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**Activity patterns and tridimensional space use by the
European catfish (*Silurus glanis*) in Belver reservoir**

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Abstract

The European catfish (*Silurus glanis*) is a non-native species with invasive character to Iberian freshwaters. Being the largest fish species in its introduced range, possessing high fecundity rates, a large life expectancy and an extraordinary predatory potential, *S. glanis* has all the indicators that it could be exerting a dangerous pressure on native fish communities. Albeit there are some studies regarding the activity and depth use of this catfish, many of them are restricted to its native range and do not portrait the circadian and annual behaviours in detail. Moreover, no studies have compared the longitudinal space use between adults and juveniles in a recently invaded territory. To fill these knowledge gaps, this study resorts to acoustic biotelemetry technology to track a set of 25 fish (10 adults and 15 juveniles) with an array of fixed receivers in a Tagus River reservoir. The adults' tags include a 3D-accelerometer and pressure sensors that allow obtaining information on activity and depth use for over a year. The results show that *S. glanis* is active throughout the year but with higher activity levels in summer and minimal in autumn, and with a crepuscular and nocturnal increase in activity. *Silurus glanis* occupies shallower depths in spring/summer, while in autumn/winter roams at relatively deeper waters. Circadian vertical movement patterns were identified; however, they vary seasonally and have some individual variability. The areas used by the adults are larger than juveniles' and increase in warmer months. Adult preferences in the use of specific areas across the year and a possible migration to a spawning site were identified. Such findings will support the development of more effective control measures, for instance, by providing information on how to allocate the fishing efforts in space and time to maximize the efficiency of mass removal actions of this invasive fish.

Keywords: European catfish; Invasive species; Activity; Depth use; Acoustic biotelemetry.

Resumo alargado

As invasões biológicas constituem uma das principais ameaças à biodiversidade do planeta, sendo consideradas como o principal fator de extinção de espécies de plantas e animais. As espécies invasoras têm a capacidade de impactar os ecossistemas a diversos níveis, desde impactos genéticos que resultam de cruzamentos com as espécies nativas até mudanças completas nas cadeias tróficas. Estas invasões têm também enormes repercussões nas economias das regiões e países afetados, sendo necessária a criação de medidas mais eficazes na prevenção e mitigação do impacto causado por estas espécies. Os ecossistemas dulçaquícolas estão entre os mais ameaçados pelas invasões biológicas uma vez que são um dos ecossistemas com maior biodiversidade e onde esta situação se verifica com maior frequência. Os impactos destas espécies em contexto dulçaquícola vão desde alterações comportamentais das espécies nativas, à reorganização integral das cadeias tróficas ou, em alguns casos, à extinção em massa da fauna nativa. As águas continentais da Península Ibérica contêm uma grande diversidade de espécies piscícolas nativas, muitas destas classificadas como ameaçadas, mas atualmente albergam também um elevado número de espécies invasoras. São conhecidas 29 espécies não-nativas de peixe (23% das espécies) nos rios ibéricos cuja principal origem é atribuída a pescadores lúdicos que promovem intencionalmente a introdução de espécies para fins desportivos. Dados recentes apontam para que o número de espécies exóticas em águas continentais ibéricas continue a aumentar. O peixe-gato-europeu (*Silurus glanis*) é um dos mais recentes invasores. Originário da Europa Central e de Leste, este predador de topo foi introduzido nos anos 70 em Espanha, tendo sido confirmada a sua presença em Portugal em 2014. Em território nacional, encontra-se na bacia hidrográfica do Tejo, tendo dispersado para jusante após introduções a longa distância e por movimentos de dispersão natural. Sendo esta a maior espécie piscícola que ocorre nos rios ibéricos, possuindo altas taxas de fecundidade, uma longa esperança de vida e um extraordinário potencial predatório, o peixe-gato-europeu tem todos os indicadores de que poderá exercer uma pressão perigosa nas comunidades piscícolas nativas, em particular nas espécies diádromas com estatuto de ameaça como a lampreia (*Petromyzon marinus*) e a enguia (*Anguilla anguilla*), espécies que este predador confirmadamente consome no rio Tejo. De forma a desenvolver medidas de gestão da espécie mais eficazes, é importante obter informações sobre a sua ecologia e comportamento nos sistemas fluviais invadidos. Apesar de existirem alguns estudos dirigidos a esta espécie que permitem caracterizar a atividade e utilização espacial, incluindo profundidade, a larga maioria foi desenvolvida em áreas onde o peixe-gato-europeu é nativo. Além disso, nenhum outro estudo comparou o uso espacial longitudinal entre adultos e juvenis em território invadido. Este trabalho procura colmatar estas falhas no conhecimento, nomeadamente no que se refere às variações anuais e circadianas no uso da profundidade e atividade do peixe-gato-europeu, assim como identificar as diferenças ontogénicas (juvenis versus adultos) nas áreas utilizadas e movimentos de dispersão. Recorrendo a biotelemetria acústica, foram monitorizados 25 peixes (10 adultos e 15 juvenis) com uma rede de 8 recetores fixos na barragem de Belver, a barragem mais a jusante do Tejo, cobrindo um troço de rio com 6 km, e a zona confluência com um afluente, a Ribeira de Eiras. Depois de capturados recorrendo a redes de pesca e pesca-elétrica, os indivíduos foram sujeitos a uma pequena incisão na cavidade abdominal onde foram introduzidos transmissores acústicos. Os transmissores implantados internamente nos adultos integram dois sensores (acelerometria tridimensional e pressão) que permitiram obter informação relativa à atividade e uso da profundidade, com uma longevidade de aproximadamente 16 meses. Os transmissores implantados nos juvenis transmitem apenas o ID do peixe e têm uma longevidade estimada de 6 meses. No total, o seguimento decorreu entre Janeiro de 2019 e Março de 2021. Devido aos diferentes tempos de monitorização, estimativas mensais das áreas utilizadas foram calculadas com recurso a um modelo de distribuição baseado no movimento dos indivíduos (modelo BRB) de forma a analisar as diferenças no uso espacial longitudinal entre adultos e juvenis. As áreas correspondentes ao uso espacial em 95% do tempo foram comparadas mensalmente entre os dois

grupos ontogénicos. As áreas vitais mensais dos peixes (uso espacial a 95% e 50%) foram mapeadas num software de sistemas de informação geográfica (QGIS). Adicionalmente, foram produzidos gráficos com a distribuição dos peixes ao longo da área durante a totalidade da monitorização. Os dados relativos à atividade e profundidade dos adultos foram analisados por estação do ano, mês e hora. Foram obtidos dois modelos aditivos generalizados (GAM), com 4 variáveis abióticas significativas e um efeito aleatório (um modelo para cada variável resposta), a partir de uma seleção de modelos e de variáveis, com o intuito de identificar os preditores ambientais que influenciam estes comportamentos. Adicionalmente, foi utilizado um modelo Hurdle de forma a identificar os preditores que influenciam registos de atividade muito intensa relacionados, por exemplo, com a atividade alimentar. A maioria da análise foi realizada em software *R*. Os resultados indicam que os peixes-gato adultos usam áreas mais extensas ao longo do ano relativamente aos juvenis. Os adultos apresentaram variações sazonais no uso espacial, aumentando tendencialmente as áreas usadas dos meses mais frios, onde usam maioritariamente as duas seções mais a montante da área de estudo, para os meses mais quentes, onde estendem as áreas usadas para jusante, incluindo a Ribeira de Eiras. Foram identificados movimentos de indivíduos para a Ribeira de Eiras desde o final de abril e até ao final do Verão, correspondendo a possíveis migrações para uma área de reprodução, tendo em conta as características físicas da ribeira e o padrão interanual consistente destas agregações. Segundo os dados dos sensores, a atividade do peixe-gato-europeu variou consideravelmente ao longo do ano, mas sem nunca ter cessado. Os indivíduos estiveram mais ativos no Verão e final da Primavera, possivelmente devido a comportamento alimentar e reprodução, e menos ativos no Outono. Os níveis de atividade foram maiores durante a noite e máximos ao crepúsculo durante todo o ano que serão os períodos em que tendencialmente a espécie caça. Foram identificadas variações sazonais no uso da profundidade, com os indivíduos a ocuparem habitats mais profundos nos meses mais frios e mais superficiais durante os meses mais quentes, comportamento que poderá estar relacionado com a alimentação e reprodução. Foram identificados diferentes padrões em movimentos verticais com uma periodicidade circadiana ao longo do ano, com alguma variabilidade individual evidente. A atividade do peixe-gato-europeu está positivamente correlacionada com o caudal, temperatura da água e intensidade luminosa da lua, e assume uma relação não-linear com o fotoperíodo. O uso da profundidade está positivamente correlacionado com o caudal e a intensidade luminosa da lua, e assume uma relação não-linear com o fotoperíodo e temperatura da água. As informações recolhidas no presente estudo podem servir de suporte ao desenvolvimento de medidas de controlo mais eficazes, por exemplo, ao fornecer informação sobre como direcionar espaço-temporalmente o esforço de pesca de forma a maximizar a eficiência das ações de remoção em massa de indivíduos. É proposto que o esforço de captura no Tejo seja focado na Primavera e Verão, utilizando redes de emalhar e/ou palangres e, para maximizar a eficiência na remoção, as artes de pesca devem ser colocadas perpendicularmente à margem durante o dia para captura de indivíduos sobretudo durante o período crepuscular e noturno, quando o peixe-gato-europeu está mais ativo e realiza maiores movimentos longitudinais. A pesca deve ser dirigida ao primeiro terço da coluna de água (5-10m de profundidade na barragem de Belver) e em potenciais zonas de reprodução (zonas pouco profundas e com águas paradas), como a Ribeira de Eiras. Considera-se que no futuro é importante avaliar o uso espacial e os padrões de atividade nos troços lóticos do Tejo de forma a maximizar a eficiência das ações de remoção nestas áreas, uma vez que são áreas de coocorrência com as espécies diádromas e com a criticamente ameaçada boga-de-Lisboa.

Palavras-chave: Peixe-gato-europeu; Espécies invasoras; Atividade; Uso da profundidade; Biotelemetria acústica.

