et al., 2019), creating protected areas and seasonal closures, limiting sizes of fish permitted to harvest, and bag limits (Bartholomew & Bohnsack, 2005). The public, both anglers and citizens should be sensitized through education and sanctions to the importance of conservation and the valuable services provided by the aquatic habitats. Fishermen could act as vessels in communities advocating environmental protection and restoration. Funds should be moved both by politicians and related industries to establish successful conservation projects and to support research

(Cooke et al., 2019). The media should spread the word in a conscious manner. When influencing the public perception communication of science should be done with public education and awareness in mind. Several examples show the spread of misinformation and misrepresentation of scientific facts leads to a distrustful public both in political conservation measurements and science (Ladle et al., 2015; Wu et al., 2018), therefore an open line of clear communication should exist between scientists and media to reduce discredit. The goal should be “fishing activities that do not cause or lead to undesirable changes in the biological and economic productivity, biological diversity, or ecosystem structure and functioning from one human generation to the next” as stated by FAO, 2009.

Given that the potential effects of catch-and-release and the tagging process should be considered, this study will examine the potential impacts on mortality and behaviour changes. C&R can result in injuries such as tissue damage and possible gill or mouth trauma, which may impair the animal's ability to feed. It is equally connected to increased vulnerability to predation if the animal is released in an inadequate environment, (Dunmall & Philipp 2002; Cooke & Suski 2005) and ultimately mortality. Furthermore, the energetic costs from the drag (McIntyre, 2015) and increase stress (Donaldson et al., 2008) add to the possible implications.

As the animals are tagged, the handling resulting from the protocol and tagging stressors could add to the unideal condition. Previous research showed that tagging with external tags as Pop-up Satellite Archival Tags (PSAT) leads to slower swimming and shallower dives in Atlantic salmon (Hedger et al., 2017) and added stress (Jepsen et al., 2015).

Nonetheless, C&R is a possible conservation approach that is becoming an increasingly used practice by anglers, either through voluntary or mandated means as a by-product of harvest regulations (Cowx 2002; Cooke & Suski 2005; Arlinghaus *et al.* 2007). C&R has the potential to reduce the direct mortality associated with catch-and-keep fisheries while conserving fish populations and maintaining the socioeconomic and cultural benefits of the recreational fishery (Policansky 2002; Lewin *et al.* 2006; Arlinghaus *et al.* 2007). Prior studies with northern pike (*Esox lucius*), smallmouth bass (*Micropterus dolomieu*), and walleye (*Sander vitreus*) revealed that air exposure due to catch-and-release angling had a reduced negative impact on fish behaviour in the short-term (Chlor et al., 2022). The same was true with halibut (Ferber et al. 2016), nevertheless, the effects of possible injuries and delayed mortality were not covered by the authors. Thus, C&R as a management approach is not without its limitations and can result in undesirable biological and ecological consequences (Cooke & Suski 2005; Arlinghaus et al., 2007).

During this study, fourteen Atlantic Salmons were tagged in Simrishamn and in Ålands hav with PSATs. To do so the salmons were removed from the water by experienced fishermen with a fishing line, remaking the usual conditions in recreational trolling, and rereleased into the water after the tagging protocol.

Advancing animal ecology through biotelemetry

We use biologging to describe the collection of data with sensors located either internally or externally on an animal, whereas telemetry is used to designate the transmission of remotely collected data (Lahoz-Monfort et al., 2021). In underwater ecosystems, animal movement studies rely on biotelemetry to remotely measure physiological, environmental, or behavioural data (Cook et al., 2004). As information on vertical and horizontal distributions is obtained, patterns can be observed and questions relating to animal migrations, social interactions, and motivations (Hellström et al., 2022) can be answered (Arostegui et al., 2017). Tags are normally equipped with tracking technology and diverse sensors. The sensors collect images, audio, environmental or physiological data, body position and movement. Tags, as the PIT tags described below, serve for important individual identification (Lahoz-Monfort et al., 2021).

Biologging uses data loggers to store biological data from sensors measuring for instance depth, light intensity, temperature, or velocity data. It allows for great data storage over long periods even when using a small-sized device. However, it requires tag recovery to retrieve this information. A good example is digital acoustic tag (or DTAG) a type of device recording sound and depth, orientation, and temperature which provides valuable insights into animals' response to noise pollution (Read, 2009).

In the 1980s passive integrated transponder (PIT) tagging (Cooke et al., 2013) with no battery and thus unlimited time use and at an inexpensive price opened the doors to the identification of a large number of individuals in confined areas (Castro-Santos et al., 1996). These small tags are coded markers inserted into the animals. The devices are used in studies about growth rates, movement patterns, and survivorship in a variety of species since proven to be more consistent than traditional methods such as external marking (Gibbones et al., 2004).

In the 1950s acoustic telemetry (Cooke et al., 2013) appeared using sound waves that allow to track and analyse movement of animals, nowadays it can be used in animals of various sizes with a longevity of up to ten years. It is cost-effective, requires low maintenance, and permits data collection in large areas as a global network of receivers detects, decodes, and stores signals transmitted by the tags attached to the animals. The tags transmit sound

waves that travel efficiently through water reaching the receivers. These receivers are fixed in the water in several habitats and in certain models, remote data extraction is possible through autonomous gliders (Hellström et al., 2022). This method allows the long-term collection of data and can be used in almost all aquatic species, with minimal behaviour changes linked to it. However, it often requires anaesthesia and a small surgery or incision performed by a trained professional (Donaldson et al., 2008). In Figure 1 the tagging of catfish with acoustic tags by Doctor Hellström and Figure 2 its return to its habitat following tagging and anaesthesia recovery.

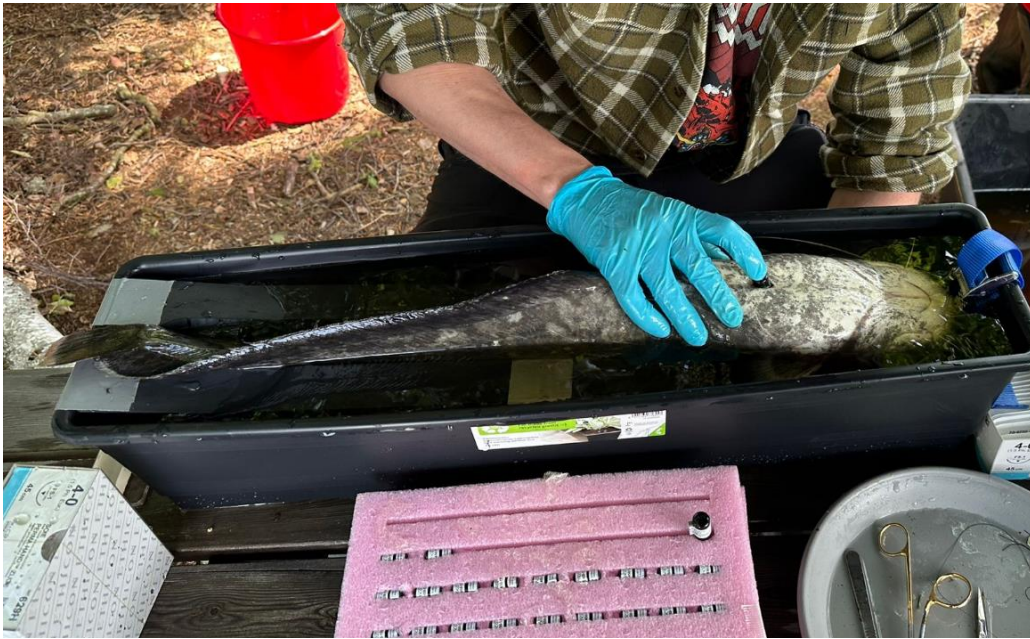


Figure 1 – Doctor Hellström performing surgery to insert acoustic tags on catfish. Photo by the author.



Figure 2 – *Releasing the catfish back into its habitat post-tagging. Photo by Doctor Hellström.*

Radio telemetry (Cooke et al., 2013) commenced mainly applied to terrestrial animals however it was later useful in some aquatic studies, mainly in freshwater conditions or in animals that surface frequently. Due to the attenuation of radio signal in the water, a medium that absorbs radio waves, the signal that reaches the receiving above-water antenna is often weak. Nevertheless, if in a small area with several antennas, precise locations might be achieved through triangulation (Monan & Liscom, 1976; McCleave et al., 1978).

Combined acoustic and radio transmitting (CART) tags also emerged combining acoustic and radio, these devices seemed to be a good option for diadromous fish as when in freshwater radio mode is activated switching to acoustic when in the ocean, the changes in water conductivity allow this alteration (Deary et al., 1998). When comparing radio to acoustic performance, the latter is poorly affected by high conductivity (Cooke et al., 2013) which not only increases longevity but also improves range (Deary et al., 1998).

The 1990s marked a leap in biotelemetry with the dawn of satellite telemetry. This allowed for real-time tracking of animal movements over vast distances and in remote areas. Satellite telemetry can be particularly helpful in the study of pelagic species as it does not demand recapture of the individual (Mate et al., 1998; Gillespie, 2001). Nevertheless, when studying marine species that do not surface or do so rarely, satellite telemetry bears many limitations as the tags need to be above water to transmit signals. Pop-up satellite archival tags combining the best of two worlds, are a great option to study teleost fish (Lutcavage et al., 1999) since these devices are buoyant and transmit stored data through satellite when at the surface thus combining stored data retrieval with satellite telemetry. Normally the tags are equipped with a wet-dry sensor to activate data recording and transmission using the antenna. Moreover, a corrodible attachment link allows release either on a programmed date (wildlifecomputers.com) or in case of premature death (e.g. deduced as the depth remains unchanged for several consecutive days) (Chittenden et al., 2012). If the tag is physically recovered archival stored detailed high-resolution data can be downloaded in contrast with the data transmitted through the satellite which frequently contain gaps of hours or even days resulting from errors in transmission (Nielsen et al., 2023). Depth, temperature, and light intensity are commonly logged with the possibility of attaching additional sensors to measure other abiotic factors such as salinity (Teo et al., 2009; Chittenden et al., 2012). This method is faster and requires less training to master when compared to acoustic tagging, nevertheless, the use in smaller species is still not possible, and the tags' drag along with attempts to remove it may cause behaviour changes in the animals (Donaldson et al., 2008).

To ascertain an animal's position the tag can either send a signal that allows it to estimate position or receive a signal to gauge coordinates, using stored light data and computer processing it is also possible to assess location by deducing solar position concerning the horizon (Lahoz-Monfort et al., 2021).

The data collected – physiological, environmental, or positioning - can be accessed remotely with radio receivers (VHF or UHF) if in short-distance or with satellite systems namely Argos, Globastar and Iridium. With acoustic tagging remote data access is possible near the receiver stations, using specialized equipment that can download the stored information without retrieving the receiver (Lahoz-Monfort et al., 2021).

Sims et al., 2006 deployed the first Global Positioning System GPS tracking device (Fastloc GPS receiver) on pelagic fish that used the Argos satellite systems (Argos Platform Terminal Transmitter) to share the locations when the tag surfaces.

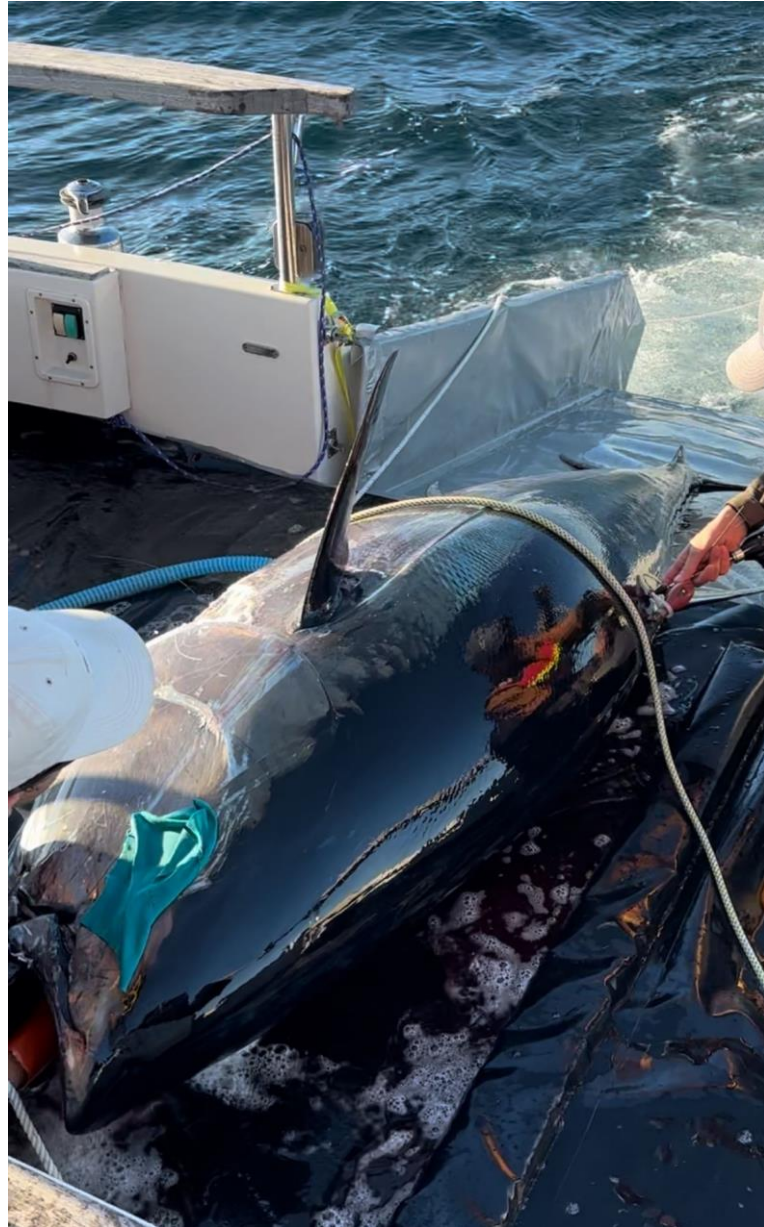


Figure 3 – Tagging bluefin tuna with PSATs Tag in red. Photo by the author.

Since its beginning biotelemetry has evolved with newer tags that are smaller and with better battery and storage capacity and consequently output (Renshaw et al., 2023).

To aid sharing and accessibility of all the data globally collected, several online data bases were created such as Movebank (www.movebank.org) (Kranstauber et al. 2011), Ocean Tracking Network (oceantrackingnetwork.org) and IMOS (the Integrated Marine Observing System; imos.org.au) (Lahoz-Monfort et al., 2021).

The everchanging fish in the slow-changing Baltic

With no solely marine species but englobing a lot of genera that migrate from fresh to seawater, the Salmonidae family retains the genera *Salmo* with Atlantic salmon and brown trout (Klemetsen et al., 2003). Both these species are found in the northern Atlantic and rivers, being that some populations only exhibit freshwater forms. Since their habitats often coexist, some hybrids have been documented. However, due to gamete formation issues from uneven chromosomes, they are infertile (SLU Artdata, 2024).

Salmo salar is versatile as such it can be found in the Atlantic, from Canada to the United Kingdom, up in Greenland all the way down to the Iberian peninsula, and even in the brackish Baltic Sea. The populations that migrate to the Baltic Sea undergo their growth period there (SLU Artdata, 2024). Whereas for *Salmo trutta* the natural habitat is the North Atlantic, but the species was diffused worldwide (Klemetsen et al., 2003).