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List of abbreviations, acronyms and symbols

3D – Tridimensional

A - Acceleration

AIC - Akaike Information Criterion

APA – Portuguese Environmental Agency

BIC - Bayesian Information Criterion

BRB - Biased Random Bridge

BRB50 - 50% Utilization Distribution using a Biased Random Bridge model

BRB95 - 95% Utilization Distribution using a Biased Random Bridge model

D - Diffusion Coefficient

GAM - Generalized Additive Model

H_0 – Null hypothesis

h_{\min} - Minimum smoothing parameter

ICNF – Institute for Nature and Forests Conservation

ID - Identification

ML - Maximum Likelihood

pdf - Probability Density Function

RMS - Root Mean Square

TL – Total Length

T_{\max} - Upper time limit

TW – Total Weight

U - Mann-Whitney statistic

UD – Utilization Distribution

ρ – Pearson correlation

χ^2 – Kruskal-Wallis statistic

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1. Introduction

Invasive alien species constitute a leading threat to biodiversity across the globe (Clavero and García-Berthou, 2005; Bellard, Genovesi and Jeschke, 2016; Blackburn, Bellard and Ricciardi, 2019). Over the last two decades, scientists have provided extensive literature about the impacts that alien species have on native biota. Invasive species might have multiple levels of impact (Cucherousset and Olden, 2011; Simberloff *et al.*, 2013). Examples are evolutionary implications due to hybridization and subsequent introgression events (Muhlfeld *et al.*, 2009), changes in the food web structure (David *et al.*, 2017), competition with natives (Blanchet *et al.*, 2007), and the propagation of parasites and diseases (Verneau *et al.*, 2011). The combination of these impacts with other environmental threats and human stressors, may ultimately lead to native species extinctions (Strayer, 2010; Bellard, Genovesi and Jeschke, 2016). Still, in some cases, an invasive species can have a much more conspicuous impact on native species. A classic example of this is the multitrophic effects of the introduction of the Nile Perch on Lake Viktoria in the 1960s, which seems to be the main responsible for the extinction of more than 500 endemic haplochromine cichlid species and the collapse of other fish populations, on a top-down effect (Marshall, 2018). Invasive species are deemed to be the primary extinction driver of both animal and plant extinctions (Blackburn, Bellard and Ricciardi, 2019).

The economic losses associated with biological invasions in the last 60 years accumulated to a total of US\$140.20 billion across 39 European countries, in a highly conservative estimate (Haubrock *et al.*, 2021). Management costs related to invasions (e.g., for prevention, control, education) accounted for 20% of this value. Yet, environmental losses correspond to less than 1% of the total economic loss (US\$938.74 million), mostly because damage and management costs are often difficult to quantify, and an estimated 33% of this value correspond to management actions. Biological invasions have, thus, a substantial negative economic impact and considering that introductions rates continue to increase globally (Strayer, 2010; Seebens *et al.*, 2017; Haubrock *et al.*, 2021), efforts to prevent and mitigate the impacts of invasive species are urgent.

Freshwater systems are highly biodiverse (Dudgeon *et al.*, 2006), accommodating approximately half of the fish in the world, despite representing only about 0.1% of the earth's surface (Nelson, Grande and Wilson, 2016). Simultaneously, this is one of the most invaded systems (GISD, 2021). Freshwater systems have historically welcomed numerous invasive species due to the multiplicity of introduction vectors related, for instance, to aquaculture, through fish escape; to shipping activities, such as ballast water; to aquarium trade, usually by the deliberate release of unwanted organisms; or to recreational fishing, by deliberate introductions or release of live bait (Lodge *et al.*, 1998; Olden *et al.*, 2021). Following these events, direct water connections and the shortage of obstacles capable of restricting movements on these systems facilitate the dispersal of the intruders, which can also be vectored by human activities. These characteristics make the freshwater systems highly invasible (Moorhouse and Macdonald, 2015) and, as the species keep being introduced and established, communities move towards homogenization (Rahel, 2002). It is proven that all freshwater invasive taxa may cause deep changes in native ecosystems, from native species' behavioural alterations, to the full reorganization of freshwater food webs, or local extinctions (Gallardo *et al.*, 2016). As a result, the freshwater intrinsic high-level invasibility, together with the large biodiversity and potential socioeconomic and ecosystem risks, make freshwater invasive species a dangerous and unpredictable threat (Moorhouse and Macdonald, 2015).

The Iberian Peninsula has half of its freshwater fishes evaluated as threatened of extinction (Hermoso *et al.*, 2016) and the presence of invasive species in the inland waters is considered a serious hazard

(Clavero and García-Berthou, 2005; Hermoso *et al.*, 2011). Iberia great biodiversity and the tremendous share of endemic species (Hermoso *et al.*, 2016) are seen as a result of the glacier periods, where the peninsula acted as a refuge for many northern species, and as a consequence of the isolation caused by the Pyrenean mountains. Moreover, its climatic, geological and ecological heterogeneity (Benito-Calvo *et al.*, 2009) promotes a great number of different ecosystems and regions (McKnight *et al.*, 2017), which in turn has favoured the existence of large freshwater biodiversity (Muñoz-Mas and García-Berthou, 2020). On the other hand, the habitat variability also increases the niche opportunities to alien species in Iberian freshwaters, as there are representatives for almost every habitat (García-Berthou, Boix and Clavero, 2007). As such, the duality of high fish biodiversity together with the abundance and threats of invasive species make this a system with an important conservationist interest.

In a recent review, Muñoz-Mas and García-Berthou (2020) reveal that the freshwater fish communities in the Iberian Peninsula count with 29 non-native species (23% of all fish species), originating mostly from Europe and the Americas and that the illegal introductions of game fish are the main vector of fish introduction, followed by the release or escapement of aquarium specimens. Anglers are responsible for many of the introductions, whether they are intentional, when introducing the preferable game fish, or accidental, for instance, when using live baits. Furthermore, anglers can travel long distances for fishing, promoting long-distance invasions (Gago *et al.*, 2016; Banha, Diniz and Anastácio, 2017). Additionally in this study, the models on the rate of introductions indicate that, for Portugal and Galicia, introductions rates show no decline in the last decades, while, for the rest of Spain, the rates are decreasing (Muñoz-Mas and García-Berthou, 2020). This phenomenon could be explained because a significant number of species were firstly introduced in the north-eastern region of the Iberian Peninsula and have been spreading westwards by following introductions into neighbouring catchments. These trends indicate that, most likely, in the next few years, Portugal and Spain will have to deal with new fish invasive species, and the situation could be more dramatic in Portugal (Muñoz-Mas and García-Berthou, 2020).

The European catfish *Silurus glanis* L. is an apex predator (Vejřík *et al.*, 2017) and recent invader of the Portuguese freshwaters (Gkenas *et al.*, 2015; Gago *et al.*, 2016). Its native range extends from Western Asia to Flanders, being now present as an invasive species in several European countries, as well as in Brazil and Tunisia (Cucherousset *et al.*, 2018). Their extremely large body size and its foodstuff value make this fish a highly prized trophy (Copp *et al.*, 2009) and an increasingly popular target species for recreational anglers, resulting in deliberate introductions outside their native range (Cucherousset *et al.*, 2018). Introduced in Eastern Spain around 1974 (Benejam *et al.*, 2007), the first official record of *S. glanis* in Portugal was in 2014, although its arrival was probably in 2006 (Gkenas *et al.*, 2015; Gago *et al.*, 2016). In Portugal, *S. glanis* dwell along the Tagus mainstem, being more common in large reservoirs. It seems that the downstream invasion across the Tagus river catchment began with long-distance introductions, probably human-mediated, followed by the current patterns of mainly short-distance natural dispersal (Gago *et al.*, 2016). Citizen science data also evidence the species presence in Douro River since 2019 (Martelo *et al.*, 2021).

Silurus glanis is a species that can reach 2.8 meters in total length and a recorded weight of 130kg, making it the second-largest freshwater fish in Europe (Boulêtreau and Santoul, 2016) and the largest species in its introduced range, doubling the biggest natives' size (Cucherousset *et al.*, 2018). *Silurus glanis* lives up to 22 years (males) and have high fecundity, building nests on woody vegetation at shallower areas (Copp *et al.*, 2009; Kuzishchin, Gruzdeva and Pavlov, 2018). Its diet includes native species and also prey on highly valuable diadromous fish (Syväranta *et al.*, 2010; Ferreira, Gago and Ribeiro, 2019). Indeed, it seems its diet becomes wider the more diverse the recipient community, and it can easily change its predation behaviour according to prey availability (Cucherousset *et al.*, 2012;

Ferreira, Gago and Ribeiro, 2019). For instance, Ferreira, Gago, and Ribeiro (2019) found that, on a lotic portion of the Lower Tagus, 81.1% of *S. glanis* prey were native species and 20% of these consisted of native fish. Moreover, because of its large body size, *S. glanis* may need to consume large amounts of prey to maintain its metabolic activity. In this invaded region, because of the high water temperatures, the consumption of prey may enlarge given the food conversion and growth optimum of 25-28°C (Hilge, 1985). These are strong indicators that *S. glanis* could be exerting dangerous pressure on native fish communities.

The preferable habitats of European catfish are slow-moving lotic or significantly deep lentic waters (Copp *et al.*, 2009), showing site fidelity and restricted movements, preferring to defend small home-range areas (Carol, Zamora and García-Berthou, 2007; Brevé *et al.*, 2014; Slavík, Horký and Závorka, 2014). Additionally, their dispersion at their native range is more likely to occur by juveniles, predominantly downstream (Slavík *et al.*, 2007). This catfish prefers warmer waters and there is a notorious increase of activity during summer (Slavík *et al.*, 2007; Daněk *et al.*, 2016), however, it seems capable of surviving at higher depths on cold winters, with low oxygen concentrations (Cucherousset *et al.*, 2018). Concerning the behaviour patterns, *S. glanis* show diel activity patterns with higher activities overnight at its native range (Slavík *et al.*, 2007), although it may be dependent on the season. In northeast Spain, *S. glanis* is found to have a strong crepuscular activity peak (Carol, Zamora and García-Berthou, 2007). They are known to have social behaviour and form aggregations of up to 44 individuals (Boulétreau *et al.*, 2011).

Silurus glanis depth use and vertical movements studies are limited, with two existing works on only one monitored fish (Ferreira, 2019; Lenhardt *et al.*, 2021). Thus, it is still unclear how the species distributes in the water column daily and along the year, and if there are any vertical movement patterns. Moreover, the existing information on *S. glanis* activity is mainly restricted to its native range and is based on longitudinal movements that may not accurately measure activity levels (Carol, Zamora and García-Berthou, 2007; Slavík *et al.*, 2007; Daněk *et al.*, 2016). Therefore, the main goal of this study is to fulfil this knowledge gap and assess how *S. glanis* depth use and activity change over time in a recently invaded territory with a Mediterranean climate. Additionally, also of interest is to identify the environmental variables that may drive such behaviours. Studies comparing the longitudinal movements and space use of adult and juvenile *S. glanis* in invaded territory are also scarce (but see Slavík *et al.*, 2007). An additional goal of this study is to provide insight on how longitudinal space use differs between these two ontogenic stages in invaded territory. The study was based on acoustic biotelemetry, which is a widely used method for movement and behaviour of aquatic animals, by remote monitoring of tagged individuals (Hussey *et al.*, 2015; Crossin *et al.*, 2017). The documented site fidelity, typical small home-range and unlikelihood of dispersal events of the catfish, makes it possible to set an array of fixed acoustic receivers that covers most of their habitat range on the study area (Ferreira, 2019). The transmitters planted on individuals transmit a signal that is received on a data-logging or relay-receiving stations, allowing to obtain the fish position and its movements. Also, sensors can be added to the transmitters for assessing environmental properties on the animals' surroundings, behavioural features, or physiological states, such as activity or depth, with great detail.

2. Methods

2.1 Study area

The site selected to monitor *S. glanis* movement behaviour was the Belver reservoir, in Tagus River (Gavião, Portugal). This reservoir is located in the central part of Portugal (Iberian Peninsula) and is subjected to dry weather summers and cold and wet winters, being classified under the Köppen Climate Classification as Mediterranean. Belver reservoir is the most downstream reservoir of Tagus, the longest river of the Iberian Peninsula, with a total capacity of 12,500,000m³ of water, with a maximum discharge rate of 18,000m³/s (Sabater *et al.*, 2009). Average monthly flows for the study period vary between 13.7 m³/s and 247.5 m³/s and water temperatures from 10.5°C in winter to 22.5°C in summer. The Portuguese Environmental Agency (APA) classifies the reservoir as an area of free use, meaning that touristic or recreational practices are allowed. In Belver reservoir, *S. glanis* represents approximately 10% of the fish caught in trammel nets and about 5% of the fish captured by electrofishing in 2019 and 2020 (Ribeiro, F., unpublished data). Other species include the Iberian barbel (*Luciobarbus bocagei*) and the big-scale sand smelt (*Atherina boyeri*). The reservoir still houses a large share of other non-native species, such as the goldfish (*Carassius auratus*), the pikeperch (*Sander lucioperca*) and the bleak (*Alburnus alburnus*).

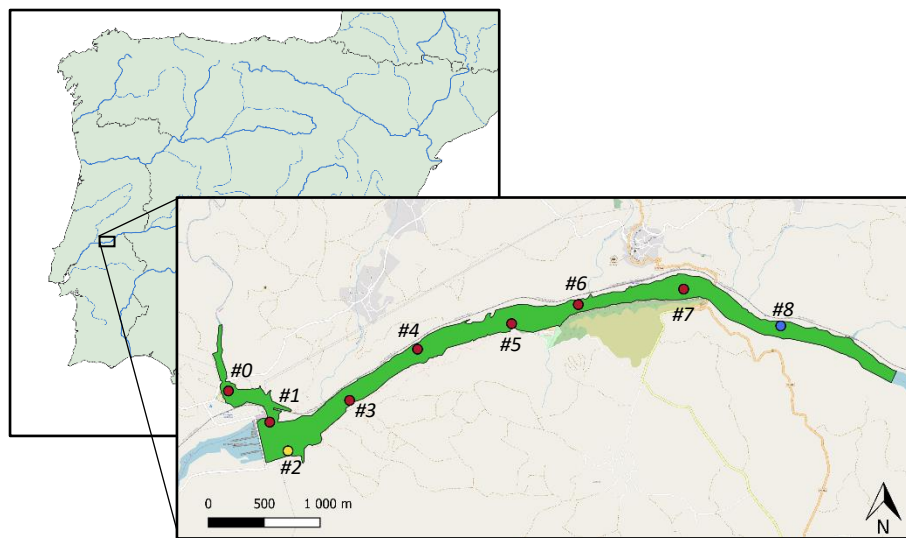


Figure 2.1 - Belver reservoir (green) and biotelemetry stations array (dots). The yellow dot represents station #2 that was discarded (18-01-2020) following the replacement by the Thelma Biotel receivers. The blue dot represents station #8, which was added as the new Thelma Biotel receivers were deployed (19-01-2020). The river flows westwards.

2.2 Fish capture, tagging and tracking

Individuals were captured by electrofishing or trammel nets placed in several locations along the study area and left overnight. A total of 25 fish were captured during three campaigns with individuals released in 2019-01-24, 2019-03-28 and 2020-09-19 (Table 2.1). The individuals were anaesthetized in a solution of 2-phenoxyethanol (0.4ml per litre of water), measured to their total length ($TL \pm 1$ mm) and weighed ($TW \pm 1$ g). Considering the size of maturation of males (78cm) (Alp, Kara and Büyükçapar, 2004), ten adults and fifteen juveniles were tagged. Acoustic transmitters were internally implanted in the peritoneal through a surgical procedure cavity. The wound was sutured and disinfected with an iodine solution. All surgical materials were sterilized with a 96% alcohol solution. Ten adult individuals were tagged with Thelma Biotel AD-HP16 transmitters (Size: 72.6mm in length, 16mm diameter, 29.6g weight in the air, 15g weight in water; transmission protocol: S256; frequency: 69kHz), which have sensors that measure tridimensional (3D) acceleration and underwater pressure, transmitting an independent ID signal for each type of measurement, with a 30 to 90 seconds interval. These sensors have an estimated battery lifetime of 16 months. Due to the size of the juvenile individuals, smaller Thelma Biotel ID-2LP7 (Size: 23.2mm in length, 7mm in diameter, 2.7g weight in air, 1.8g weight in water; transmission protocol: R64K; frequency: 69kHz) transmitters were implanted on fifteen individuals of this group. These tags are not equipped with sensors, transmitting information about the fish location only (i.e., just the ID information), with a 40 to 100 seconds interval and have an estimated lifetime of six months. Because of the shorter battery lifetime of the transmitters of this ontogenic group, two sets of juvenile fish were released to ensure an annual cycle of monitoring. All tagged fish were marked with an external mark (the juveniles with a Tbar, the adults with an anchor tag) for identification purposes in case of recapture. After tagging, all fishes were released at the capture location after a two-hour recovery period.

The 3D acceleration sensor on Thelma Biotel AD-HP16 S256 69kHz computes a Root Mean Square (RMS) of the horizontal (x), vertical (y) and lateral (z) acceleration (A) values (m/s^2) during a time window with N samples before it transmits the result value:

$$A_{RMS} = \sqrt{\frac{\sum_{n=1}^N a_x^2 + a_y^2 + a_z^2}{N}}.$$

For simplicity, this 3D acceleration (A_{RMS}) will be considered as a fish activity measurement. The pressure sensors on these transmitters provide adjusted depth values in meters, with a resolution of 0.2 meters for a maximum depth of 51 meters.

A total of 8 fixed biotelemetry acoustic receiver stations were deployed along the study area using three different models of acoustic receivers (VEMCO VR2W, VEMCO VR2Tx and Thelma Biotel TBR 700) (Figure 2.1). Deploying the receivers underwater requires securing the receiver on a steel cable attached directly to the bedrock on the bottom and, on the other end of a cable placing a buoy that assures the cable stays in a vertical position. VEMCO receivers were first deployed on the study location, and they were replaced at the beginning of 2020 by the Thelma Biotel receivers, which have the same features as the previous VEMCO's. The arrangement of the receivers was slightly adjusted at the time of this replacement with the addition of receiver #8 to increase the study area from 5km to about 6km long (Figure 2.1). The signal range of the transmitters varies between a minimum of 200 meters for the smaller and less powerful transmitters used in the juvenile fish and up to 1000 meters for the adults', meaning that, according to the stations' displacement, it might allow range overlapping between neighbouring receivers on certain locations and that a single signalling event can be detected by two or more receivers. This redundancy was key to minimize the risk of missing the transmitted signals.

VEMCO receivers' data was downloaded by scuba divers in late January 2020 and Thelma receivers' data in August 2020 and April 2021.

Table 2.1 – Identification (ID) of the tagged *S. glanis* with capture and tagging periods, release date, Total Length (TL), Total Weight (TW), code of external mark, ontogenic group and monitoring days

ID	Capture and Tagging date	Release date	TL (cm)	TW (kg)	External mark	Group	Monitoring days	ID	Capture and Tagging date	Release date	TL (cm)	TW (kg)	External mark	Group	Monitoring days
#1*	21 January 2019	24 January 2019	132.0	18.2	2442	Adult	473	#14*	24-28 March 2019	28 March 2019	111.0	9.91	2430	Adult	101
#2	23 January 2019	24 January 2019	44.0	0.5	2414	Juvenile	241	#15*,†	24-28 March 2019	28 March 2019	105.0	8.07	2433	Adult	494
#3	24-28 March 2019	28 March 2019	62.0	1.39	2440	Juvenile	179	#16	24-28 March 2019	28 March 2019	62.0	1.42	2435	Juvenile	132
#4	24-28 March 2019	28 March 2019	69.0	1.81	2438	Juvenile	178	#17	24-28 March 2019	28 March 2019	64.5	1.48	2420	Juvenile	26
#5*,†	24-28 March 2019	28 March 2019	88.0	4.05	2417	Adult	289	#18	24-28 March 2019	28 March 2019	67.0	1.49	2428	Juvenile	3
#6	24-28 March 2019	28 March 2019	66.0	1.64	2425	Juvenile	190	#19	24-28 March 2019	28 March 2019	64.0	1.02	2449	Juvenile	56
#7*	24-28 March 2019	28 March 2019	114.0	10.29	2416	Adult	493	#20	13-19 September 2020	19 September 2020	44.2	0.49	292	Juvenile	171
#8*	24-28 March 2019	28 March 2019	126.0	12.98	2431	Adult	393	#21	13-19 September 2020	19 September 2020	24.7	0.08	288	Juvenile	19
#9*,†	24-28 March 2019	28 March 2019	92.5	7.21	2423	Adult	493	#22	13-19 September 2020	19 September 2020	22.1	0.09	286	Juvenile	164
#10	24-28 March 2019	28 March 2019	52.0	0.75	2427	Juvenile	8	#23	13-19 September 2020	19 September 2020	37.5	0.49	285	Juvenile	65
#11*	24-28 March 2019	28 March 2019	111.0	7.8	2445	Adult	278	#24	13-19 September 2020	19 September 2020	46.1	0.57	284	Juvenile	176
#12*	24-28 March 2019	28 March 2019	96.0	4.75	2422	Adult	395	#25	13-19 September 2020	19 September 2020	18.5	0.04	283	Juvenile	168
#13*	24-28 March 2019	28 March 2019	101.0	6.55	2421	Adult	383								

*Transmitters equipped with sensors that record tri-dimensional acceleration (i.e., measure of fish activity) and pressure (i.e., depth use).