Although salmonids share comparable lifecycles as they begin with a juvenile phase (parr) in freshwater streams where they stay for a period of 1 to 8 years, undergo smoltification, and usually migrate to the sea for feeding where they go from post-smolts with a total length of 10 to 20 cm to 45-135cm when in salt waters the development is hasty, with massive weight gains. This period is determined for their survival and reproductive success as 1 to 5 years later (Thorstad et al., 2011) they return as adults to their birthplace rivers to spawn (Heggberget et al., 1986). Two groups can be formed when comparing fish one year after fertilization: the small individuals choose not to migrate into the sea, spending an additional year in the rivers before doing so, nearly ceasing growth. Whereas the larger individuals that grow over the winter, smolt and migrate earlier to sea waters (Valdimarsson, et al., 1996). With the smolts' size having a clear relation with survival, when food sources are available the juvenile salmon prosper and grow faster migrating earlier (Klemetsen et al., 2003). The time spent at sea varies among individuals and is influenced by environmental cues (Thorstad et al., 2011), as some decide to prolong their growth opportunities (Alm, 1934; Svardson and Fagerstrom, 1982, Kallio-Nyberg et al., 2006).

With increasing daylight and rising temperatures, juvenile Atlantic salmon (*Salmo salar*) begin their migration from rivers into the Atlantic Ocean, as well as the Northern and Baltic

seas, transitioning into pelagic fish. Parr can start their smoltification after 1 or up to 5 years, these differences are also reported in the same populations possibly to maximize survival chances (Klemetsen et al., 2003). With this journey, many biological adaptations come as they change from a freshwater to a saltwater fish. Their previous brownish/green colour changes as they become silver and streamlined, their salinity tolerance upsurges as the gills, kidney and intestines adapt (McCormick, 2012), and their size significantly increases in a process known as smoltification (Farrel et al., 2020). Even though this term is used with salmonids, it is driven by different aspects depending on the species (Stearns, 1992; Mobley et al., 2021) and its duration is individual and environmentally contingent (Boeuf et al., 1985). In the studied species as well as in rainbow trout (*Oncorhynchus mykiss*) and coho salmon (*Oncorhynchus kisutch*) photoperiod and temperature are the main factors influencing smolt development, however for other species as chum salmon (*Oncorhynchus keta*) and pink salmon (*Oncorhynchus gorbuscha*) photoperiod may be less significant since the salinity tolerance is matured much earlier in the lifecycle. Water flow and temperature appear to be central cues in initiating migration for *Salmo salar* (Farrel, et al. 2020), whether the fish inhabit the northern or the southern water the environmental cue to start migration is when water temperature reaches 8°C (Klemetsen et al., 2003).

These physiological adaptations involve various hormones such as growth hormones, thyroid hormones, and cortisol (McCormick, 2012). Interestingly, the time each individual was in the freshwater or sea phase can be determined by examining scale growth rings (Mobley et al., 2021).

The completion of smoltification varies within individuals as smaller (Bjerknes et al., 1992) and in earlier stages (McCormick et al., 1989; Sigholt and Finstad, 1990) fish take longer to adjust to the osmotic stressor and, once more, with habitat cues including temperature (Sigholt and Finstad, 1990) and photoperiod (Handeland et al., 1998).

As this transformation reaches its end salmonids acquire different degrees of hyperosmotic tolerance depending on their marine habitat (Haraldstad et al., 2017).

Different individuals are shown to express different migratory behaviours, this variation could be linked to population dynamics related to genetic variations (Kallio-Nyberg et al., 1999). Some will perform incomplete migrations, with individuals migrating to the sea (anadromous) and freshwater residents (Birnie-Gauvin et al. 2019). In fact, distinct sea migration patterns were reported in several studies. Kallio-Nyberg et al., 1999 noted that prey availability (i.e. herring), stock influence, and smolt size determined such variations. One population presented shorter migrations and preferred the Bothnian Sea (the northmost area of the Baltic) but all stocks were more abundant in the area in years when food abundance was higher. When testing the distribution patterns of ten different populations, Jacobson et al. 2019 concluded that populations from the southernmost

regions initially migrate northward before moving towards the southern Baltic whereas the northernmost populations are the first to arrive at the southern region, doing so at a smaller size. However, all ten populations ultimately reach the southern Baltic Sea reaching feeding areas. Individuals originating from distinct populations aggregate to feed in similar locations in the Baltic (ICES 2007) since waters with higher salinity are usually associated with higher biodiversity (Ojaveer et al., 2010) the migration tends to be southward (Jacobson et al., 2019) but varies yearly, with and within stocks (Kallio-Nyberg, et al., 1999). Other factors could help explain this as body size and photoperiod greatly influences salmon's migration and diet not only because it is a visual predator but also because its predators are as well, so survival depends on visual cues (Haraldstad et al., 2017).

Kallio-Nyberg et al. 2006 pointed out that nowadays most of the remaining populations depend on hatchery fish releases, largely due to the effects of hydropower regulation and river damming. Their migratory nature makes these species an easy target for fishing, their time at sea is usually the most vulnerable stage although the river populations also struggle with hydropower construction (Klemetsen et al., 2003). In a conservation effort, many are bred and stocked in the rivers after the dams (SLU Artdata, 2024).

After this marine period salmon reach the rivers, the sea and freshwater migrations are complementary but very distinct as salmon endure long periods of starvation as they enter the rivers, consequently after spawning the surviving fish are called kelts. Kelts show reduced fitness and can be more vulnerable (Brobøl et al., 1996) regardless, some can live up to fifteen years (SLU Artdata, 2024). As they return to the river females usually display a pattern of migration divided into three phases, namely, fast movement upriver, afterward an elongated residence period, next a rapid upstream migration preceding spawning that occurs at similar times with the rise of water temperature (Hawkins & Smith, 1986; Heggberget et al., 1988; Baglinière et al., 1989). In species as *Salmo salar*, frequently this spawning migration is recurring however some fish die after the first cycle (Birnie-Gauvin et al., 2019). Distinct from the Pacific salmon, they can spawn more than once in their lifetime doing so in their natal river (Klemetsen et al., 2003). The spawning can take place in distinct months from September to February, the females lay their eggs in the gravel in one or more redds that are fertilized by the returning males or males that chose to stay in the rivers. The cool water temperatures cause a delay in egg development as such, populations inhabiting the north tend to lay their eggs earlier to compensate (Thorstad et al., 2011). Klemetsen et al., 2003 stated the differences in reproduction strategies among the Atlantic salmon's populations. It appears to be a trade-off between size, which increases offspring survival, and the number of eggs laid, with a correlation between fish and egg size – larger individuals lay larger eggs and tend to be more fertile (Jonsson et al., 1996).

Individuals with distinct life histories and migration patterns coexist in the same location, providing evidence for the optimization of their fitness strategies (Thorstad et al., 2011).

Therefore, as the fish reach the brackish Baltic Sea where better growth opportunities await, coming from different rivers spread throughout the Nordic countries they are met with new risks to their survival as a novel environment, predators, and unfamiliar food resources test their fitness (McCormick et al., 1996.). Mainly predated by burbot (*Lota lota*) and pike (*Esox lucius*) (Larsson, 1985), these fish start their post-smolt lives in the sea feeding mainly on insects (Jutila and Toivonen, 1985) gradually changing their diet to fish like herring (*Clupea harengus*), and in smaller quantities, three-spined sticklebacks (*Gasterosteus aculeatus*) and sand lances (*Ammodytes* sp.) (Salminen et al., 2001; Kallio-Nyberg, 2006).

The Baltic Sea has particular characteristics with massive gradients throughout the 10 regions, see figure 6 (Kattegat, Belts and the Sound, Arkona, Southwest, Eastern and Northwest of the Baltic Proper, Gulf of Riga, Gulf of Finland, Bothnian Sea and Bothnian Bay), declining from southwest to northeast. In the Kattegard region, the average salinity is 22.3 psu whereas in the northern region of the Bothnian bay 3.1 psu. Bordered by nine countries and home to over 85 million people in its coastal areas (Ehlers, 2002), it has a shallow morphology with a maximum depth of 460 meters and an average depth of 60 meters (Ojaveer et al., 2010). Moreover, when compared to the Atlantic Ocean this ecosystem has higher temperature and salinity gradients, and fewer predators and prey species as the biodiversity is lower (Hvidsten et al., 1998, Salminen et al., 2001; Kallio-Nyberg et al., 2006). The deeper areas have two layers of water separated by a constant halocline at 70-100 meters (Ojaveer et al., 2010). The oxygen-rich saline water enters from the North Sea in the southmost region, the freshwater comes from the various rivers influenced by precipitation. In the summertime water temperatures on the coast can go up to 25°C opposed to the deep waters below the thermocline with low oxygen and temperatures, and high salinity (Ojaveer et al., 2010).

The non-tidal Baltic possesses distinct characteristics. It is nearly isolated from the open ocean, with narrow straits, a complex topography, and deep basins separated by shallow sills, all of which hinder water exchange (Reckermann et al., 2022). The residence time is around 25 to 35 years (Lass et al., 2008). These features create a habitat for diverse organisms with varying origins and levels of complexity, such as freshwater, marine, migratory, and even relict glacial – cold-adapted, common through glacial periods – species. There are about 200 fish species inhabiting this sea, with herring, sprat, and cod as the most common. In regions with lower salinity, freshwater species like pike, perch, roach, and ruffe prevail. In the cold north, below the thermocline one might find relict glacial species in their habitat, eelpout, lump sucker and sea snails chose the Baltic as their home. It is also home to mammal species such as seals (see Figure 4). A study done in the area found

salmonids in these animals' stomachs (Suuronen & Lehtonen 2012). When it comes to migratory species, salmon, trout, and eel pose as the ones with the highest commercial value (Ojaveer et al., 2010).



Figure 4 - Grey seals in the Baltic sea close to Bornholm. Photo by the author.

However, these unique conditions, combined with human activities, cause significant threats to the region (Stramska & Chudziak, 2013; Meier et al., 2022) through the accidental or illegal discharge of nitrogen and phosphorus from agricultural runoff, as well as heavy metals and petroleum from industrial processes, shipping, and offshore operations (Ehlers, 2002). In fact, the many ships crossing the Baltic daily are a vessel for invasive species that disturb the ecosystem (Ojaveer et al., 2010). Overfishing was also a growing threat in the Baltic, the salmon populations were being affected by many stressors as hydropower plants started being constructed and rivers dammed. Nevertheless, conservation measures were set in place and prevailed allowing for the slow recovery of these populations (Ojaveer et al., 2010).

Atlantic salmon has been named by some authors as “the chicken of the sea” (Torrissen et al., 2011), while not that many years ago this fish was considered a delicacy not available to many, the mass farm production and extensive fishing led to two rather contrasting outcomes: the cost decreased making it accessible to the masses and the wild populations became vulnerable resulting in restricting fishing measurements to conserve the vulnerable populations (Jonsson & Jonsson 2011).

Therefore, to fill in the existing knowledge gap in understanding (i) salmon migration in the Baltic Sea and (ii) how catch-and-release practices are affecting salmon populations, we

tagged 14 Atlantic salmon with PSAT. The study area, deployment and pop-up locations are depicted in Figure 5. The novel use of pop-up satellite tags equipped with additional sensors to determine survival and sublethal effects, namely changes in migration patterns, provided unparalleled details. In summary, our work focused in understanding the impact of C&R on Atlantic salmon survival and overall behaviour and movement (sublethal effects). Hence, the two main objectives were to assess post-release mortality following C&R, and the influence of abiotic factors on movement (vertical and horizontal migration).

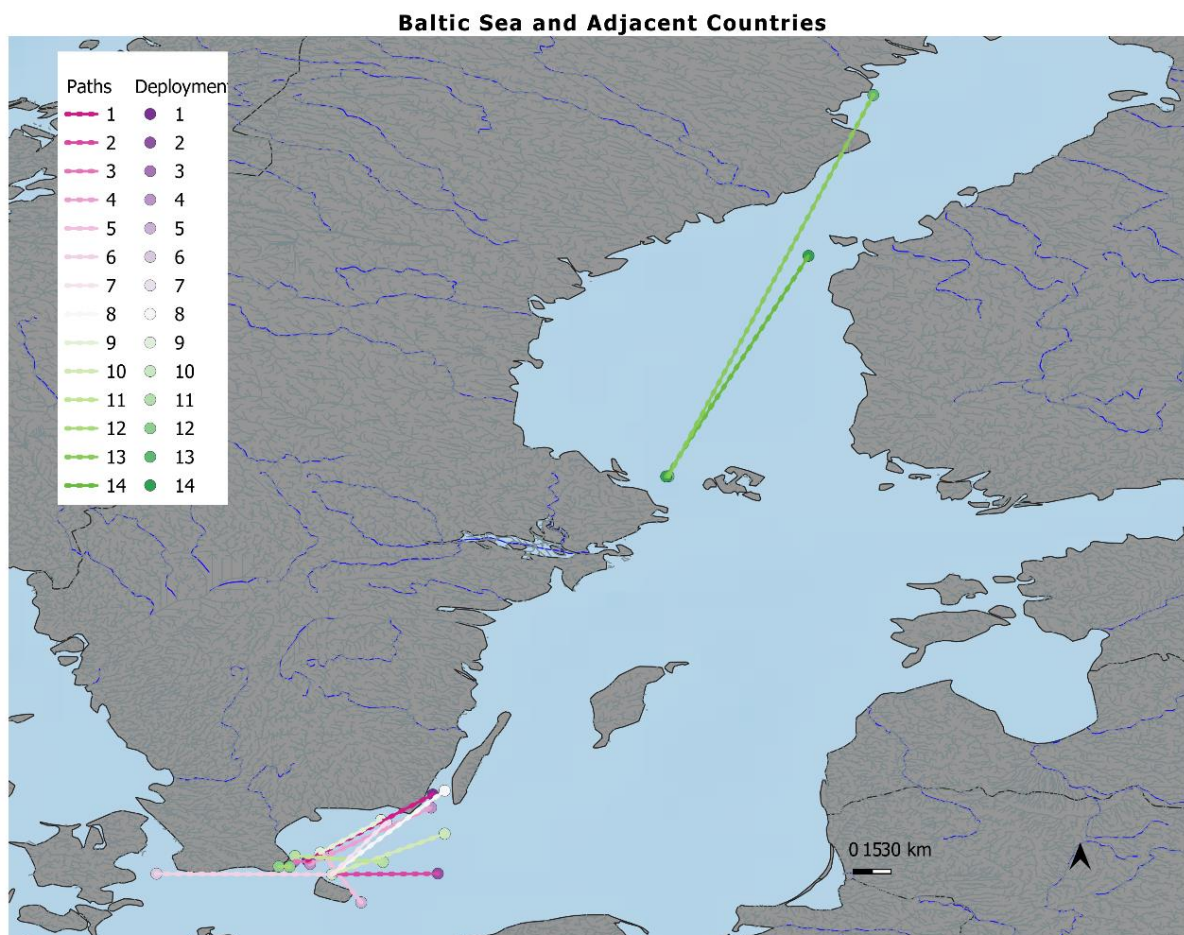


Figure 5 – Study area with interpolated paths of the tagged fish and deployment and pop-up positions. Image by the author using QGIS.