†Transmitters with problems in the accelerometric sensors.

2.3 Data analysis

The data analysis was mainly conducted on R 4.0.3. Collected data was filtered with Thelma (ComPort 3.1.2) and VEMCO (VUE 2.7.0) software to remove ‘type A’ false detections that may occur when signals from two or more transmitters collide, creating a different signal with an unknown tag ID code (Simpfendorfer *et al.*, 2015). For each ID detection, a ‘lag’ time was assigned in R, corresponding to the time interval between detections. Detections with ‘lag’ times inferior to 30 seconds for the adult transmitters and 40 seconds for the juvenile transmitters (minimum tag signalling intervals) were considered as duplicates (i.e., the same signal detected by two or more receivers), the result of the receiver detection range overlap, and they were eliminated.

For analysing the longitudinal space use, individual Utilization Distributions (UDs), i.e., the probability distribution that defines animal’s space use (Winkle, 1975) were calculated for each tagged individual, for the entire detection period. With the UD, home-ranges (typically the smallest area associated with a 95% probability of finding the animal within a year period) and core-ranges (the smallest area associated with a 50% probability of finding the animal within a year period), were obtained for each tagged individual. Because of the battery life of the smaller juvenile transmitters (up to 6 months), a typical annual home-range comparison between adults and juveniles was not possible. To overcome this limitation, monthly 95% Utilization Distributions were calculated for all months (2019-02 to 2020-03), allowing to compare monthly UD values between the two ontogenic groups (juveniles vs. adults). These were not produced in months with less than 100 observations/detections, as they were considered to possibly inaccurately reflect the area used by the fish. The estimation of the UD was based on a biased random bridge model (BRB), which is a movement-based Kernel method that considers animal movements generated by a biased random walk (Benhamou and Corn elis, 2010; Benhamou, 2011). This model consists of dividing each step (the movement between receivers) into several interpolated steps (bridges) before computing a classical kernel estimation (Figure 2.2).

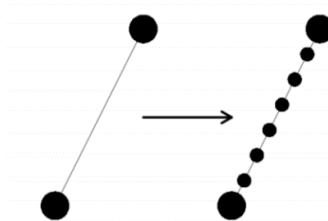


Figure 2.2 - Illustration of the division of a single movement step into several interpolated intermediate steps between receivers.

The Biased Random Bridges approach estimates a probability density function (pdf) that the animal is located at a certain place $r = (x,y)$ at time t_i (with $t_1 < t_i < t_2$), given that it is located at r_1, r_2 at times t_1, t_2 , and considering that the animal moves according to a biased random walk with an associated advection component (‘drift’), which is a general tendency to move in the direction of the next relocation (i.e., a tendency to move from r_1 and r_2). An additional diffusion coefficient ‘D’ that considers a possibility of movement in other directions than the direction of the drift is also added to this model (Benhamou and Corn elis, 2010; Benhamou, 2011)

As the drift component is allowed to vary between steps, an upper time limit (T_{\max}) must be set to ensure homogeneous movements (i.e., no marked drift changes). Steps with a longer duration are not considered in the estimation of the UD. Uncertainty over the relocation of an animal increases as t_i moves from t_1 towards t_2 . Thus, a minimum smoothing parameter (h_{\min}) is added to the model, portraying the minimum uncertainty over the location of the fish (Benhamou and Cornéris, 2010; Benhamou, 2011). R packages *adeHabitatHR* and *adeHabitatLT* provide the functions needed for calculating the BRB-based UD's. The function *as.ltraj()* creates an object with the fish trajectories that afterwards is applied in *BRB()* function, which computes the UD. A T_{\max} of 1 hour and a minimum distance between successive relocations (L_{\min}) of 100 meters were chosen for *BRB()*. The resting period filter of the *BRB()* function was disabled so that continuous detections at one receiver are accounted for in the UD production. An h_{\min} corresponding to the uncertainty on the fish location (location error) around the receiver was set to 200 meters because this is the minimum range of the transmitters used for the juvenile fish. Since this parameter affects the size of UD areas and although adults' transmitters have a larger minimum range, to establish comparisons between ontogenic groups (adults and juveniles) the h_{\min} values had to be the same for both groups and thus, the minimum location error was chosen considering the two sets of transmitters. The diffusion coefficient 'D' was chosen automatically for each UD with the *BRB.D()* function. Annual and monthly 95% and 50% contours, i.e., the areas corresponding to the 95% UD (BRB95) and to the 50% UD (BRB50), respectively, were extracted using *getverticeshr()* function, clipped to the study area shapefile and plotted as shapefiles on QGIS 3.16.2. The clipped BRB95 and BRB50 areas were also calculated on R. Using *ggplot2* package, boxplots of the annual and monthly UDs were computed and a non-parametric Mann-Whitney test (*wilcox.test()* function on *stats* R package) were performed to test for significant differences between adults and juveniles' UDs, considering a significance level of 5%.

The acoustic biotelemetry dedicated R package - *Actel* - was used to complement the space use analysis, as it provides useful graphical outputs for examining residency areas and movement patterns, throughout time (Flávio and Baktoft, 2021). Moreover, this package also provides outputs with an overview of the input data, as well as information regarding the receivers' performance. For the optimal usage of *Actel* and better data adjustment, the receivers (arrays) were clustered into designated river sections (Figure 2.3) and with its semi-automatic function *residency()*, multiple outputs were produced. Only tags with more than two consecutive detections at a given section were considered as valid events. Events in which a tagged fish jumped over more than two receivers were considered invalid. These events may happen due to not filtered 'type B' false detections, which are false detections that have the same tag ID as another transmitter that has been released, and thus *a priori* harder to detect (Simpfendorfer *et al.*, 2015). *Actel* outputs include plots of the fish arrival and departure times for each receiver and section, and residency plots with fish location over time. The results of both ontogenic groups, i.e., adults and juveniles, were then compared. An integrated analysis of the longitudinal results together with the activity and depth sensors information should provide a better insight into the behaviour and 3D spatial use of *S. glanis* adult individuals in the Belder reservoir.

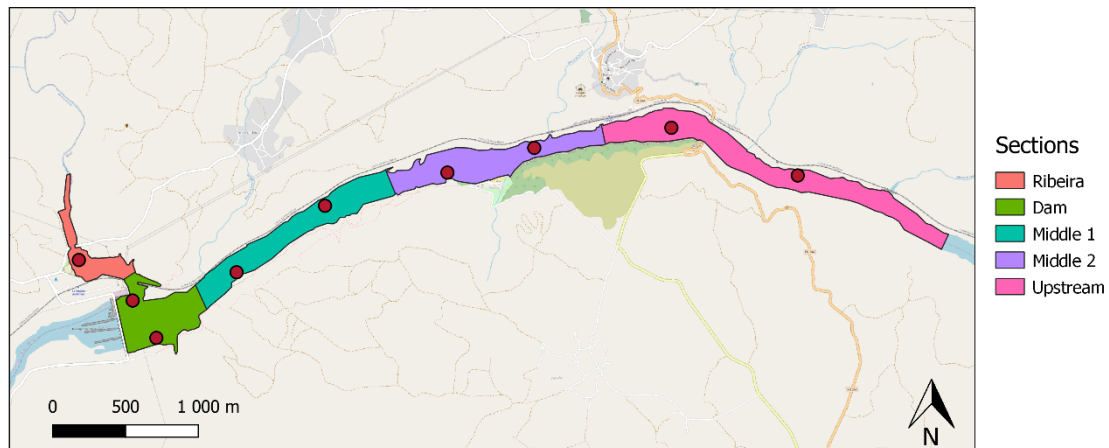


Figure 2.3 – Acoustic receivers clustered into designated river sections in Belver Reservoir.

Depth and activity data corresponding to the sensors present only in the adults' transmitters were grouped according to season, month and hour with *dplyr* package and plotted using *ggplot2* package in R. *lubridate* package was used for formatting the datetime data. For testing the significance of the seasonal variations in activity and depth use, Kruskal-Wallis rank sum tests were performed using *kruskal.test* function on the base R. To determine which seasons were significantly different from the others, a post-hoc Dunn's test was conducted, using *dunn.test()* function from *dunn.test* package. The p-values from Dunn's test were adjusted with the Bonferroni method, by choosing this option in the *dunn.test()* function. A significance level of 5% was chosen for all tests (Zar, 1999).

Explicative models were computed to find environmental variables that may be drivers of activity and explain depth use, the two response variables analysed. As it was expected non-linear relationships between the response variables and some predictors, Generalized Additive Models (GAMs) were the chosen model family (Wood, 2017) and were created using *mgcv* package in R. For both models, the response variables are the daily average activity and depth values. The set of predictors includes water temperature, river flow, photoperiod and moonlight intensity (Table 2.2A). Water temperature values were measured by all active VEMCO VR2TX and Thelma Biotel receivers at approximately half the water column depth (~5 m) and were averaged for each day. Photoperiod data was not available with daily values. Instead, discrete data with single values (in daylight minutes) for 10 days periods were used in the models. The river flow data corresponds to the Belver dam daily mean affluent flow. The moonlight intensity represents the moon illuminated fraction, between 0 and 1, where 0 is the new moon and 1 is the full moon. In the context of GAMs, nonlinear correlations among predictors must be assessed. These nonlinear correlations are called 'concurvity' (Wood, 2008) and were assessed using *concurvity()* in *mgcv* package. An arbitrary cut off value of 0.7 for the most pessimistic measure of concurvity was established when selecting predictors. A random effect to account for the inherent individual tagged fish variation in behaviour and to avoid pseudo-replication was included in the models (Brewster *et al.*, 2021). The Maximum Likelihood (ML) method was used on the estimation of the smoothing parameter, allowing model comparisons (Wood, 2017). A forward variable selection was conducted with AIC (Akaike Information Criterion) and BIC (Bayesian Information Criterion), with the former being chosen as the main selection criteria when comparing models. In addition, on the model with all predictors, another selection method was performed to confirm their significance – the double penalty method (Marra and Wood, 2011). The chosen models were validated by examining Q-Q plots, histograms of residuals, response versus fitted values and residuals versus linear predictor.

Given the high number of outliers in the activity data, an additional model was created for analysing behaviour associated with periods during which fish activity is very high. There was an interest in finding what environmental conditions can promote highly intense peaks of activity, which could be associated with a predatory burst movement or agonistic behaviour. The chosen response variable was the hourly ratio of the number of outliers per number of detections. This zero-inflated count data was handled through a two-part Hurdle model (*hurdle()* function from *pscl* R package), consisting of a Hurdle component that models the zero counts through a logistic regression, and a truncated count component for the positive counts (Zeileis, Kleiber and Jackman, 2008). Thus, it is possible to separately test the effects of a set of predictors on the presence-absence of extreme activity events (outliers) and the effects of another set of predictors on the number of outliers. The absolute number of outliers was introduced as the dependent variable but an *offset* parameter on the *hurdle()* function adjusts the count number to the number of detections, meaning the true response variable is the rate (or proportion) of extreme activity events. Two distribution families were tested for the count part of each of the hurdles - Poisson and Negative Binomial. The latter is usually best suited for overdispersed data (Ver Hoef and Boveng, 2007). The chosen predictors include hourly water temperatures, light periods along the study period (dawn, daytime, dusk and night-time), water flow and the photoperiod (Table 2.2B). Predictor correlations (Pearson correlation) were assessed with *cor()* function in *stat* package, and a cut off value of 0.7 was defined on variable selection. The light period significance was tested through a likelihood ratio test (*lrtest()* from *lmtree* R package) between the best model including this variable and the model lacking it. A rootogram was the chosen graphical tool for assessing the fit of these models. It compares the frequencies of the observed distribution on a square root scale with the curve of the fitted count model (Kleiber and Zeileis, 2016). Annex III contains the references for all the installed R packages.

Table 2.2 – List of predictors analysed in the Generalized Additive Models (GAMs) with activity (3D accelerometer data) and depth use (pressure data) as response variables (A) and in the Hurdle models with activity hourly ratio of the number of activity (3D accelerometer data) outliers per number of detections as the response variable (B)

A				
Generalized Additive Models				
Variable	Range	Unit	Abbreviation	Source
Mean daily water temperature	10.5 - 22.5	°C	Temp	VEMCO VR2TX & Thelma Biotel receivers
Photoperiod	567 - 893	minutes	Photo	Observatório Astronómico de Lisboa
Moonlight intensity	0 - 1	fraction	Moon	Observatório Astronómico de Lisboa
Mean daily water flow	1.8 - 704.0	m ³ /s	Flow	Sistema Nacional de Informação de Recursos Hídricos

B				
Hurdle models				
Variable	Range	Unit	Abbreviation	Source
Mean hourly water temperature	10.7 - 22.7	°C	Temp	VEMCO VR2TX & Thelma Biotel receivers
Photoperiod	567 - 893	minutes	Photo	Observatório Astronómico de Lisboa
Light period	'dawn', 'daytime', 'dusk', 'night-time'	factor	Light	Observatório Astronómico de Lisboa
Mean hourly water flow	0 - 3052	m ³ /s	Flow	Sistema Nacional de Informação de Recursos Hídricos

3. Results

The fish were passively and continuously tracked between 2019-01-24 and 2021-03-14. After the raw data filtrations, a total of 1,609,714 datetime stamps were used for analysis, of which 480,940 correspond to the adults' activity data, 778,797 to the adults' depth use data and the remaining 349,977 to the juvenile ID data.

3.1 Longitudinal space use

Most of the tagged fish have stayed consistently within the study area. Considering the receiver where the fish were last detected (Dam section) and the unusual shorter detection period, it is likely that two juvenile fish have dispersed downstream and another four individuals were, eventually, recaptured by fishermen. Three adult individuals, however, have left the study area, between September and December.

The 95% Utilization Distribution (UD) areas (BRB95) for the full detection periods are presented in Figure 3.1. The maps of individual BRB95 and BRB50 (50% UD) areas can be found in Annex I (Figure I.1). For the adult fish, these areas represent the home-range, since the detection period for every fish (except individual #14) corresponds to almost or more than one year cycle.

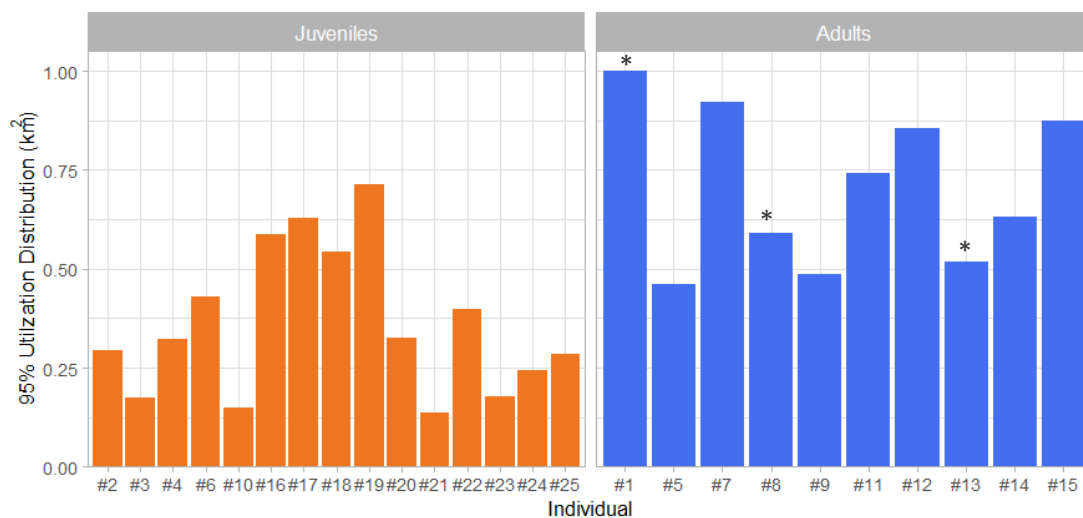


Figure 3.1 – Juvenile (orange) and adult (blue) *S. glanis* 95% Utilization Distribution (BRB95) values for the entire individual tracked period (maximum 8 months for Juveniles and 16 months for adults). *Tagged fish that left the study area upstream for a period of time. The ID of each fish can be found in Table 2.1.

Adults have significantly larger monthly BRB95 areas than juveniles (Figure 3.2). The Mann-Whitney test rejects the null hypothesis (H_0) that the BRB95 areas of the two groups are the same, i.e., that they belong to the same population ($U = 5742$, p -value $< 0,0001$). However, there are large individual variations in the size of the areas used in every month (Figure 3.3). The adults' group have an interannual variation in BRB95 areas sizes, with quite stable values in spring and summer of 2019, followed by a drop to minimum values in November 2019 and then a constant increase until the end of spring of 2020. Juveniles show less individual variation and more stable BRB95 areas across the year. As a precautionary note, some adult fish might have, in some months, larger BRB95 values than the ones presented, in the case they leave the study area in the upstream direction for a period of time. An example of the monthly BRB95 areas can be found in Annex I (Figure I.2).

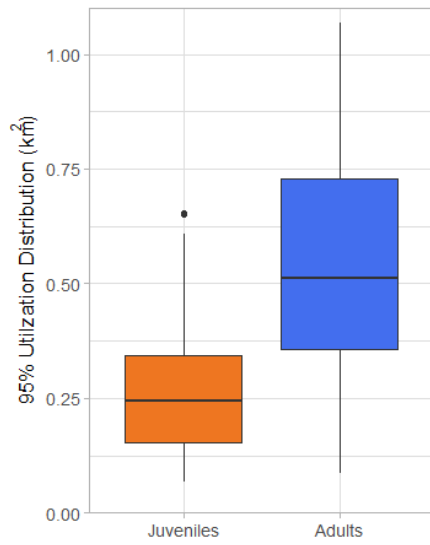


Figure 3.2 – Tagged *S. glanis* monthly 95% Utilization Distribution (BRB95) values clustered in boxplots for each ontogenic category (juveniles vs. adults).