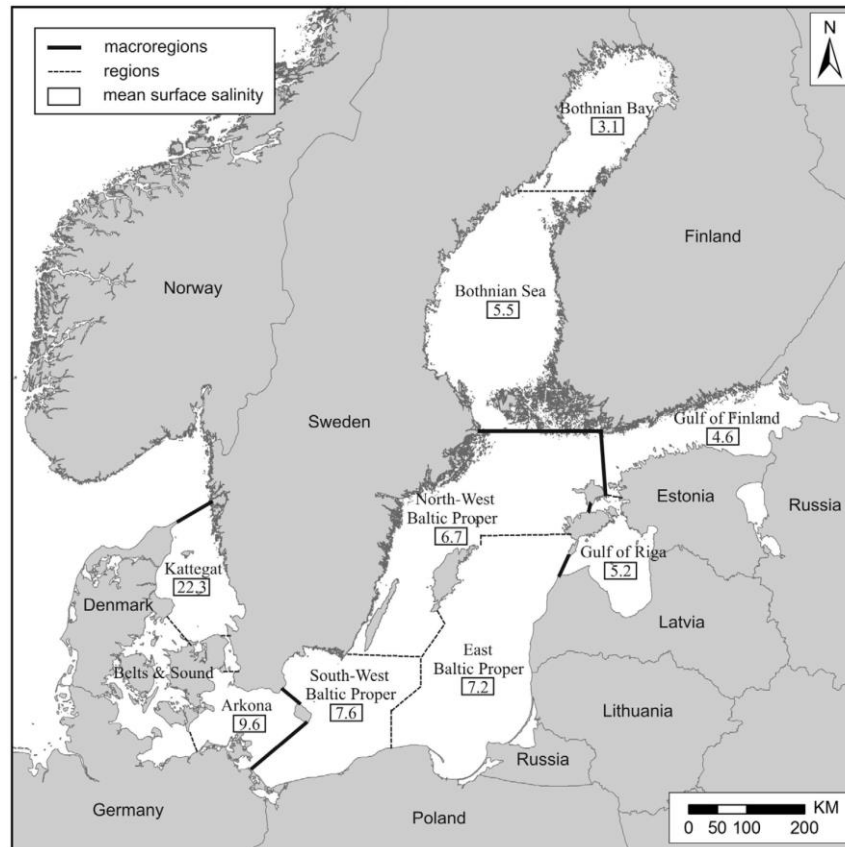


Figure 6 – Baltic sea regions and salinity. Ekeröth, N., Lindström, M., Blomqvist, S., & Hall, P. O. (2012). Recolonisation by macrobenthos mobilises organic phosphorus from reoxidised Baltic Sea sediments. *Aquatic geochemistry*, 18, 499-513.

Materials and Methods

Tagging

In May and June of 2023, fourteen Atlantic salmon (*Salmo salar*) were tagged with PSATs developed by WildLife Computers. The following table (Table 1) shows the tags identification (ID) and serial numbers and a number attributed randomly to the individuals, for this point on these numbers will be used to address the different fish:

Table 1 – Table identifying the individuals.

Attributed Number	Serial Number	PTT ID
1	23P0222	242922
2	23P0429	242930
3	23P0228	242924
4	22P1084	242903
5	23P0121	242915
6	22P1337	242907
7	23P0258	242928
8	23P0310	242929
9	22P1097	242904
10	22P1458	242910
11	22P1219	242906
12	23P0453	242931
13	23P0216	243273
14	22P1478	242911

Of these, thirteen salmon were tagged with Survivorship Tags (sPAT) tags, while one with a miniPAT tag equipped with a Conductivity Temperature and Depth (CTD) sensor (StarOddi) (Figure 8), this sensor allows for the collection and analysis of conductivity data.



Figure 7 – Insertion hook (on the left); Wildlife Computers pop-up satellite archival tag (in the middle); and conductivity and temperature sensor developed by Star-Oddi (on the right). The picture shows how the CTD was attached to the tag in a novel manner. Photo by the author.

The tags were programmed to detach after thirty days (sPat) and forty-five days (miniPat). They were all identical in size, measuring 118 mm in length and 38 mm in diameter, and were designed with a hydrodynamic shape to minimize drag, ensuring that the tags had minimal impact on the swimming efficiency of the fish. The tag's design makes it possible to be recovered as it floats after detaching from the animal (www.wildlifecomputers.com). The tagging was conducted near Simrishamn and Ålands hav. A geographic information system software namely, QGIS software was used to create a map of the study area (Figures 5 and 6). For better context and analysis, a layer containing the surrounding countries along with another with the relevant water conditions and freshwater influxes of the region was added.

An open-source map with detailed daily temperature data from the Baltic Sea was accessed on:

https://data.marine.copernicus.eu/viewer/expert?view=layers&dataset=BALTICSEA_ANALYSISFORECAST_PHY_003_006 of the deployment and pop-up dates.

Capture and Handling

The salmon were captured by trolling fishing, using rods and 4 to 6 fishing lines by experienced fishermen operating from motorboats as seen in Figures 8 and 9. Thirteen fish were caught using a triple hook, and one was caught with a single hook. Once hooked, the fish were brought onboard using a landing net as seen in Figure 10, with no efforts made to remove the hook. The deployment coordinates were recorded and obtained through the boat's GPS. The fight time, time between hooking and netting the fish, was kept under ten minutes.



Figure 8 – Tagging boat. Photo by the author.

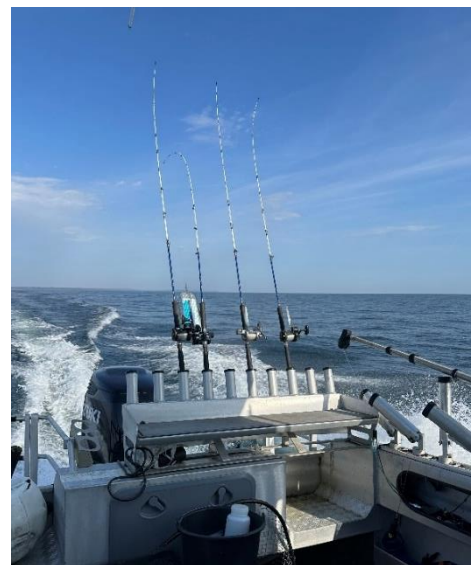


Figure 9 – Rods in the tagging boat. Photo by the author.

Once onboard, the salmon were placed in a holding box (check Figure 10) filled with seawater, which was changed after each tagging session to maintain optimal water quality.



Figure 10 – Holding box with salmon and net. Photo by the author.

While on the box, each salmon was measured for total length, and the hook type, as well as the depth at sea at which the hook was inserted, were recorded. These measurements were later used to assess the impact of these factors on post-release mortality. A DNA sample of each animal is kept in record and for such a scale was taken as seen in Figure 11.



Figure 11 – DNA collection. Photo by the Doctor Hellstrom.

The tags were inserted intramuscularly just behind the dorsal fin, to minimize interference with natural swimming motion. The tag was towed using its anchor ensuring secure attachment (see Figure 12). The entire tagging process was completed as quickly as possible, typically within 3 to 10 minutes, to minimize the duration of handling and potential stress on the fish.

To ensure that the tags did not significantly affect the fish, only salmon longer than 60 cm were selected for tagging. This size criterion was implemented to reduce any potential impact of the tag on the swimming performance of the fish and lessen possible drag and injuries.

Tagging procedures were conducted in full compliance with Swedish law, under the supervision of an authorized researcher (Doctor Gustav Hellström) with an Animal Welfare permit issued by the Swedish Animal Welfare Council (dnr:5.2.18/1153818). The primary researcher followed all ethical guidelines, ensuring that the welfare of the animals was prioritized throughout the process.



Figure 12 – Tagged salmon held by the fisherman pre-release. Photo by the author.

Tag recovery

The retrieval of the pop-up satellite archival transmitting tags was carried out using the same motorboats that were employed during the tagging process (see Figure 8). The recovery operation relied on an Argos goniometer CLS RXG-234, a device made by CLS that specifies in finding active tags in the field in a range of 100km (www.telemetry.groupcls.com) (see Figure 13).

Its antenna white pointer (Figure 14) was placed facing the front of the boat in a high position to minimize possible interference and maximize reception which was crucial for accurately locating and retrieving the floating tags after they detached from the salmon.



Figure 13 – Goniometer connected to the antenna. Photo by the author.

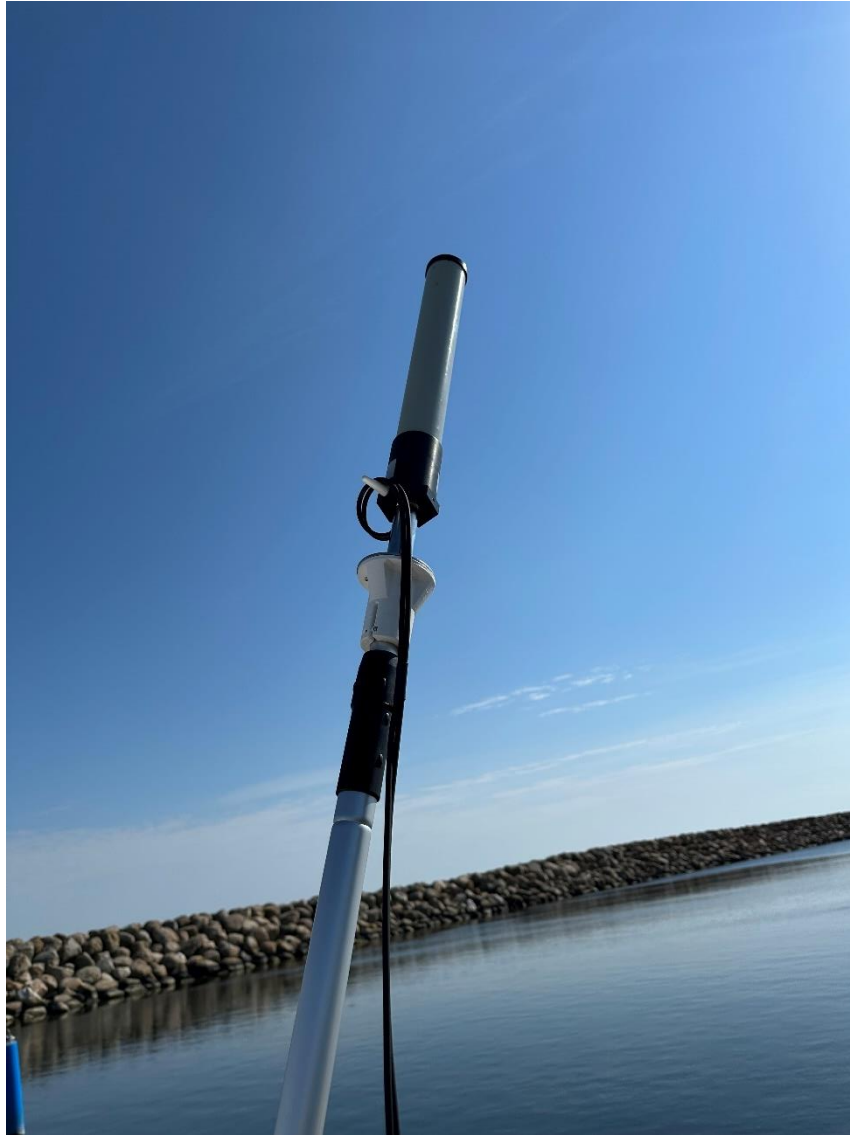


Figure 14 – *Antenna and pointer. Photo by the author.*

The goniometer was used as indicated by its manual and set to operate in “Gonio mode display” where the direction is presented relative to the antenna’s pointer, granting detection and consequent navigation towards the signal emitted by the PSATs. The recovery team routed the boat towards a general area where the tags were prone to be found as the last known GPS coordinates transmitted by the tags were read on the platform.

The tags' identification number was programmed into the device so when in proximity to this last known location, the goniometer began to detect the real-time signal emitted by the drifting tag. The directional antenna provided real-time feedback on the signal strength and direction, guiding the boat directly toward the tag. The area was circulated by the boat until the visual identification of the device was possible. Once the tag was visually identified at the surface, the team used a long-handled net to collect it from the water. The recovered tags were then brought onboard and secured for subsequent data retrieval and analysis.

Data analyses and processing

Following the deployment, the PSATs and the CTD sensor recorded several environmental parameters, including light levels, depth, temperature, and conductivity. The tag data was sampled every second however, if the tag could not be recovered and thus transmitted through satellite only ten-minute intervals were obtained. CTD data was logged in ten-minute intervals.

The depth profiles allowed mortality to be deducted if the fish remained at the same depth for more than 3 consecutive days (Chittenden et al., 2012).

The data collected from the PSATs was processed to ensure accuracy. To do so, firstly the raw data was either downloaded from the tags following their recovery or from the tags' supplier portal in case the tag was not physically retrieved.

The initial step in data processing involved identifying and removing periods where the tag might not have been recording properly or where it had detached prematurely and surfaced (popped up). Such periods were identified through anomalies in the data, namely persistent periods at the surface – identified visually on the depth plots, or inconsistent depth measurements that did not align with the possible behaviours of the tagged salmon. To attain this the noise was filtered by flagging and removing data points where the tag displayed abnormal patterns such as brisk and non-physiological changes in depth or temperature possibly due to obstruction or debris. The pop-up events were equally excluded from the analysis.

Post-release mortality analysis

The fish length and hook depth were analysed as potential factors influencing post-release mortality using boxplots.

Determination of Day and Night Periods

To evaluate if diel patterns existed and check for behaviour differences between day and night, light data recorded by the PSATs was used to validate the data extracted from the R package "suncalc". These periods were established based on the geographical coordinates of the deployment and pop-up locations, using the package to distinguish daylight and darkness.

First, the average coordinates between the deployment and pop-up locations were calculated to serve as a reference point for the study area. Three average coordinates were calculated: pop-up, deployment, and combined pop-up and deployment. Using the "suncalc" package in R, nautical dawn and dusk times were extracted for these averaged coordinates, providing accurate time frames for day and night. The analysis showed no significant difference in dawn and dusk times between the deployment and pop-up locations and the combined average was used. This enabled the use of consistent time frames across the entire dataset. Specifically, 03:00 hours was identified as dawn, and 21:00 hours as dusk. This was then plotted against the light data recorded by the tags to validate its accuracy (see Figure 18). By categorizing the data into day and night periods, it was possible to plot depth profiles and examine changes in salmon activity and diel behaviour relative to the time of day. This analysis was crucial for understanding how the salmon's depth preferences varied between daylight and darkness, providing insights into their diel vertical migration. Subsequently, to assess for differences in depth behaviour at night vs day period two approaches were followed. Once the day periods were set from 3:00 hours until 21:00 hours as explained, depth was plotted with this data. Then a percentual time at depth (TAT) histogram dividing night and day periods was done for each individual and two containing averages for series (tag not recovered) and archival (tag recovered) data. 5 meter bins were defined and the percentage of time spent at each depth bin was obtained.

Path linear interpolation

The daily positions between the deployment and pop-up locations were interpolated. This interpolation was performed under the assumption that the tagged salmon moved at a constant pace along a direct, straight-line path between the known locations. The movement of the salmon was modeled as a straight line between the deployment and pop-up points. The time interval representing the total number of days the tag was attached to the fish was divided into equal segments. The position for each day was estimated with the assumption that an equal distance was traveled each day. The interpolated positions were then integrated with the deployment and pop-up positions, into the study area map using QGIS, a geographic information system software.

Environmental Data to evaluate vertical behaviour changes

To visualize the possible influence of mean temperature in mean depth a scatter plot was generated that contained hourly data for each individual followed by the calculation of R^2 and statistical significance.

Subsequently, time at temperature histograms were plotted to visualise possible temperature preferences.

Salinity and temperature data retrieved by the sensors in the tag and Conductivity-Temperature-Depth CTD was analysed against vertical behaviour. To do so, plots showing depth vs time were coloured with different shading representing temperature and salinity (for individual 13) gradients were generated. Since a noticeable behaviour change was noted in individual 13 the plots were divided into two periods. For each period the following metrics were calculated: hourly maximal depth, mean depth, and depth range were determined.

To investigate if the period of the day (night or day) had influenced depth behaviour before conducting analysis based on hourly averages, a Wilcoxon test Rank-Sum (as the normality criteria was not met) was applied to compare maximum hourly depths between day and night within each period. This ensured that when comparing data from the two different periods the time of day did not influence our results.

A Wilcoxon Rank-Sum test was then applied to check if: 1 - determine if there were statistically significant differences between stated depth metrics and 2 – abiotic factors differed as well, so the hourly mean and maximal temperature and salinity between the two periods were also checked for statistical significance. If the p values were $< 0,05$ statistical significance was determined. To test robustness in our analysis minimal depth was tested and in 31% of the repetitions, statistical significance was found.

Since the two periods represented a small sample and uneven distribution (5 and 6 days), a bootstrap resampling was used in the analysis to improve the reliability of the estimates. With a resample size of 72, 72% of the data (equivalent to 3 days from the smaller 5-day set) was resampled with replacement over 1000 simulations. The Wilcoxon rank-sum test was run on each bootstrap sample with a significance level of 0,05 to assess the statistical significance of differences between the two periods, as the data were not normally distributed.