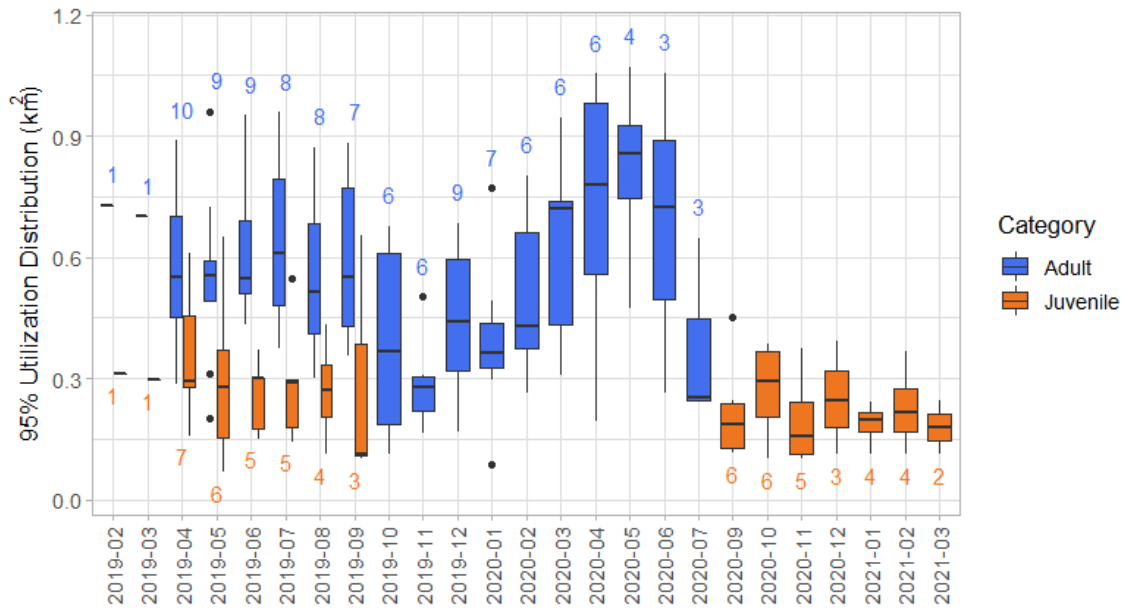


Figure 3.3 – Juvenile (orange) and Adult (blue) *S. glanis* 95% Utilization Distribution (BRB95) values clustered in monthly boxplots. The number of individuals included in each month is shown above (adults) and below (juveniles) the respective boxplots.

The *Actel* residency plot shows that the Adult *S. glanis* used all the study area during the entire study period (Figure 3.4A). However, a preference for the usage of certain river sections in specific time periods is evident. From April to August, the usage of more downstream sections increases ('Mid1', 'Dam' and 'Rib' sections), whilst off that period fish tend to use predominantly the most upstream sections ('Up' and 'Mid2' sections). Some fish often used the 'Ribeira de Eiras' tributary ('Rib' section) from late April until August 2019, with just a few entries after that period. Unfortunately, from the 15th of November of 2019 until the 29th of January of 2020, 'Rib' section receiver stopped working. After the 'Rib' receiver replacement, no tagged *S. glanis* was detected until April 2020. From April 2020 until the end of the study, 'Rib' section had been used by at least one or two tagged fish almost continuously. During these periods, the rest of the tagged fish were spread across sections and each fish was found restricted to one or two sections. A brief predominance of usage of the upstream section ('Up') is found at the end of summer (August 2019), however, after this period, there is an overall upstream movement with more than half of the fish being detected in the two most upstream sections until April 2020. During a short period in December 2019, nine of the ten tagged adult fish were located within these two last sections. The least used section by the adult fish was the dam section ('Dam').

Seasonal variations in the longitudinal use of study area use are not evident in the juvenile group (Figure 3.4B). Contrary to the adult fish, only one juvenile fish from the first released group used continuously 'Rib' section after April 2019. In the second group, only two fish used 'Rib' section continuously in October 2020, however, this was the site of their release. In general, the fish of the second group had a bigger site fidelity (Annex I, Figure I.3). Again, the least used section by the juvenile fish was the dam section. Unfortunately, the monitoring period of six juvenile fish was significantly inferior to the six months expected.

The arrival times of the tagged fish on each receiver (Annex I, Figure I.4). indicate that longitudinal movements occur more often during the night in both groups.

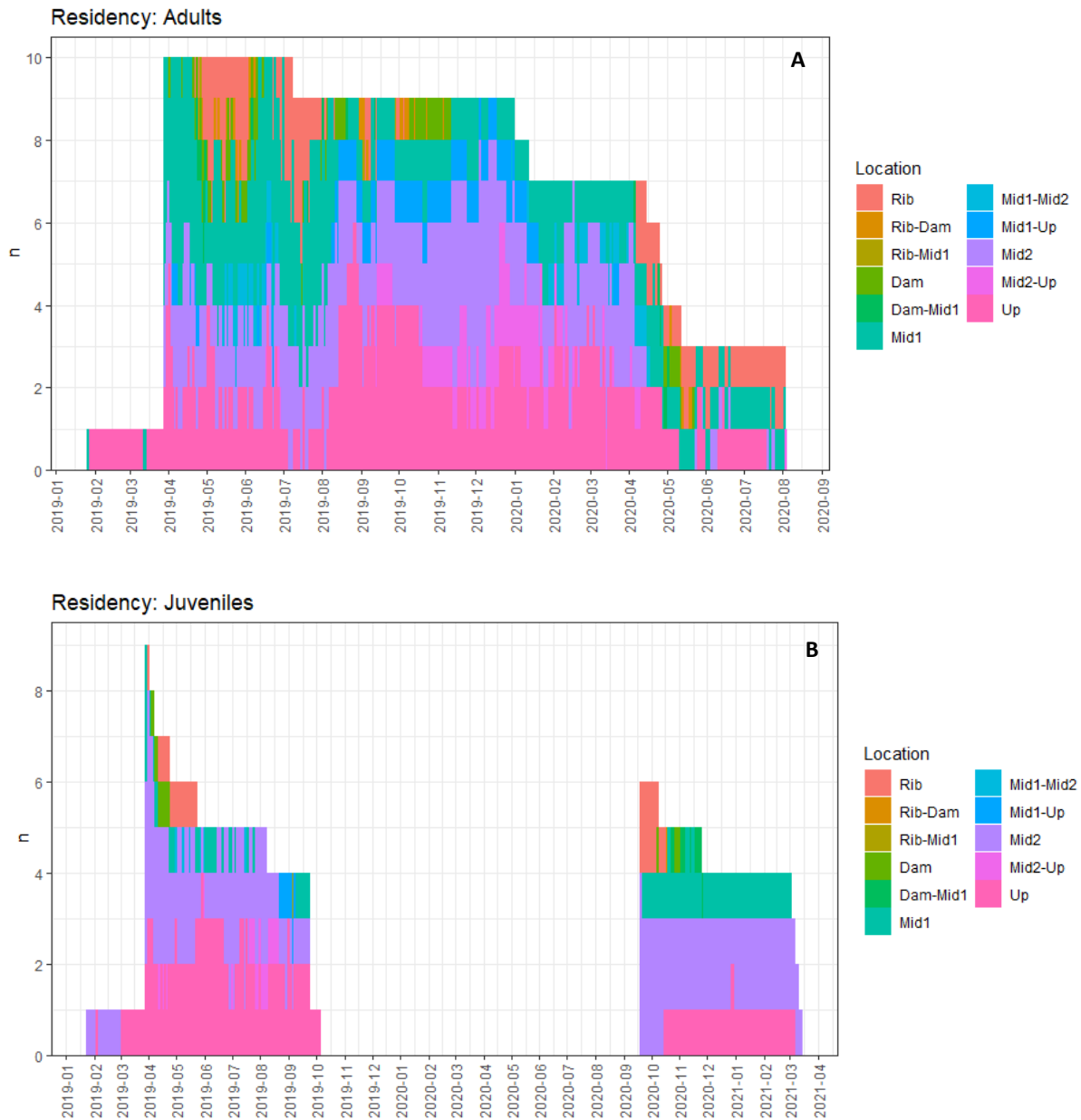


Figure 3.4 – Actel residency plot showing the location where *S. glanis* Adults (A) and Juveniles (B) spent the most time each day. The vertical axis indicates the number of individuals included in the analysis at each day. The locations include the ‘Ribeira de Eiras’ tributary section (‘Rib’), the dam section (‘Dam’), the middle section 1 (‘Mid1’), the middle section 2 (‘Mid2’), the upstream section (‘Up’), as well as the intermediate locations between sections (e.g., ‘Rib-Dam’). These intermediate locations are generated when a tagged fish travels undetectably between sections or when it is being simultaneously detected by two receivers of different sections. Occasionally, a fish (or at least the transmitter’s signal) jumps over a section, creating non-adjacent intermediate sections (e.g., ‘Rib-Mid1’).

3.2 Activity and depth use

The data collected with the transmitters equipped with the 3D accelerometer sensor show some seasonal and monthly variations in activity (Figure 3.5), with higher values being registered in spring and summer months but also during two of the coldest months (December and January). The peak of *S. glanis* activity was observed in August 2019 and May 2020, however, the latter correspond to data of two fish only. autumn is the season with the lowest activities. Autumn is the season with the lowest catfish activity values. The accelerometer sensors rarely registered values close to 0, however, such values were more recurrent in autumn and winter.

The depth sensor (pressure sensor) data show a strong seasonal variation in *S. glanis* depth use (Figure 3.6). The tagged fish generally occupied shallow waters during spring and summer seasons, with median values ranging from 1.8m in May 2019 to 4.6m in September. Between October and March, *S. glanis* occupied deeper water layers, as much as 3 times larger than in warmer months, with median depths of around 10m. When compared to the homologous period of 2019, there is a significant increase in depth values in 2020; nevertheless, these results are based on a small sample size of only three fish. Maximum depths of nearly 30m were registered several times, mostly between August and December.

The Kruskal-Wallis test indicates that there are significant differences in seasonal activity ($\chi^2 = 11486$, p-value <0,0001) and depth use ($\chi^2 = 114058$, p-value <0,0001) values. Similarly, Dunn's test indicates there are differences in activity and depth for any of the seasons' pairwise comparisons (all p-values <0,0001).

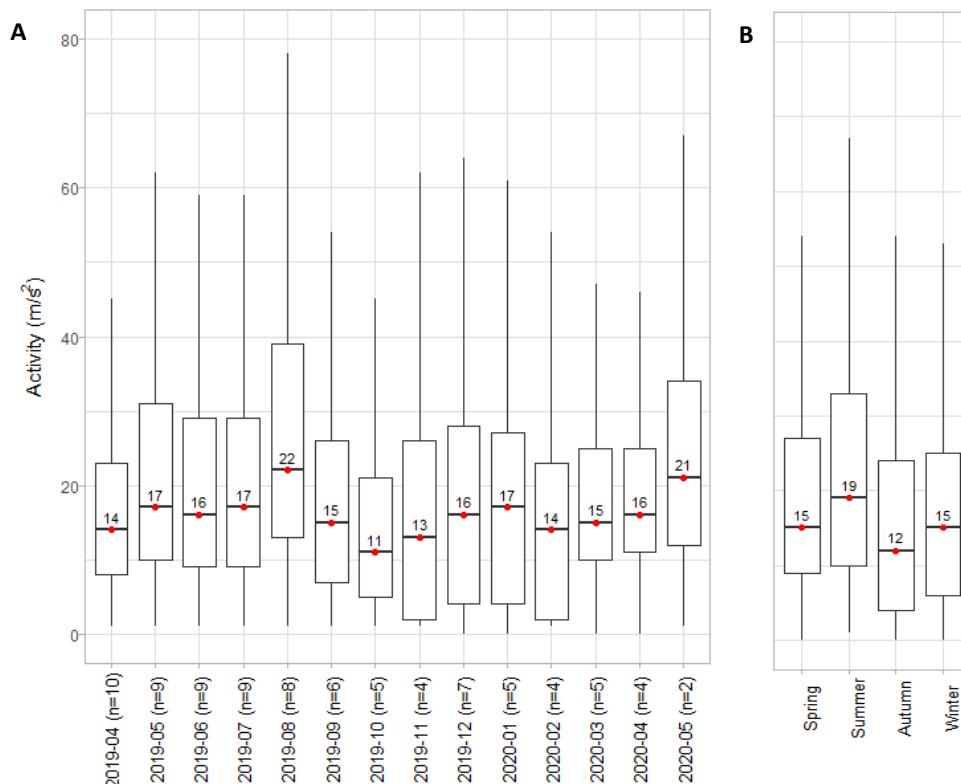


Figure 3.5 – Adult *S. glanis* activity (ARMS) boxplots for each month (A) and annual season (B). Median values are presented. Outliers are omitted as they did not portrait useful information on the activity variations throughout the year and they shrink the scale of the graph.

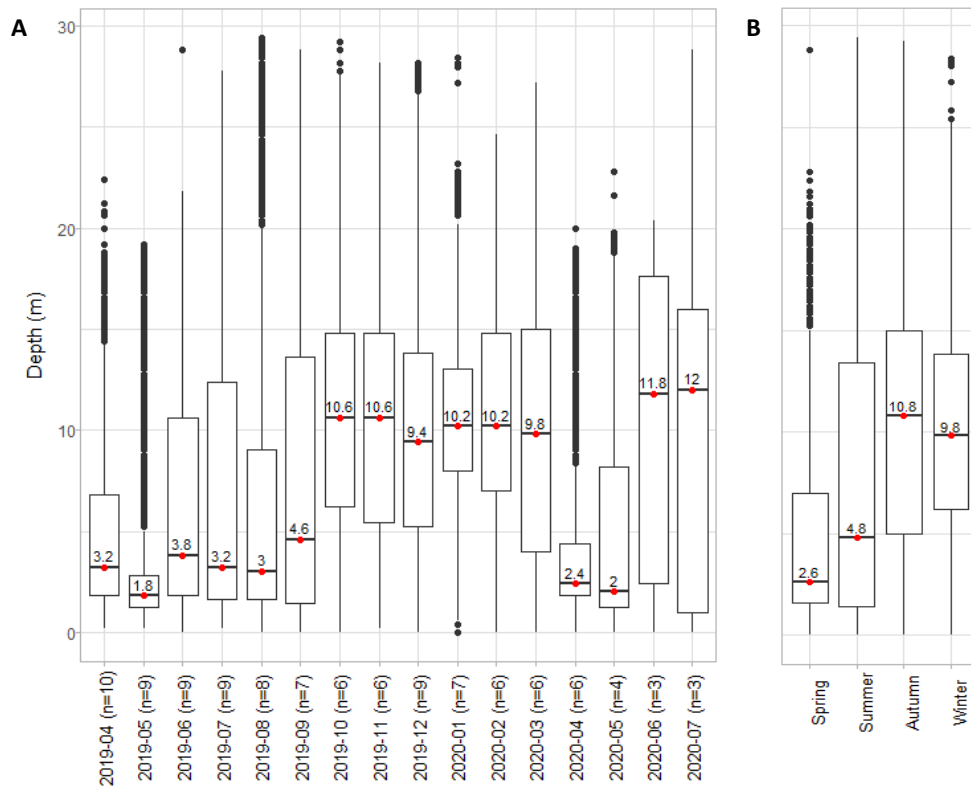


Figure 3.6 – Adult *S. glanis* depth use (ARMS) boxplots for each month (A) and annual season (B). Median values are presented.

Silurus glanis activity displayed a diel pattern that is generally consistent throughout the year: activity reached a peak around dusk, then drops gradually, eventually to a minimum value during the daytime (Figure 3.7). December is the month that deviates more from this pattern, with higher activities taking place during the day. Between October and December, an activity peak at dawn is also identified. In August, after the minimum value at dawn, activity increased gradually along the day.

Circadian patterns in *S. glanis* depth use were found with this study (Figure 3.8). Between December and March, the tagged fish performed clear vertical movements from deeper waters at night to shallower waters at daytime, but rarely reaching the surface. In March, these movements have amplitudes of up to 15 meters. In April and May, the diel amplitude is much smaller than in the rest of the year. Two different patterns are found from June to October: while some fish had considerably stable depth values, others present large variations in depth along the day with distinct interindividual patterns (Annex II, Figure II.1).

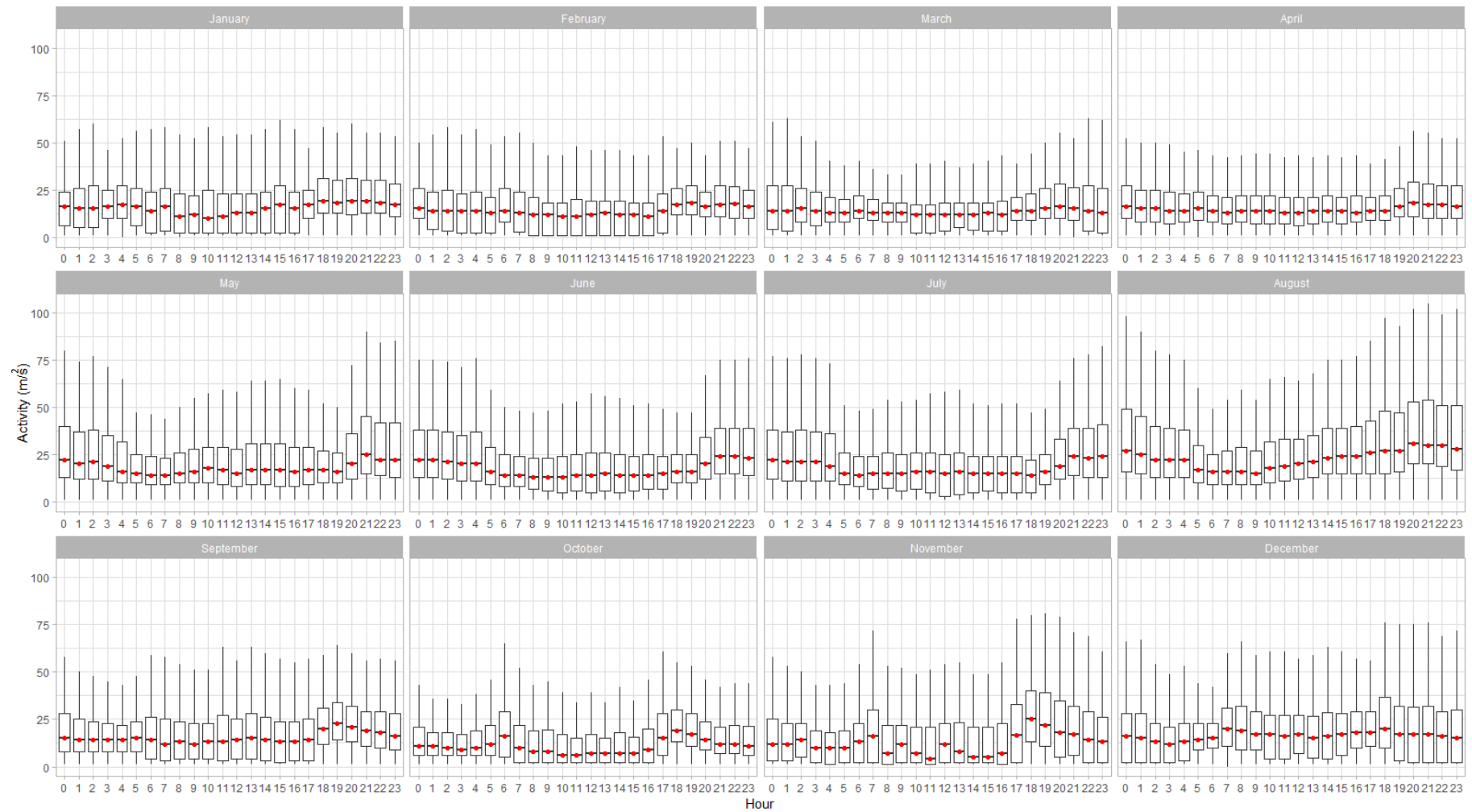


Figure 3.7 – Adult *S. glanis* circadian activity (A_{RMS}) boxplots for each monitored month.