All data was processed and analysed using R version 4.3.2.

Results

Mortality assessment

With a success rate of 57%, 8 of the 14 tags were recovered.

One of the subjects died right after tagging, the following plot shows that it stayed in the same depth, presumably the bottom, since its tagging until tag pop-up with no movement (Figure 15).

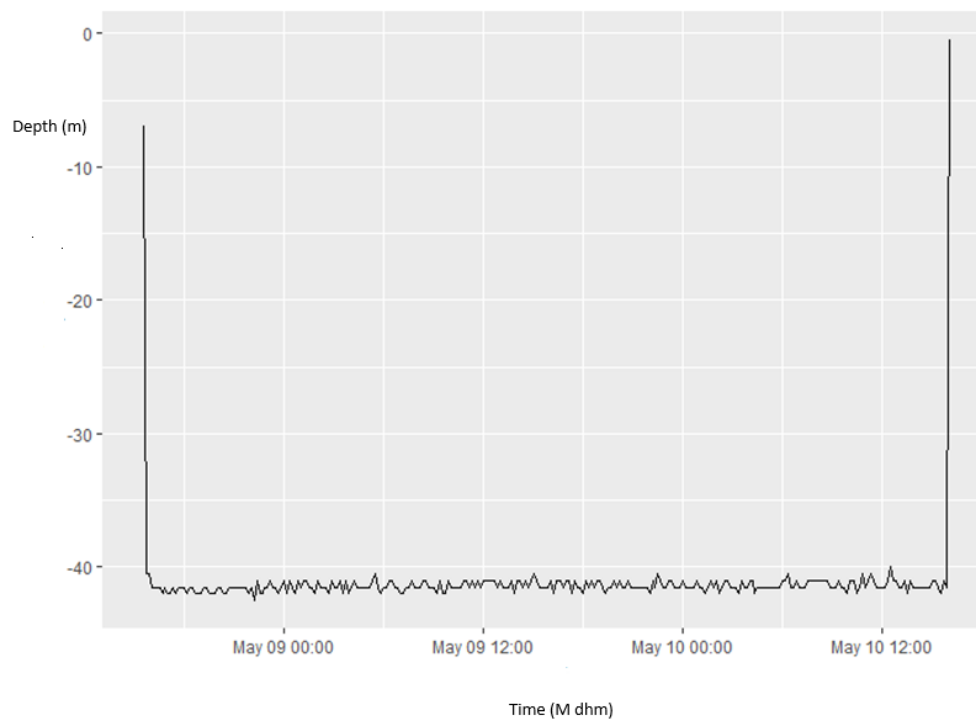


Figure 15 - Plot showing death of salmon 3, through lack of movement in consecutive days. Depth in meters (reversed in Y-axis) over Time.

As individual 3 had a smaller size (76cm) than the observed mean (89cm) and it was hooked deeper (21m) than the average (17m) refer to Table 2, boxplots were made to visually analyse such differences (Figure 16 and 17).

Table 2 – *Salmons' Total lengths (cm); hook depths (m) and relevant meta data.*

Salmon's attributed number	Total length [cm]	Hooking depth [m]	Deployment date	Pop-up date	Time at liberty	Release	Type of tag
1	81	17	2023-05-08	2023-05-24	16	30 Days	sPAT
2	96	12	2023-05-08	2023-05-15	7	30 Days	sPAT
3	76	21	2023-05-08	2023-05-10	2	30 Days	sPAT
4	92	22	2023-05-13	2023-05-20	7	30 Days	sPAT
5	86	29	2023-05-13	2023-05-18	5	30 Days	sPAT
6	87	30	2023-05-14	2023-05-20	6	30 Days	sPAT
7	106	4.5	2023-05-14	2023-05-21	7	30 Days	sPAT
8	83	28	2023-05-14	2023-05-22	8	30 Days	sPAT
9	88	5	2023-05-14	2023-05-23	9	30 Days	sPAT
10	85	26	2023-05-18	2023-05-26	8	30 Days	sPAT
11	76	18	2023-05-18	2023-05-25	7	30 Days	sPAT
12	106	2	2023-05-21	2023-05-24	3	30 Days	sPAT
13	87	13	2023-06-03	2023-06-16	13	45 Days	miniPAT
14	92	6	2023-06-05	2023-06-14	9	30 Days	sPAT
Mean	89	17			8		

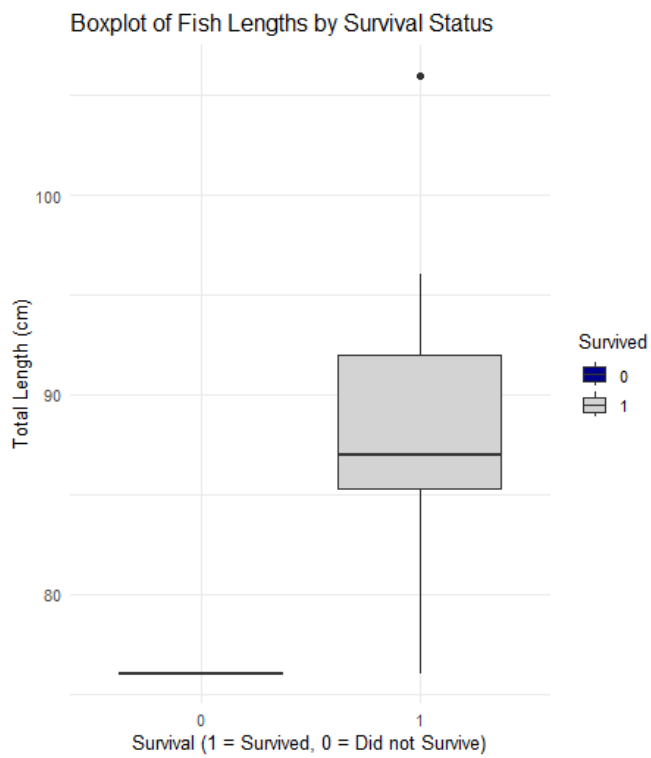


Figure 16 – Boxplot total length and survival.

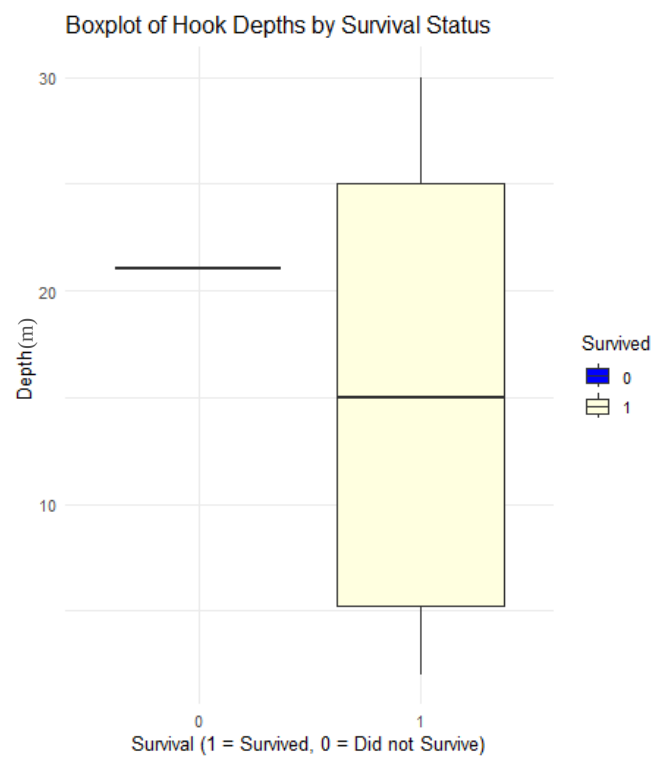


Figure 17 – Boxplot hooking depth and survival.

Both factors differ from the normal distribution when mortality is assessed.

Night and day variations

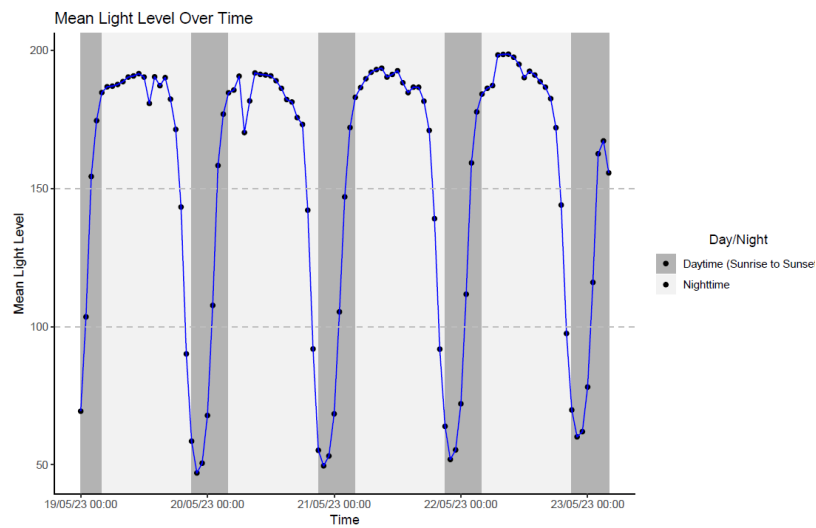
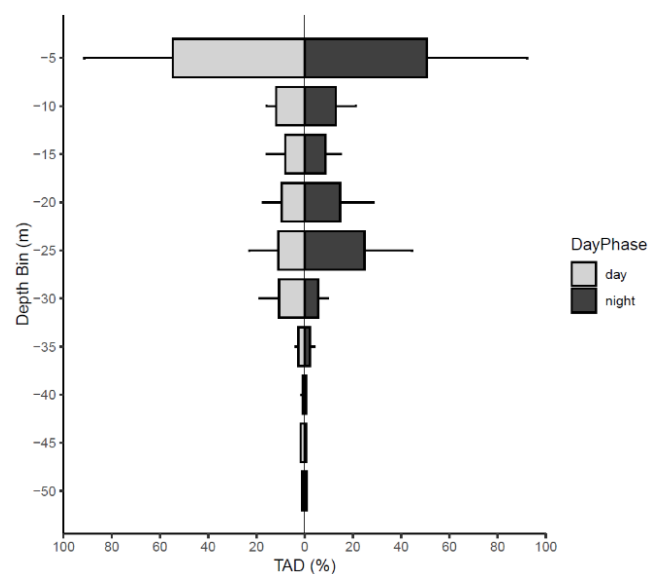
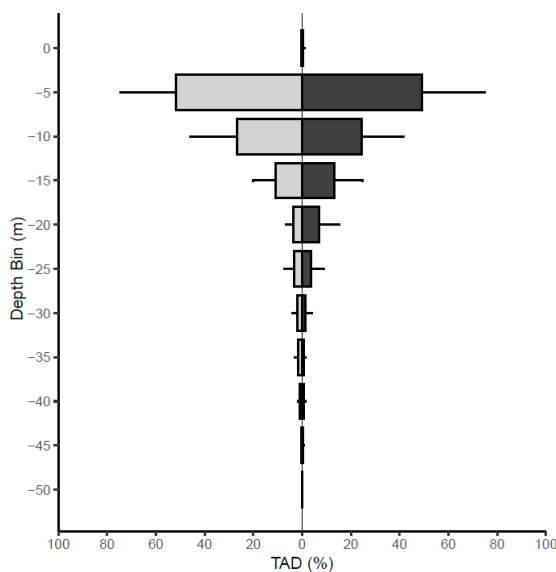


Figure 18 – Light levels measured by the tag (in blue). Day and night intervals represented by the different shadowing retrieved for the study location, through pop-up and deployment coordinates, from the sunlac pack (nautical sunrise at 3 am and nautical sunset at 9 pm).

Overall, there was activity recorded both in day and night periods and the individuals occupied shallower depths of the water column most of the time, with some dives occurring in both periods (check Figures 19 and 20). The fish were mainly found in the first 15 meters:



Figures 19 and 20 – Time at depth histograms showing average occupancy of depth bins in day and night periods, for archival data (Tags retrieved) on the left and series (not retrieved) on the right.

Some salmon had equally distributed patterns with activity and dives in both periods. The individual shown has deep irregular dives up until more than 60 meters, considering the Baltic's bathymetry one can state it is a deep dive:

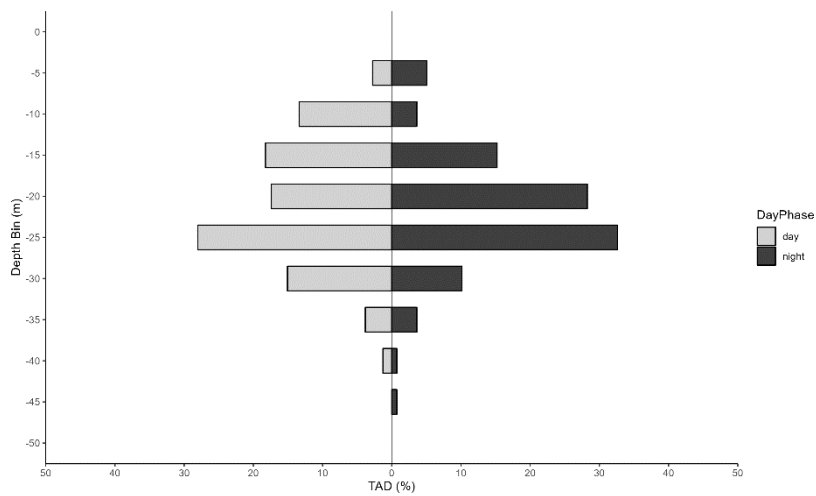


Figure 21 – Time at depth histogram showing similar occupancy of depth bins in day and night periods.

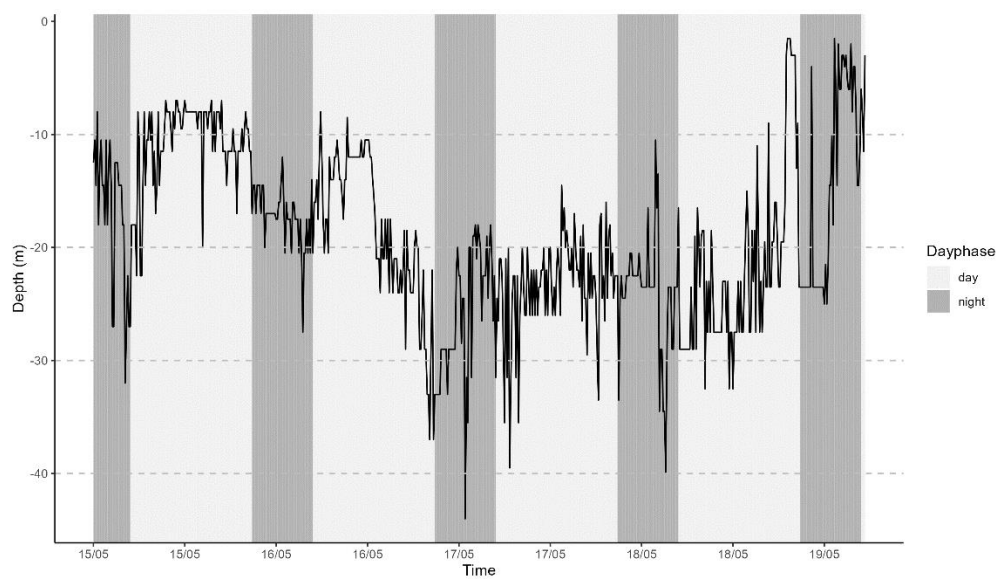


Figure 22 – Depth over time plot for the same individual that displayed activity both in night and day periods. With night and day represented in different shades.

Some individuals were in deeper water layers and dived more frequently during the day:

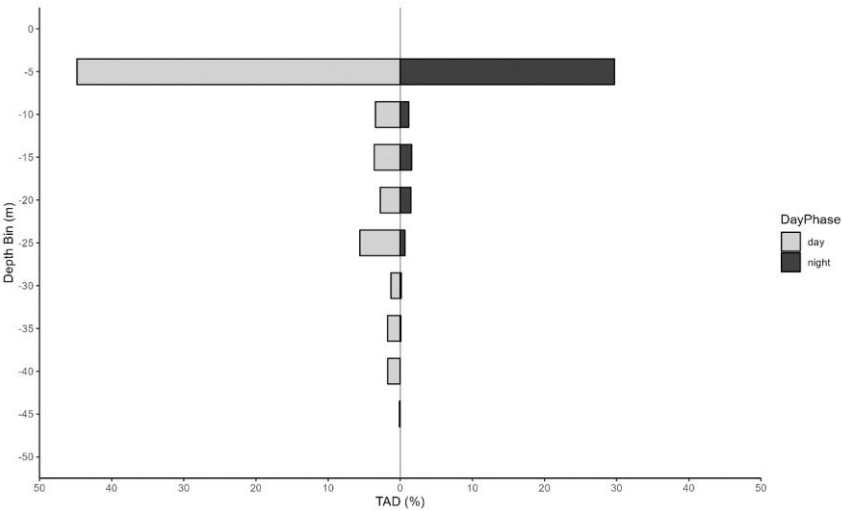


Figure 23 – Time at depth histogram showing larger range of depth occupancy during the day.

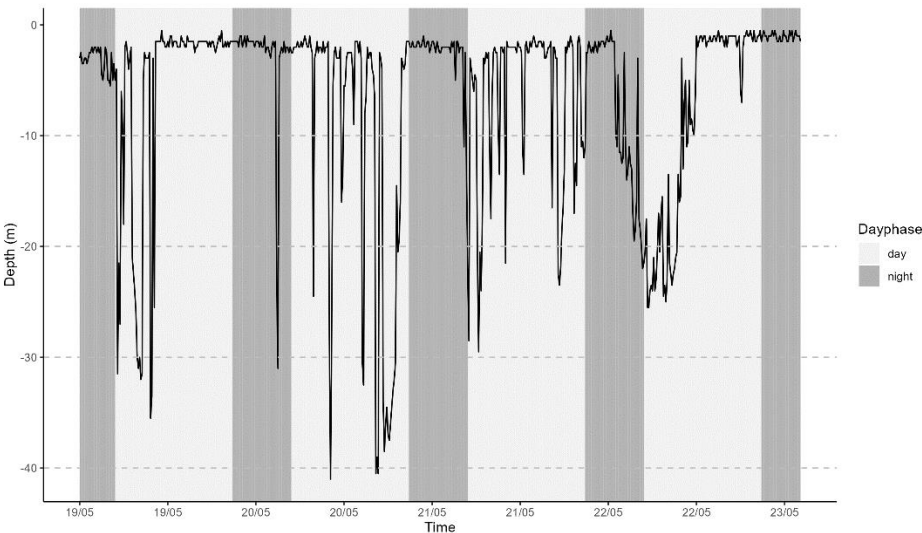


Figure 24 – Depth over time plot for the previous individual with deeper depths in the daytime.

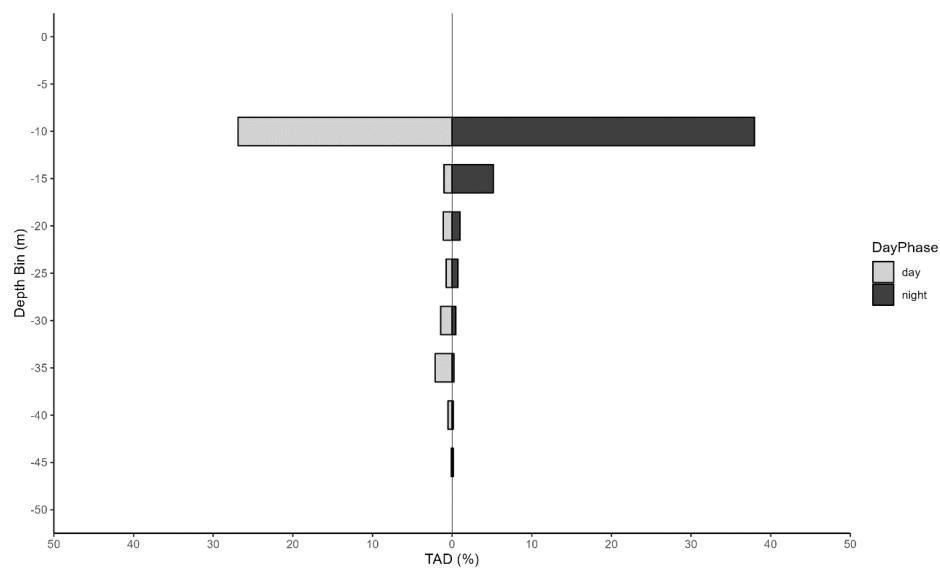


Figure 25 – Time at depth histogram showing a larger range of depth occupancy during the day.

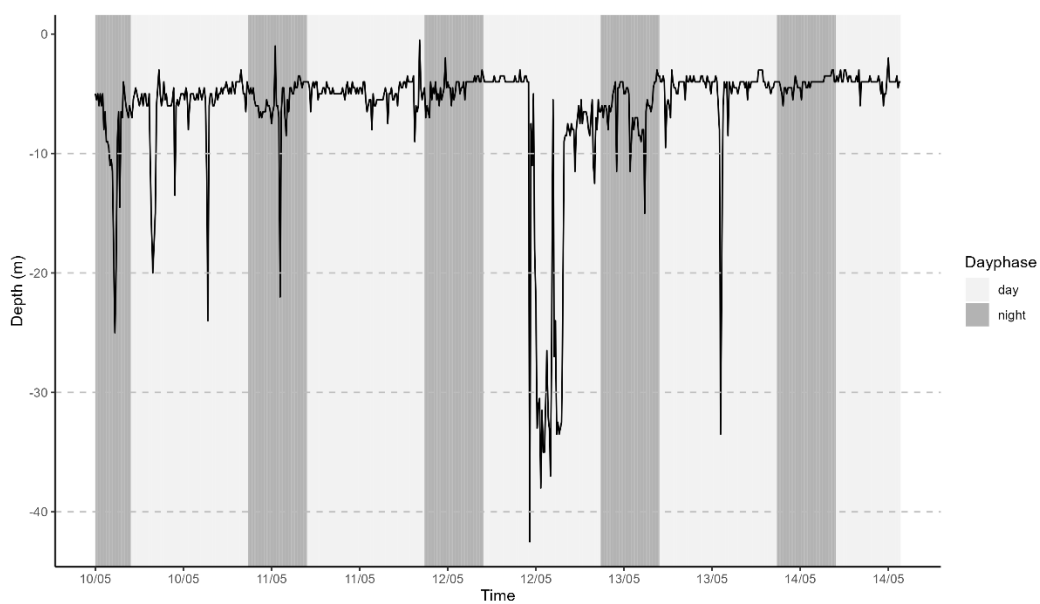


Figure 26 – Depth over time plot for the previous individual with deeper depths in the daytime.

Influence of abiotic conditions

There was an effect of mean temperature on the mean depth of tracked salmon. A negative relationship was observed between these variables as demonstrated by the scatter plot analysis (Figure 27). The increase in mean temperature corresponded to a decrease in mean depth. With an R^2 value of 0.34 indicating that 34% of the variation in depth could be explained by temperature changes. Additionally, the low p-value ($p < 2.2e-16$) shows that the effect is significant (<0.05).

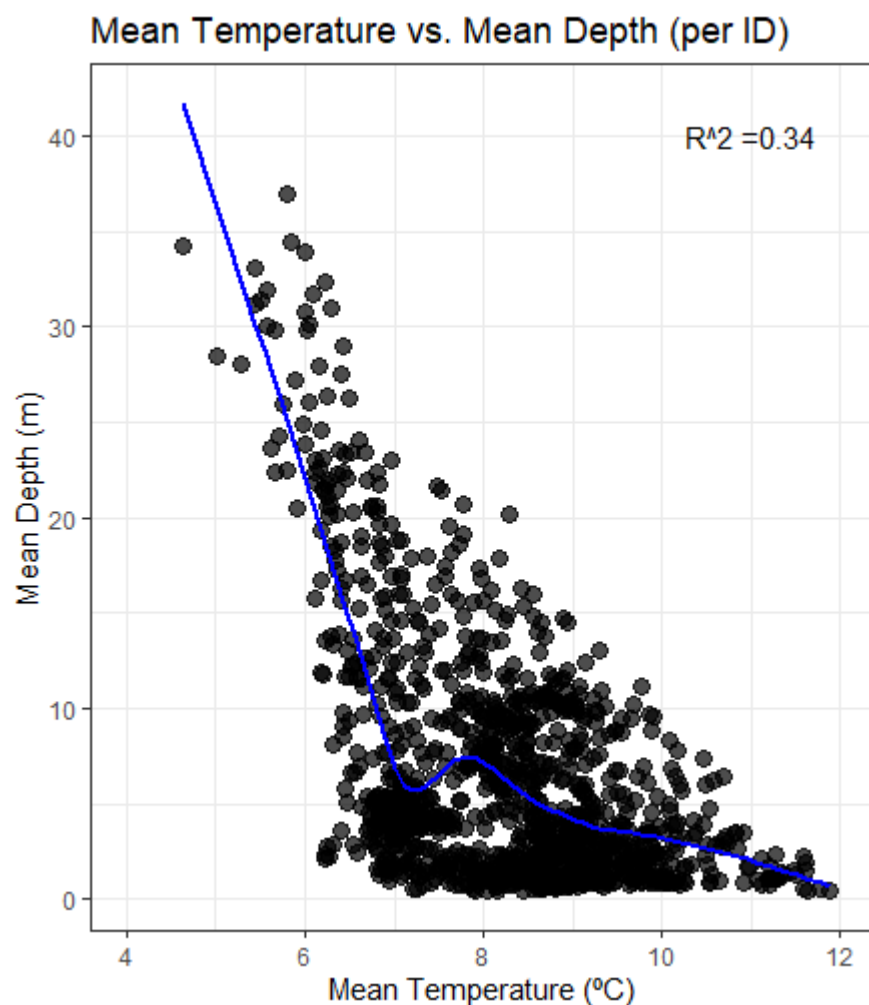


Figure 27 – Scatter plot showing relationship between Temperature and Depth.

This tendency is also visible in the plots showing vertical movement and temperature gradients (Figures 28 and 29):

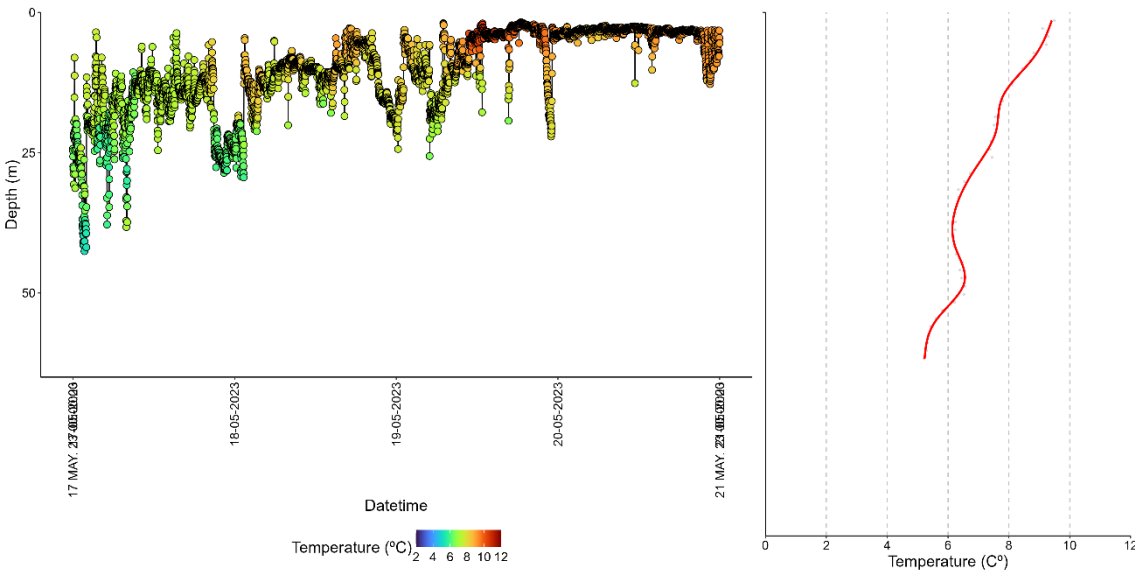


Figure 28 – Depth plot and temperature profile displaying depth with gradient temperature scale and temperature profile.

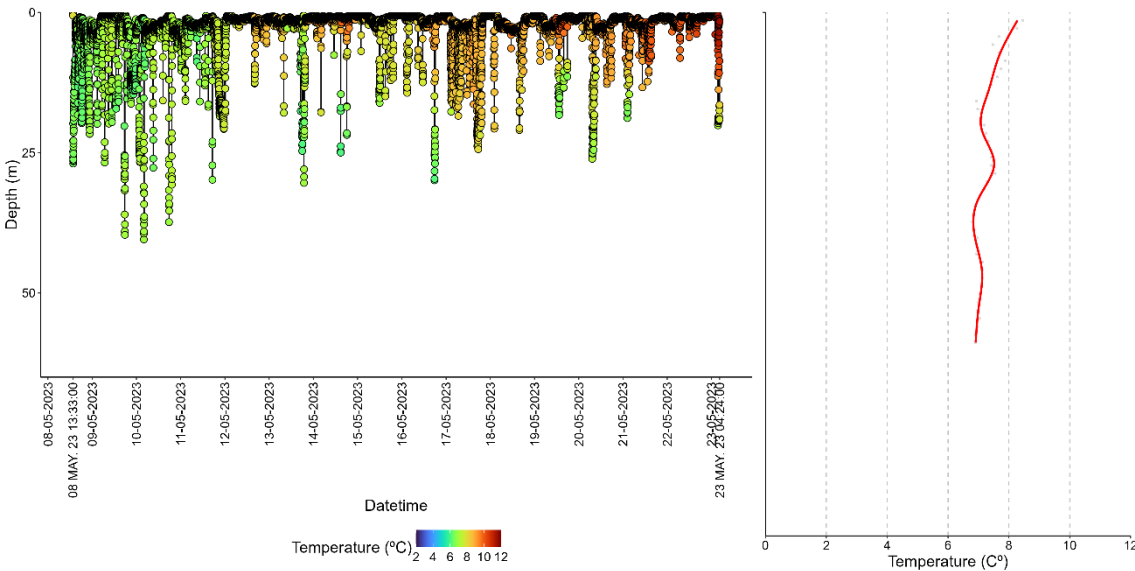


Figure 29 – Depth plot and temperature profile displaying depth with gradient temperature scale and temperature profile.

In general, the individuals preferred to stay between 5°C and 9°C although the temperatures experienced ranged from 1°C to 12°C (Figure 31):

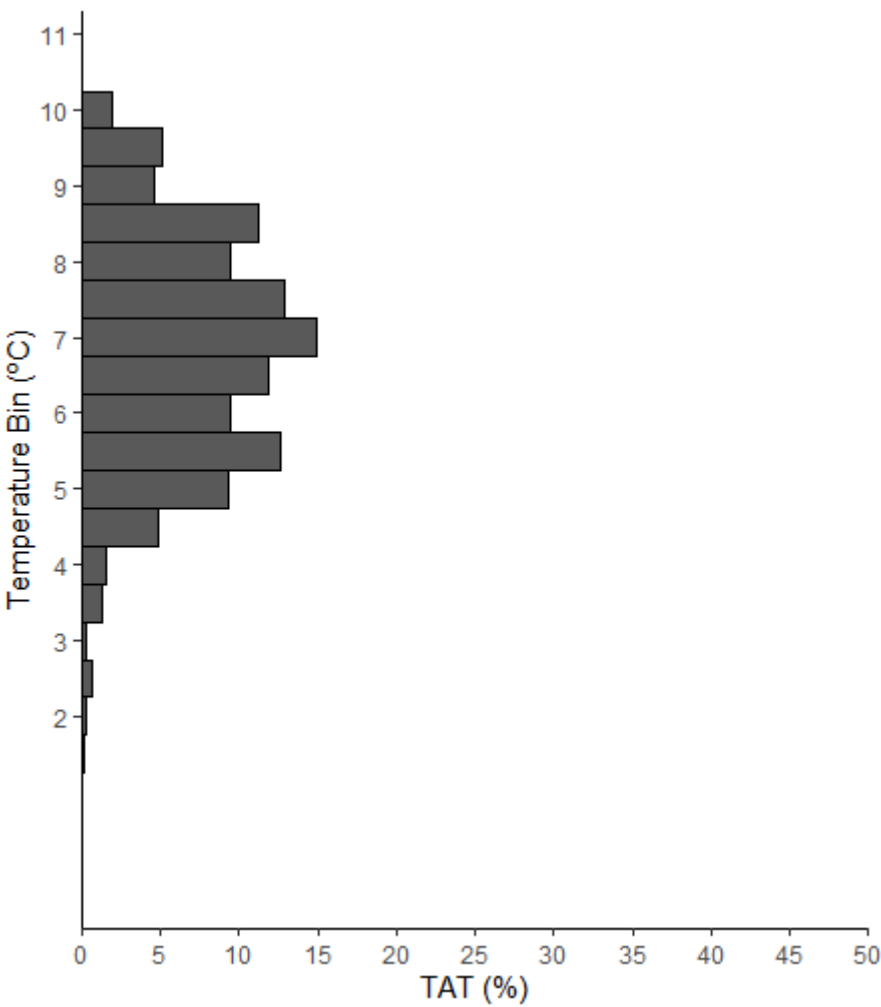


Figure 31 – Time at temperature histogram showing average values for all individuals with temperature measurements.

For salmon 13 two periods corresponding to behaviour changes were defined, separated on the 10th of June as per the following graphs 32 and 33:

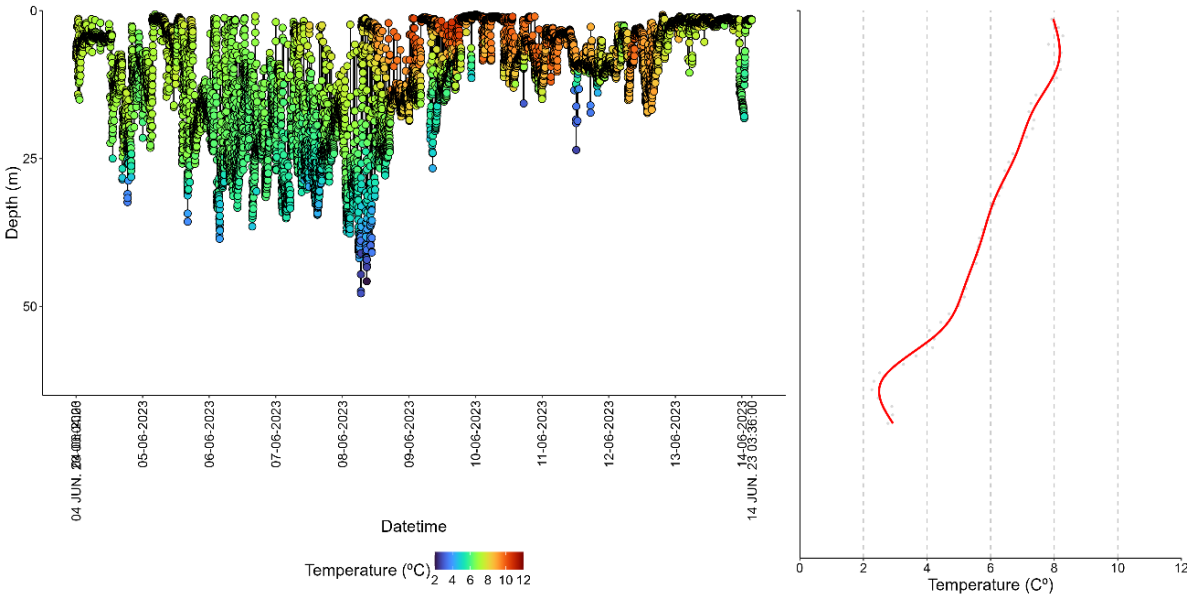


Figure 32 –Depth plot and temperature profile displaying depth with gradient temperature scale and temperature and salinity profile for salmon 13 with disruption on 10/06/2023.

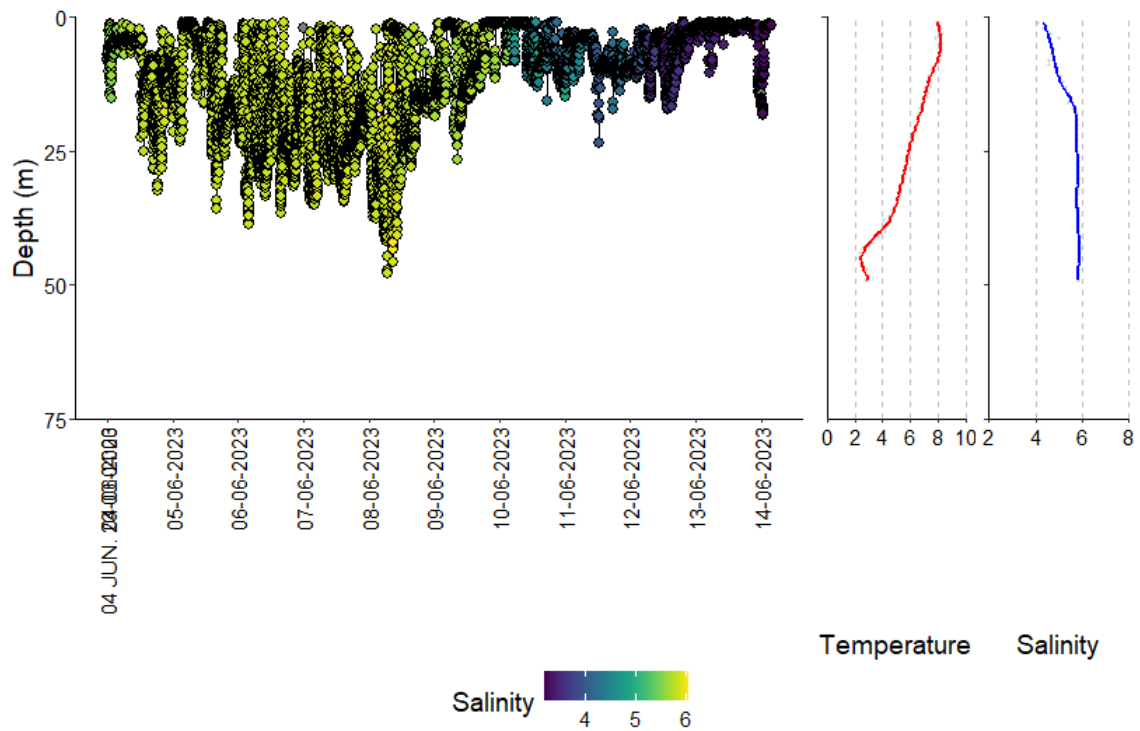


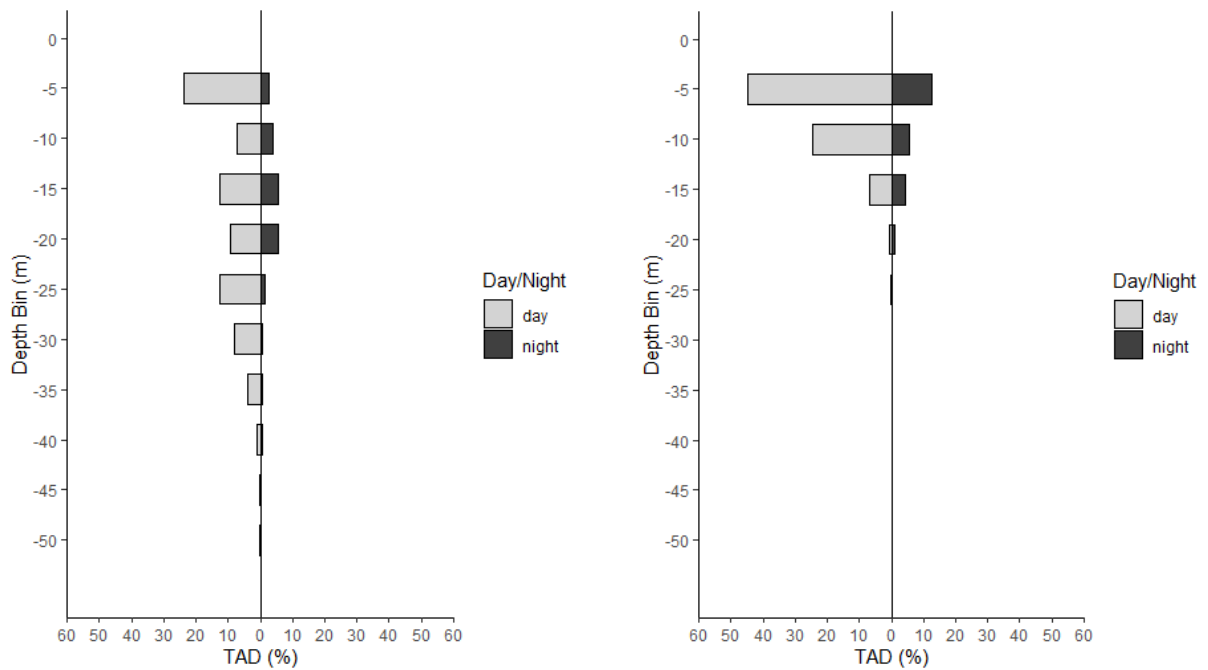
Figure 33 –Depth plot and salinity profile displaying depth with gradient temperature scale and temperature and salinity profile for salmon 13 with disruption on 10/06/2023.

To ensure the time of day was not influencing the animal's behaviour, prior to conducting analysis based on hourly averages, a Wilcoxon test Rank-Sum was applied to compare maximum and mean hourly depths between day and night within each period. No statistically significant differences were found as Table 3 shows.

Table 3 –Wilcox test results for the two periods.

Period	Metric	Day/Night	W- statistic	P- value	Significance
First Period	Max Depth	Day vs Night	1935	0.2693	Not Significant
First Period	Mean Depth	Day vs Night	1744	0.8691	Not Significant
Second Period	Max Depth	Day vs Night	887	0.9935	Not Significant
Second Period	Mean Depth	Day vs Night	788	0.4269	Not Significant

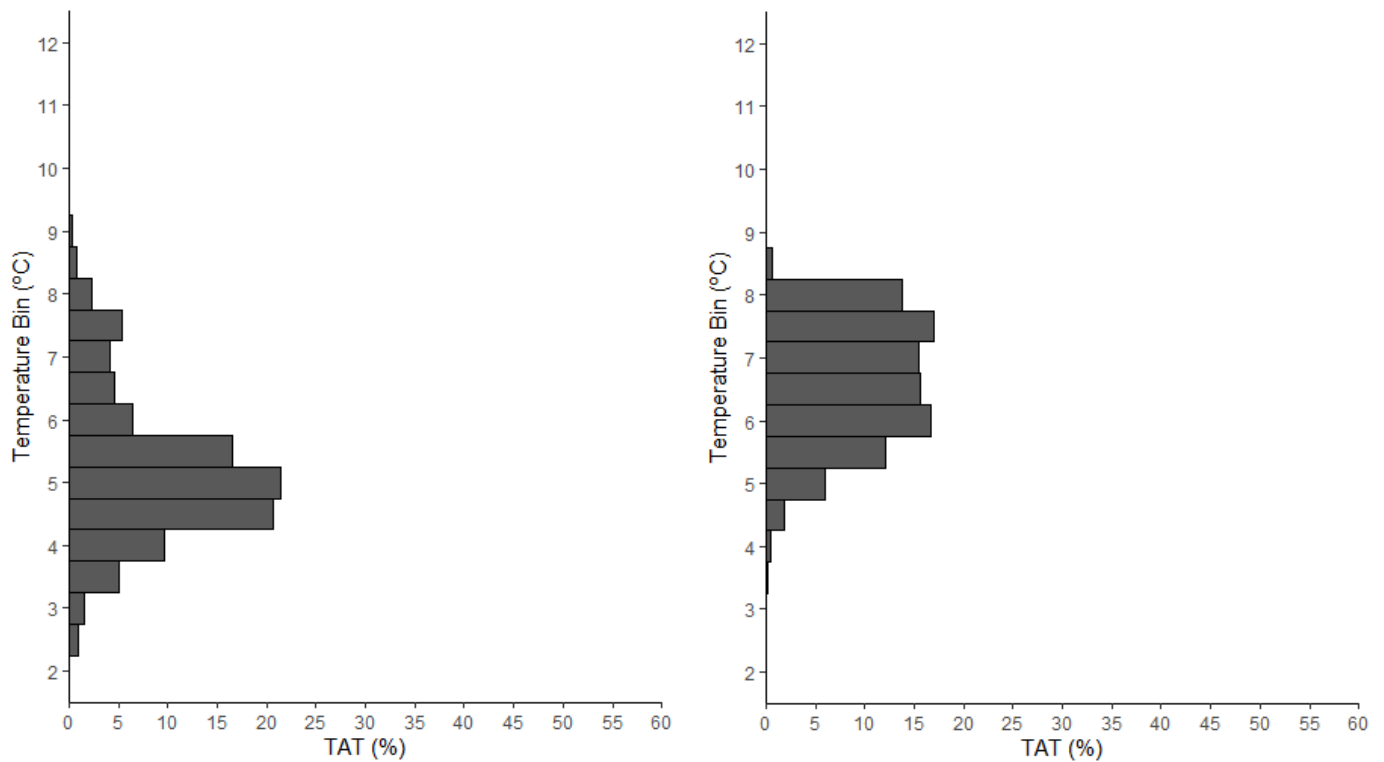
For each period the time spent at each depth in the day and night was visualized on histograms. This clarified that in the second half, the animal did not swim in deeper waters, preferring shallower depths above 15 meters.



Figures 34 and 35 – Time at depth histogram for the first period on the left and second on the right showing a larger range of depth occupancy during the day in the first half of the analysis.

In all the 1000 repetitions included in the bootstrap, statistical significance (p -value $< 0,05$) was found when evaluating: mean hourly depth, maximal hourly depth, depth range, mean hourly temperature, and mean hourly salinity.

To assess variations in temperature preferences, we created percentual histograms of time spent at different temperature ranges (refer to Figures 36 and 37). During the second period, the individual showed a preference for warmer temperatures, with time spent at these temperatures being more evenly distributed. On the first, the salmon was found more frequently below the preferred temperature ranges.



Figures 36 and 37 – Time at temperature histogram for the first period on the left and second on the right.

Since the study was done in the Baltic Sea, an area that offers limitations in the application of light-based geolocation due to the high latitude that obstructs accurate solar positioning, it was necessary to employ an alternative method to estimate the path of the studied animals between the known deployment and pop-up locations of the pop-up satellite archival tags. Maps modelling the sea temperatures at the time of deployment (Figure 38) and pop-up (Figure 39) were accessed in the Copernicus Marine Service (<https://data.marine.copernicus.eu>).

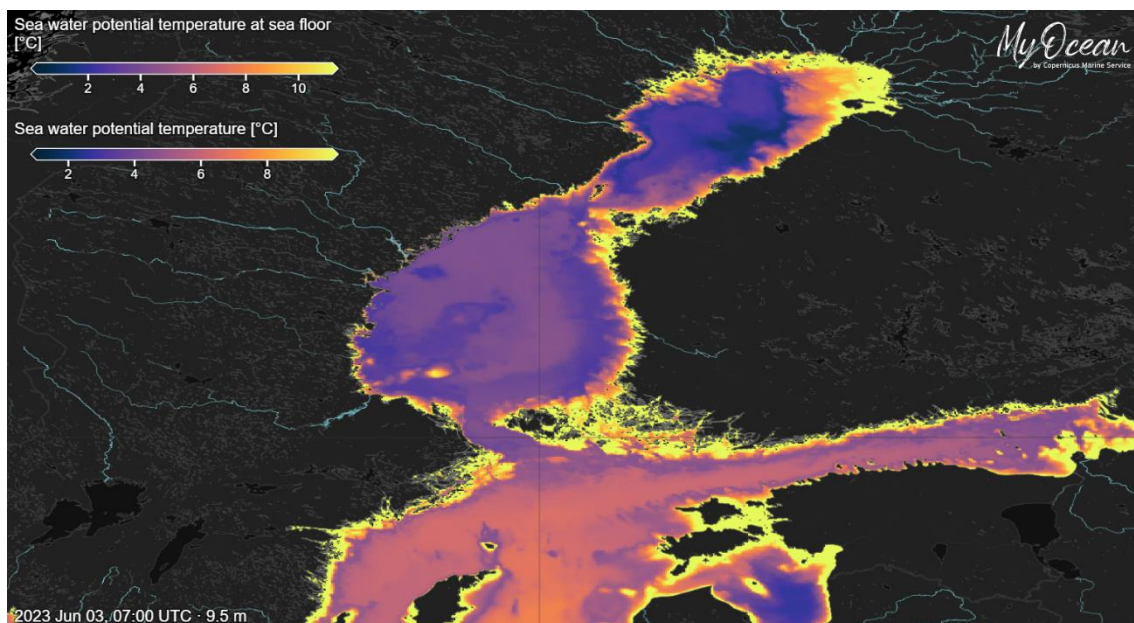


Figure 36 – Copernicus Marine Service model displaying temperature at the time of tag deployment. (<https://data.marine.copernicus.eu>)(Product DOI:<https://doi.org/10.48670/moi-00010>).

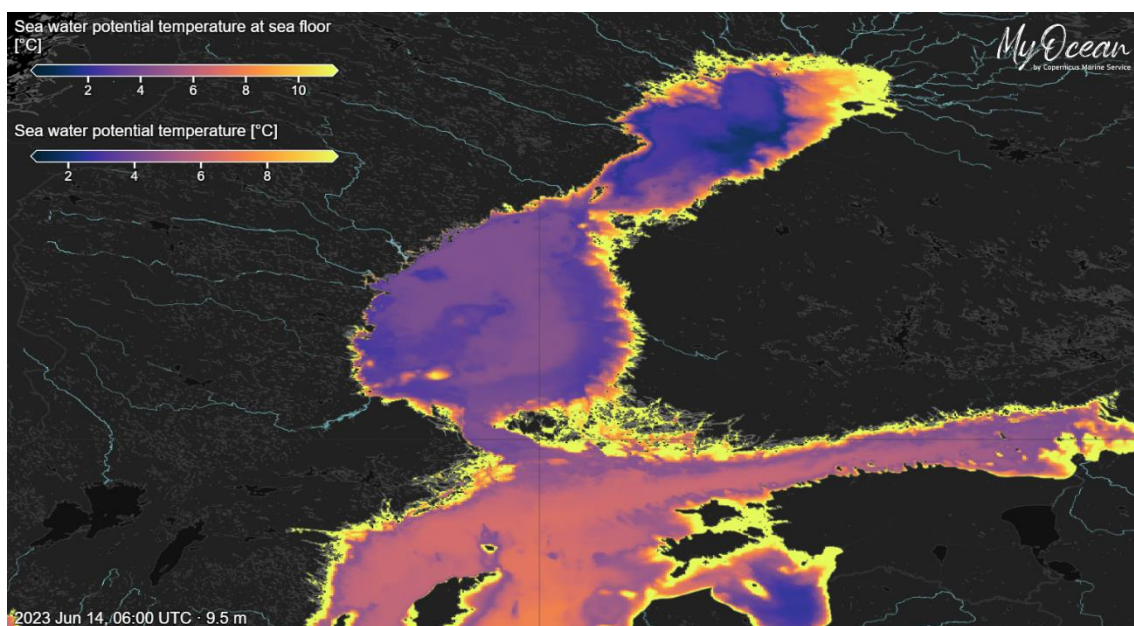


Figure 37 – Copernicus Marine Service model displaying temperature at the time of tag pop-up. (<https://data.marine.copernicus.eu>)(Product DOI:<https://doi.org/10.48670/moi-00010>).

Discussion

Should you catch them if you can?

In the present analysis, one of the fourteen fish (7%) died immediately after release. The same proportion was documented in other papers on *Salmo salar* such as: Havn et al., 2015 and Lennox et al., 2017.

Immediate mortality is defined as mortality during landing, pre-release, or immediately following release (Pepperell and Davis 1999; Donaldson et al., 2008). Short-term mortality is defined as occurring 24h to 72h after release and long-term if it happens more than 72h post-release (Pollock and Pine, 2007). Two other tagged fish died (fish 1 and 9 from table 2), however, the deaths occurred 15 and 7 days after tagging. According to the above cited references, these deaths were considered long-term mortality, likely due to natural causes. Especially as handling time was minimised to the lowest possible during the tagging since air exposure and handling time lead to compromised survival for salmonids such as rainbow trout (Bartholomew & Bohnsack, 2005) and only fish bigger than 60cm were tagged.

Post-release mortality in this species has been examined in several reviews as discussed further, with mortality rates found to be relatively low compared to other species, where rates can reach as high as 88% (Hühn and Arlinghaus, 2011; Stålhammar et al., 2012). Other salmonids have a comparably low mortality rate as the proportion described in this work nonetheless, as mentioned, mortality varies immensely in different species as size, robustness, and physiology can be determining factors. In some species, there was an inverse relationship between size and mortality, for Chinook salmon (Bendock & Alexandersdottir, 1993) and lake trout (Loftus, 1986) mortality increased for smaller individuals. For striped bass (Malchoff and MacNeill, 1995) and nonanadromous trout (Taylor and White, 1992) the opposite was true. For some salmonid species like rainbow trout, spotted seatrout, and cutthroat trout no size-related differences were reported (Pauley and Thomas, 1993; Murphy et al., 1995; Schisler and Bergersen, 1996). For pike, salmon's predator in the Baltic and affluent rivers, the mortality rates reported are also low, staying below 10% (Burkholder, 1992; Arlinghaus et al., 2008). However negative effects on foraging - as physical condition decreased coupled with amplified avoidant behaviour learned from the negative experience - were described (Stålhammar et al., 2012).

With mortality rates generally ranging between 0% and 8% (Booth et al., 1995; Whoriskey et al., 2000; Dempson et al., 2002; Thorstad et al., 2007; Halttunen et al., 2010; Jensen et al., 2010 and Gargan et al., 2015) studies on Atlantic salmon show the species resistance to angling events. It has also been observed that Atlantic salmon show learned hook avoidance behaviour after capture events (Lennox et al., 2015) as does its predator, pike

(Stålhammar et al., 2012) and, even though recapture does exist recapture rates are higher if different gears are used (Lennox et al., 2015). Whoriskey et al. 2000 observed fish that were angled three times in a river in Russia which on the one hand contradicts this learning possibility for some individuals but on the other hand, stands for their resilience to C&R. Despite the extensive literature on salmonids, the previously mentioned research differs from this study both in the choice of tags and in the study area. The majority was conducted in North America, a proportion used cages instead of natural conditions (Gargan et al., 2015) and various were in freshwater. Also, the previously mentioned papers worked with radio or acoustic tagging. Thus, the study of C&R mortality of Atlantic salmon in the Baltic Sea employing PSATs was, to our knowledge never previously done.

In the Baltic Sea, as discussed before there were no found studies conducted to analyse the post-release survival of salmon. However, when addressing the reproductive success of its anadromous predatory fish the pike in the area Flink et al. 2021 did not find a relation between the increased stress induced by angling and egg viability or quality, spawning arrival timing, and maturity stage. Nevertheless, a different paper on bass reproduction post C&R events noted contradicting tendencies as C&R resulted in nest abandonment and therefore reduced reproductive success (Suski et al., 2003).

Of the fourteen fish caught in the Baltic Sea the only one that died was fished with a single hook opposing to the other thirteen hooked using a triple hook. Which perhaps led to deeper injuries, in fact when the individual was brought to the tagging box it was already lethargic and showing signs of compromised health. Bartholomew & Bohnsack 2005 reviewed previously published analyses on the factors leading up to death after C&R events hooking location, the type of hook, and whether it was removed or not were the central determinants of survival. The type of gear, fishing method, and kind of bait might lead to hooking in life-threatening locations like the gills, esophagus, brain and gut. The shape of the hook may lead to a deeper lodge of it in the animal, as such J-hooks cause more damage than circle ones (Cooke & Suski, 2004) that fixate in fish mouth corners (Bartholomew & Bohnsack, 2005). Similarly, removing the hook led to higher mortality in rainbow trout (Schisler & Bergersen, 1996) as doing so often results in further injuries. However recent studies done on other species such as the threatened eel *Anguilla rostrata* show no difference in cutting the line or removing the hooks (Litt et al., 2020). In our work the hook was not forcibly removed in any case.

The subject that did not resist the injuries was hooked at a deeper depth than average (Table 2), which resulted in added fighting time. This demise could be explained by higher mortality levels formerly linked to excessive exercise (Wood et al. 1983). In fact, after

analysing muscle lactase levels Booth et al., 1995 reported a peak level following angling. In this event since the individual in question was fighting for a longer period, the level of lactase must have been higher than the other surviving fish. The same was true for other fish species as increased depth resulted in increased mortality for red grouper (Wilson and Burns, 1996) and black sea bass (Rogers et al., 1986; Collins et al., 1999). To these and other species the barotrauma resulting from the subsequent expansion of the swim bladder poses as a frequent cause of death resulting from catch. Physoclistous fish do not have a connection or duct between the organ and the intestinal tract making them more vulnerable to barotrauma (Stallings et al., 2023). Swim bladder expansion can cause internal injuries, such as the intestines protruding through the anus, the stomach being expelled through the mouth, and the eyes being pushed outwards (Bartholomew & Bohnsack 2005). To enhance survival a common method used is venting, where a puncture with a hollow needle serves as a canal to the exterior allowing gas release. Despite its popularity, the technique is not always efficient and can result in internal injury (Wide, 2009). A recently exploited and evidently more effective method is recompression, with the use of weighted descending devices the fish are returned to higher depths. Stallings et al., 2023 found that even when released at depths shallower than those of capture, the fish had higher chances of survival when compared to the former venting methods.

Atlantic salmon being physostomous fish can fill their swim bladder by gulping air from the surface, which makes them less affected by barometric changes (Macaulay et al., 2020).

When addressing mortality, an especially vulnerable group would possibly be kelts, post-spawning individuals that could be more prone to suffer from the stressors associated with catch-release since the energy required to spawn and the starving period results in lower fitness (Brobbe et al., 1996). However, in two studies with kelts 0% (Brobbe et al., 1996) or low (Halttunen et al., 2010) mortalities in this group were documented. Nonetheless, Brobbe et al., 1996 verified three fatalities in salmon entering the river to spawn post-angling. Even though, these fish had more energy reserves this led to longer fighting periods which is connected to lower survival rates (Wood et al. 1983). Halttunen et al., 2010 documented low mortality rates even with the stated lower body condition. Fish were in river conditions at a temperature between 3-12°C with a control group – fish that had been previously tagged months earlier and thus deemed unaffected by tagging. Other research shows that these temperatures might have influenced these low rates as Dempson et al., 2002 also conducted the study in freshwater in small fish, total length below 63cm, and a control group where the fish were caught in traps, kept in cages and exposed to tagging and handling as the experimental group, none of these individuals kept in the control conditions died. In this study, temperature appeared to be the only abiotic factor influencing

survival as higher temperatures (higher than 18°C) resulted in higher mortality rates. In fact, temperature variations are a factor conditioning survival for many species as rainbow trout (Wydoski et al., 1976) and striped bass (Tomasso et al., 1996) showed reference blood levels alterations (e.g. high levels of glycemia, cortisol and lactase) in response to higher temperatures. This could be explained by the decrease in oxygen dissolved in the water and higher susceptibility to diseases (Bartholomew & Bohnsack 2005). Indeed, for Atlantic salmon warmer water temperatures lead to increased mortality rates in other previous studies (see Wilkie et al., 1996,1997; Anderson et al., 1998). Especially when it rises over 18° C (Havn et al., 2015).

Since this analysis was conducted in the spring, between May and June, the temperatures fell below such threshold (see Figure 31) preventing any sublethal effects. Nonetheless, the Baltic Sea surface temperature (SST) can overcome 20°C in the summer months (Siegel et al., 2015) consequently, it could be a relevant comparison for future work. As some salmon stay in the sea for a year or more or might be still migrating during these warmer months (Jonsson et al., 1997) and if fished by anglers it would be expected that the mortality rates would rise. Additionally, rising water temperatures from climate-linked ocean warming will likely shift the onset of the 18°C threshold to an earlier point (perhaps even in the spring), overlapping the salmon sea migration phase. The Baltic Sea is especially susceptible to warming due to its shallow depth (CIT). In fact, when analysing regional patterns Belkin 2009 found that from 1985 until 2006 the warming rate in this sea surpassed 1° C per decade, at a rate 3 times faster than the global trend.

Past research using control groups e.g. Jensen et al., 2010 to determine C&R mortality and migratory behaviour deployed external radio transmitters on 117 Atlantic salmon, 10 of these previously tagged subjects (total length similar to this study, between 86-102cm) were caught and released by anglers whereas the remaining fish posed as the control group, no differences in mortality or migration were found between the two groups. For Thorstad et al., 2003 and 2007 studies on freshwater specimens, even though the mortality rate was 0% the catch and release events appeared to delay spawning migration or alternated migration patterns as fish displayed up and down migrations along the river stream. Regardless, egg viability in *Salmo salar* (Booth et al., 1995) and other salmonids seems to be unaffected by the stress induced by C&R (Pettit, 1977; Smukall et al., 2019; Flink et al, 2021). Our results show that long migrations occurred following release. In fact, this was validated by a video of a salmon in a fish ladder in river Byske, Swedish Lapland since the only fish tagged with PSATs were tagged during this project this image sustains the data acquired through tags (check Figure 38). Other papers on *Salmo salar* migration after C&R events corroborate our findings (see Jensen et al., 2010). In Figure 5 are the deployment

and pop-up coordinates for each individual, the ones tagged in the northmost locations appeared to have migrated more even though the other group also showed migratory behaviour. As discussed before, Atlantic salmon shows different migratory behaviours in and between populations as staying in the sea comes with better feeding opportunities some individuals do so for longer periods of time (Alm, 1934; Svardson and Fagerstrom, 1982, Kallio-Nyberg et al., 2006). In addition, it has been shown that populations from northern rivers tend to migrate more as they move to the south portion of the Baltic basin (Jacobson et al., 2019).

When studying the effects of catch-and-release on species such as salmon, particularly considering the methodology of this study, the impact of tagging should not be overlooked. External tagging was the best fit in this case as it allows for environmental variables to be measured additionally, it is a fast method (Jepsen et al., 2015). However, the tag's attachment exposes the fish to additional stressors, explicitly extended handling, and prolonged time on the boat. Increased predation and changes in social interactions might equally be at risk. Also, a possible window of infection is opened through the anchoring wound, as tissue damage is a frequently reported issue (Jepsen et al., 2015). Since the current study was done on wild animals, with pop-up satellite tags the effects of tagging and catch-and-release might be intertwined. Previous research showed that even though dives and return migration still occurred, when compared to internally tagged salmon, the fish with PSATs were slower, dived less, and to shallower waters (Hedger et al., 2017). A possible approach to address the stress level related to the tagging procedure and thus observe more concretely the effects of C&R, would be to examine a blood sample collected pre and post-tagging that could provide biomarkers such as cortisol or glucose that would later be compared to reference levels (Rozas-Serri, et al., 2022). If a significant increase after tagging was observed then the elevated level of stress-related hormones in the bloodstream could be linked to the tagging procedure and not the fishing practices (Casanovas et al., 2021). However, increased stress might not represent altered behaviour, and stress resulting from angling alone might not be prominent as determined by Booth et al., 1995. In their study, they quantified plasma glucose, counted as a significant indicator of stress in fish, post-catch, and recounted negligible changes in comparison to base levels. An alternative method could involve maintaining a control group of fish in cages post-angling, where the fish are captured and released into these cages without the tagging procedure as employed in previous studies (see Dempson et al., 2002).

Too hot to handle?

The surviving individuals continued their migration journey, the two that were tagged in the north close to Stockholm showed extensive horizontal migration, with the last locations (pop-up in Figure 5) close to Lapland. Understanding how abiotic conditions might be influencing animals' movement behaviour is crucial to comprehend triggers and variations, to predict how they will respond to environmental changes, and properly plan and manage species (Hellström et al., 2022).

When examining salmon depth patterns, we observed that the studied fish spent most of their time in the first fifteen meters of the water column (see TAD% in Figures 19 and 20). This preference was reported in other studies on the species, Strøm et al. 2018 and Hedger et al., 2017 documented that all individuals were in the tenth upper meters 67% and 82% of the time, respectively.

Regardless, vertical movement with some individuals showing more frequent and deeper dives during the day was seen in our study (check individuals in Figures 23 and 24, and 25 and 26). Usually, vertical movements can be related to searching and foraging behaviour (Strøm et al., 2018), natural and artificial light (Juell & Fosseidengen, 2004; Riley et al., 2012), temperature regulation (Brill et al., 1999; Einarsson et al., 2018) and prey avoidance (Valdimarsson et al., 1996). These variations in occupancy of the water column can be dependent on day and night shifts with several species preferring to stay deeper in the water column during the day and the opposite at night. This behaviour is described as Diel Vertical Migration (DVM) and although less frequent, the inverse situation also occurs with animals occupying shallower depths during the daytime (Sims et al., 2005; Arostegui et al., 2017). Previous studies have shown that DMV in *Salmo salar* is typically season-dependent and happens in fresh and marine water stages. As ectotherms salmon are less active in the winter with increased activity during the night in comparison to the daytime, this behaviour has been explained as a predator avoidance tactic coupled with the fact that food resources available for the salmon are not significantly different between the two periods (Valdimarsson et al., 1996). As the low temperatures of the northern winters reduce their ability to escape, they become easier prey for endotherm predators like seabirds, and seals (Suuronen & Lehtonen 2012) if active during the day. In addition, the decreased light intensity in the waters along with the physiological alteration in their retina in the winter - an increase of porphyrins in proportion to rodopsins leads to better night vision (Fraser et al., 1993) - results in escaping its visual hunter more efficiently, the pike. Moreover, these behaviour shifts result in lower energy demands that can be fulfilled during the night, so these fish choose the winter darker hours to forage as it provides safer conditions

(Valdimarsson et al., 1996). In the summertime, the previously nocturnal Atlantic salmon leave the gravel and its hiding locations and forage in bright daylight (Rimmer et al., 1986). DVM with Atlantic salmon displaying more activity in the day periods during their marine stage has been documented several times. Einarsson et al., 2018 and Davidsen et al. 2008 reported DMV in all studied subjects with irregular occasional dives and deep dives in some cases. Also, a negative relation between light intensity and swimming depth was observed, with most fish choosing to swim closer to the surface and diving in the first six meters of the water column. Additionally, similar patterns were described for other salmonid species such as rainbow trout (Contor & Griffith, 1995).

With their work, Gregory & Griffith 1996 and Riley et al. 2012 showed that this is not an innate behaviour related to the circadian rhythm but in fact, a response to light alterations. The first authors connected ice coverage and turbidity with the number of fish hiding. The latter authors studied the influence of artificial light on migration patterns noticing random migrations if artificial light was incident on the water column. As opposed to when the light was turned off and the fish migrated similarly to the control group.

In our analysis, DVM was present with individuals going into deeper waters during the daytime i.e. Figures 24 and 26. Yet not all fish displayed this behaviour as some were active during the day and night (see Figures 21 and 22) with an overall TAD percentage spent at each depth similarly distributed through the day and night. Thus, on average, it appears to be vertical activity at all hours of the day as graphs - check Figures 19 and 20 - shows. As spring is a transitional period with long periods of light and short night periods, especially in the study area as it is clear in Figure 18, these light patterns might have resulted in the long periods of activity displayed by some fish. Moreover, the individuals were likely undergoing their feeding migration before spawning (Kallio-Nyberg et al., 1999; Thorstad et al., 2011 and Einarsson et al., 2018), as such dives could be associated with foraging. In fact, an increase in foraging would be expected as energy reserves should be filled before reproduction and the fasting ahead. In the Baltic, salmon feed mainly on herring, pelagic fish that show DMV behaviour, aggregating in the bottom during the day and dispersing at the surface during the night (Cardinale et al., 2003). Thus, these patterns would be in line with possible foraging as reported previously (Einarsson et al., 2018).

Additionally, fish occupying the same geographical area displaying individual adaptations consequence of different life stages or to improve fitness have been reported previously and are characteristic of the species (Thorstad et al., 2011) so as some might display DVM patterns others showed a more incoherent pattern.

The archival tags gave us data on temperature along with depth and light alterations. Therefore, investigating how temperature, an important abiotic condition in an ectothermic

animal's life cycle (Valdimarsson et al., 1996), could have influenced vertical variations was a logical progression in this research. When analysing time at temperature histograms the study group preferred to stay between 5°C and 9°C, ranging from 2°C and 12°C (see Figure 31). This is consistent with previous observations where individuals from the same species chose 6°-15°C (Guðjónsson et al. 2015) and 8°C to 12°C (Friedland et al., 2000; Einarsson et al., 2018).

We found that temperature influenced depth as higher temperatures were linked with decreased mean depth (see Figure 27). The animals displayed a reduction in depth range and maximal and mean depth as temperatures rose. This pattern is consistently observed in several individuals, as shown in Figures 28 and 29. In other studies, foraging behaviour is inversely influenced by temperature in both marine and terrestrial experiments (i.e. Jayatilaka et al., 2011 and Nowicki et al., 2012). Some ant species rely on temperature as a cue to initiate foraging choosing to do so within their optimal thermal range (Jayatilaka et al., 2011). Whereas for coral fish food intake and foraging decreased with augmented temperatures (Nowicki et al., 2012). As the efficiency of aerobic behaviours is directly influenced by the cardiovascular system's ability to transport oxygen to the muscles (Farrell, 2009; Pörtner et al., 2005), when water temperatures rise beyond a species' thermal ideal range this oxygen delivery to the organs and muscles becomes less effective, resulting in reduced physical performance (Beamish, 1981; Brett, 1971). Elevated temperatures can therefore weaken the ability to perform key behaviours such as seeking and preying. So, in a cold water species that relies heavily on environmental thermic conditions (Valdimarsson et al., 1996) a similar response could have succeeded to reduce metabolic stress.

Nevertheless, this association might not explain the behaviour response. Since, as stated the study is conducted in a natural environment, one should not rule out the possible influence of other external and internal factors. Additional abiotic conditions not considered in this study could have weighted on the change as often animals respond to the environment and not an isolated variable (Wong & Candolin, 2015). In fact, it has been shown that migratory behaviour can be affected not only by natural and artificial light (Juell & Fosseidengen, 2004; Riley et al., 2012), and temperature as discussed but also by some anthropological pollutants such as those found in anti-anxiety medication, namely GABA_A receptor agonists. Since salmonids have the same receptors for the drug diluted in the water, migration intensified as fish that express bold personality traits tend to be more prone to horizontal migration (Fahlman et al., 2016). With the study area being susceptible to human pollution (Ehlers, 2002) the influence of chemicals and drugs diluted in the water should not be excluded.

Alternatively, as salinity in the Baltic affects prey distribution, salinity gradients may help explain why salmon from mixed populations tend to aggregate in certain locations to feed (Chaput, 2012). According to the map in Figure 5, individuals tagged in the south remain close to that geographical area, likely due to higher food availability as herring migrate southward to spawn in nursery areas at sea (Nielsen et al., 2001). However, being an anadromous species, salmon are adapted to cope with salinity changes as they migrate between freshwater and saltwater. As such, their body composition (Krogdahl et al., 2004) and the metabolic capacity of their kidneys and gills (McCormick et al., 1989) are not significantly altered.

Salinity data was available for one of the individuals tagged with a CTD sensor, which revealed a behavioural change occurring simultaneously with a temperature shift (see Figure 32). We examined the salinity profile to determine whether any alterations in salinity coincided with this behaviour and temperature shift. Visual inspection indicated a salinity change during the same period (refer to Figure 33). Additionally, a statistically significant difference in salinity, temperature, and various depth metrics (maximum depth, mean depth, and depth range) was observed between the two periods.

These changes in abiotic conditions may help explain the contrasting behaviours. However, the increase in water temperature during the south-to-north migration was unexpected, as it contradicts the anticipated temperature gradient (Ehlers, 2002)

On closer examination, the tag's pop-up location was near a river, suggesting that freshwater inflows could explain the higher temperature and lower salinity in this region. This likely indicates the individual moved into or near a freshwater stream or remained close to a river mouth, where such changes in environmental conditions are expected (Ojaveer et al., 2010).

As per map analysis (Figure 5), the individual was close to a river that flows into the Baltic at the time of the pop-up which is coherent with the hypothesis that the behaviour change was linked to a change in environment. After the pop-up event a salmon with an attachment lacking the tag was spotted on a fish ladder in river Byske, a connecting river to the one found close to the pop-up location (see Figure 38).



Figure 38 – Salmon with tag attachment on a fish ladder located in a northern river close to the pop-up location.
Image from a video on: fiskdata.se

To further investigate this assumption, the sea temperatures at the time of deployment (Figure 36) and pop-up (Figure 37) were observed in a highly detailed model from the Copernicus Marine Service (<https://data.marine.copernicus.eu>). In line again with our proposition, the warmer areas are close to the shore which would help explain why there is an increase in temperature as the fish moved north. When comparing TAT% plots between the periods (Figures 36 and 37), the first half shows an irregular distribution with long periods spent below the preferred temperature, this would be consistent with foraging behaviour expected in the sea feeding migration (Kallio-Nyberg et al., 1999; Einarsson et al., 2018). Whereas in the second half of our study salmon 13 showed a different pattern in preferred temperature, remaining in warmer temperatures and throughout a more evenly distributed outline. This pattern would conform with the ceasing of foraging as post-smolts enter the rivers to spawn and start their freshwater migration (Thorstad et al., 2011).

The importance of combining data collected from the CTD sensor along with the data from the tag was highlighted in our analysis. The salinity measurements coupled with temperature and location data painted a much broader picture of the environment and the animal's interaction with its changing surroundings. Possible sites chosen by the animal, what abiotic conditions it might have encountered in that route, and how such conditions might have influenced its behaviour, namely vertical and horizontal migrations were obtained. In our understanding, if such metrics were available in all our subjects it would be

of value as more abiotic variables would be examined. In the past, the use of combined sensors has enabled important breakthroughs. Zimmer et al 2003, linked behaviour disruption in sperm whales to artificial noise with the combination of tag data, several sensors (i.e. pressure and motion sensors, a hydrophone), and a passive sonar system. A program of the Census of Marine Life, the Tagging of Pacific Pelagic Predators (TOPP) provided valued data on large marine predators on habitat range and choices, migrations, and behaviour. The sensors collected important data and acted as a bridge between biology and oceanology since the abiotic data collected by the tagged animals reaching hard-to-survey areas, was later incorporated into ocean models (Costa et al., 2010).

Nevertheless, we showed once more how biotelemetry, using tags and sensors deployed in wildlife, plays a critical role in the management of species and populations. Allowing the analysis of anthropogenic impact in populations (Hellström et al., 2019) – in our case study survival to a stress-inducing event was assessed. Enabling the identification of critical feeding areas, migration routes, and the identification of such locations for vulnerable populations (Jacobson et al., 2019). Giving insights into habitat use and resource selection, and into interactions in the food web and between conspecifics (Hellström et al., 2019).

Casting the final net – in conclusion:

Biotelemetry persists as a vital component in the study of animal movement allowing important questions, such as where and why the animal is moving, to be answered. The development of tags with increasingly available sensors and the usage of novel attachment techniques allowed the synergy of animal behaviour with environmental factors to be better understood. We are now permitted to look at each animal as a unique and important factor in the ecosystem and unveil how survival is affected, intra and interspecific interactions, and how the environment is weighing on decision-making.

The conservation measures that have been put into practice in the past and reinforced in the present years come with hope for the recovery of the Atlantic salmon. Provided that these essential measures are maintained, we believe that the recovery of vulnerable *Salmo salar* populations in the Baltic Sea is achievable and C&R can return to this sea. The evidence suggests relatively low mortality rates for these species following C&R however, in populations under strain, each spawning individual plays a critical role in sustaining population numbers. It is to our understanding that balancing this recovery with C&R practices will depend on creating optimal conditions, including fishing only when appropriate water temperatures are met, adequate hooks, and minimizing stress during catch-and-release practices by limiting fight time. One can thus enhance survival rates and create more fishing opportunities for the avid anglers who visit the Baltic coast each year, seeking a good catch. Boosting the local economy, as they often stay in small villages that benefit from the tourism income.

Through this work in close proximity to the fishermen community, it was also clear that their motivations are more complex than economic profit, and thus their role in conservation and spreading awareness should not be overlooked. They are often passionate about wildlife and deeply connected to nature with a broad knowledge of legislation and the species in question. However, even though many are well intended as shown by Blyth & Rönnbäck 2022 in their survey about release motivations for anglers regarding trout in the Baltic, there is a need to fill the knowledge gap when it comes to how fishing techniques and handling affect survival. As community representatives, education for this group and the general population will lead to more effectively implemented laws. In addition to this, the responsibility of media and how the communication is shared with the public is also crucial to success.

When studying a species that displays great behaviour plasticity, found in freshwater and marine environments, that is this charismatic and with such economic and social value the research opportunities are numerous.

So where to navigate next? – future work:

- The use of the HMMoce state-space-model – SSM (Braun et al., 2017), that incorporates temperature at-depth data (and possibly salinity at-depth data from the tag and CTD sensor) will help minimise the spatial errors, thus improving light-base geolocation. Since the tagging area is located close to the Arctic, the Wildlife Computers' GPE3 SSM failed to properly correct the salmon tracks, likely due to the long periods of light in the northern spring (Ekstrom, 2004) coupled with frequent cloud coverage in the area (Thiebot & Pinaud, 2010). SSM models like HMMoce can be used to improve and correct mismatches as 3D oceanography data and available tag data is used to improve position estimates (Braun et al., 2017).
- Some of our tags had premature release which was previously reported in other studies where the tag might have been relatively large in comparison to the animals' total size as noted in Jepsen et al., 2015 review paper. A different attachment method could benefit both the fish and the study, however more research is needed.
- As mentioned, addressing the stress level related to the tagging procedure and thus observing more concretely the effects of catch-and-release, as well as ensuring the best possible animal welfare would be possible if a blood sample was collected pre and post-tagging. As it could provide biomarkers such as cortisol that could be compared to reference levels. If a significant increase after tagging was observed, then the stress induced could be linked to the tagging procedure and not the fishing practices.
- It would be interesting to investigate the differences between smoltification in the Baltic and other marine locations as salinity is one of the drivers and leads to different salinity tolerances, no studies were found on the subject.
- In the present report, no chlorophyll data was analysed yet, it would be beneficial to investigate how primary productivity affects this species' movement especially DVM and migration along the Baltic Sea. Moreover, if in addition herring were tagged acoustically various food web relations could be established.

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