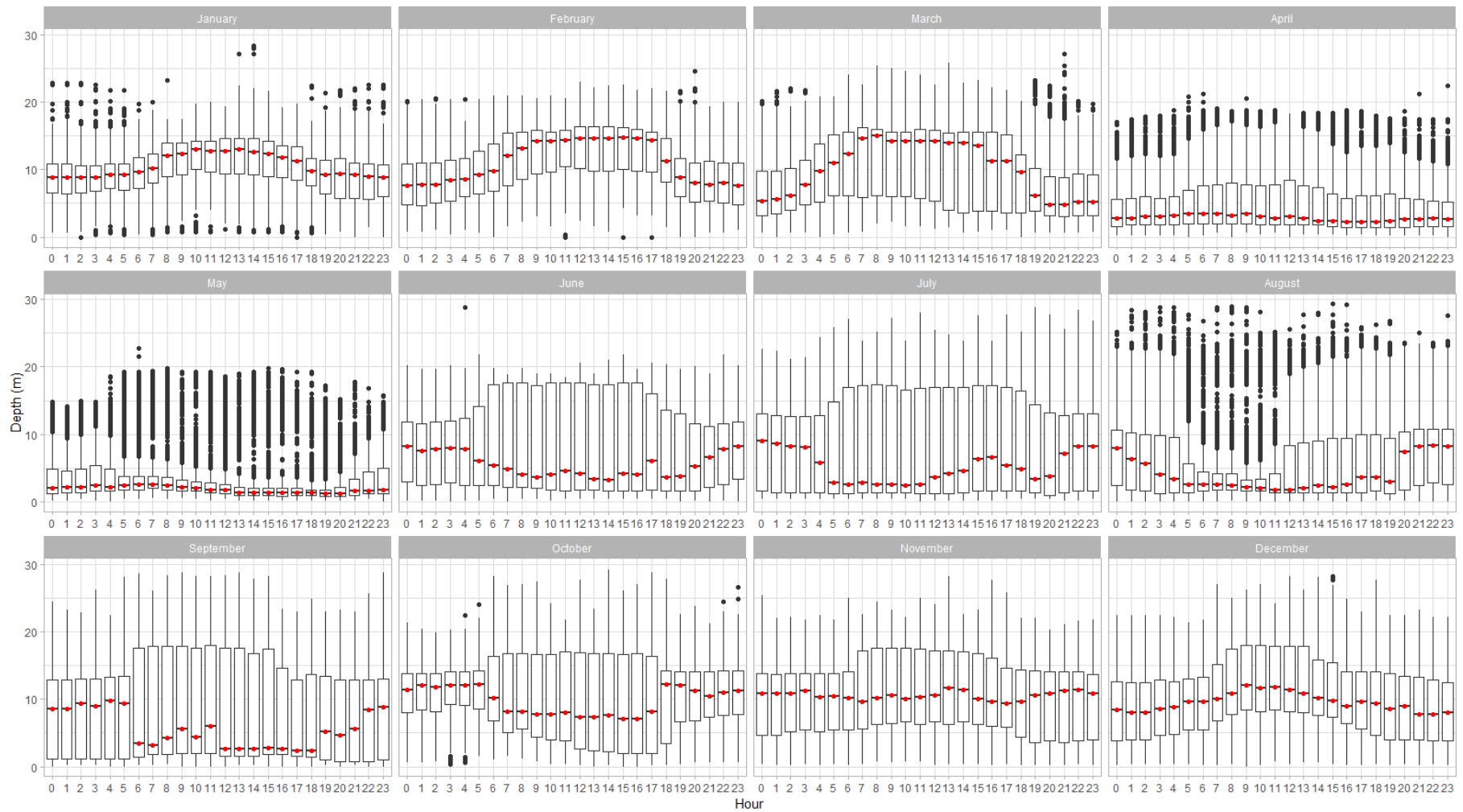


Figure 3.8 – Adult *S. glanis* circadian depth use for each monitored month.

Ten explicative models for activity were created. The log-linked gamma distribution was the chosen family distribution for this strictly positive continuous data. The best-fitted model includes all chosen predictors (Table 3.1). Although the level of correlation between photoperiod and temperature predictors is high (concurrency of 0.669), both variables were used on model creation. The penalized p-values, obtained using the double penalty method for GAMs, confirms the significance of these variables. The large variance in the data, which include a great number of outliers, may explain the considerably low deviance explained value. Nevertheless, both AIC and BIC values, as well as the deviance explained, are comparably better on this model than on the remaining models. Model 10 partial plots (Figure 3.9) reveal a positive and non-linear relationship between water flow and *S. glanis* activity values, and between water temperature and activity. A linear positive relationship is found between moonlight intensity and activity. The photoperiod assumes a non-linear relationship with activity. According to the model, minimum activities occur with photoperiods corresponding to the end of March and beginning of April and to the last 3 weeks of September. On the contrary, maximum activity values happen during the end of April to mid-May, and August. There is also another smaller peak of activity on photoperiods corresponding to the last two weeks of October and mid-February.

Table 3.1 – Forward selection process of the predictors on Generalized Additive Models (GAMs) of the daily mean activity of adult *S. glanis* as the response variable. The Akaike Information Criterion (AIC), the Bayesian Information Criterion (BIC) and the deviance explained are presented for each fitted model

Model ID	Activity Model Formula	AIC	BIC	Deviance explained (%)
1	Y ~ Temp + (1 Ind)	15319	15418	15.40
2	Y ~ Flow + (1 Ind)	15265	15330	8.41
3	Y ~ Moon + (1 Ind)	15373	15439	8.05
4	Y ~ Photo + (1 Ind)	15282	15386	16.40
5	Y ~ Flow + Temp + (1 Ind)	15095	15199	16.10
6	Y ~ Flow + Moon + (1 Ind)	15166	15237	8.88
7	Y ~ Flow + Photo + (1 Ind)	15054	15165	17.80
8	Y ~ Flow + Photo + Temp + (1 Ind)	15001	15129	20.10
9	Y ~ Flow + Photo + Moon + (1 Ind)	14957	15073	18.20
10†	Y ~ Flow + Photo + Moon + Temp + (1 Ind)	14905	15038	20.50

†Model selected as the best fitted.

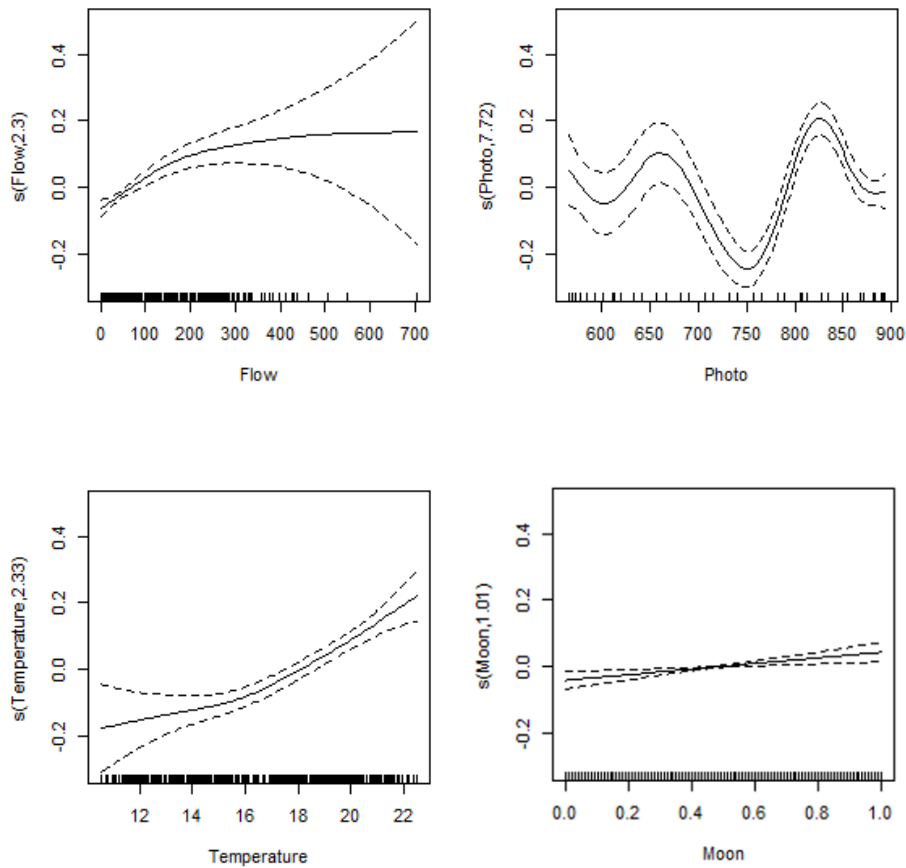


Figure 3.9 – Partial plots of the chosen activity GAM model (model 10) revealing the correlations between the predictors and the activity response variable.

Ten explanatory models were created for the depth use. The chosen distribution family was a log-linked gamma distribution for the strictly positive continuous depth data. The best-fitted model includes all the explanatory variables, which were significant when using the double penalty method (Table 3.2). This model has better AIC and deviance explained but not the best BIC. The best AIC value was the criteria for choosing this model over the others. Looking at the deviance explained, this model, with the same dependent variables as the previous activity models, seems to be better at explaining the response variable. The partial plots for this model show a positive non-linear relationship between water flow and depth use (Figure 3.10). Fish seem to dwell at deeper habitats when the amount of light is lowest, corresponding to the winter period, and use shallower depths in photoperiods corresponding to the spring and late summer period. There is an increase in the depths used when the photoperiod is maximum, in late June. A positive and almost linear relationship exists between the moonlight intensity and depth. The depth use relationship with temperature assumes a non-linear form, with larger depths occurring at ~14°C and when the water temperature reaches its maximum value (22-24°C), around April 2019 and 2020. Perspective plots of the models' predictions (Figure II.2 and Figure II.3), water temperature and water flow (Figure II.4) daily values in Belver reservoir can be found in Annex II.

Table 3.2 – Forward selection process of the predictors on Generalized Additive Models (GAMs) of the adult *S. glanis* depth use response variable. The Akaike Information Criterion (AIC), the Bayesian Information Criterion (BIC) and the deviance explained are presented for each fitted model

Model ID	Depth Use Model Formula	AIC	BIC	Deviance explained (%)
1	$Y \sim \text{Temp} + (1 \text{Ind})$	13587	13701	29.00
2	$Y \sim \text{Flow} + (1 \text{Ind})$	13665	13761	22.10
3	$Y \sim \text{Moon}^* + (1 \text{Ind})$	13750	13829	20.40
4	$Y \sim \text{Photo} + (1 \text{Ind})$	13248	13361	16.30
5	$Y \sim \text{Photo} + \text{Temp} + (1 \text{Ind})$	13241	13380	37.10
6	$Y \sim \text{Photo} + \text{Flow} + (1 \text{Ind})$	13041	13177	38.20
7	$Y \sim \text{Photo} + \text{Moon}^* + (1 \text{Ind})$	13108	13234	36.90
8	$Y \sim \text{Photo} + \text{Flow} + \text{Temp} + (1 \text{Ind})$	13023	13196	38.90
9	$Y \sim \text{Photo} + \text{Flow} + \text{Moon} + (1 \text{Ind})$	12912	13054	38.40
10[†]	$Y \sim \text{Photo} + \text{Flow} + \text{Moon} + \text{Temp} + (1 \text{Ind})$	12891	13070	38.90

[†]Model selected as the best fitted.

*Non-significant variable for a 5% significance level.

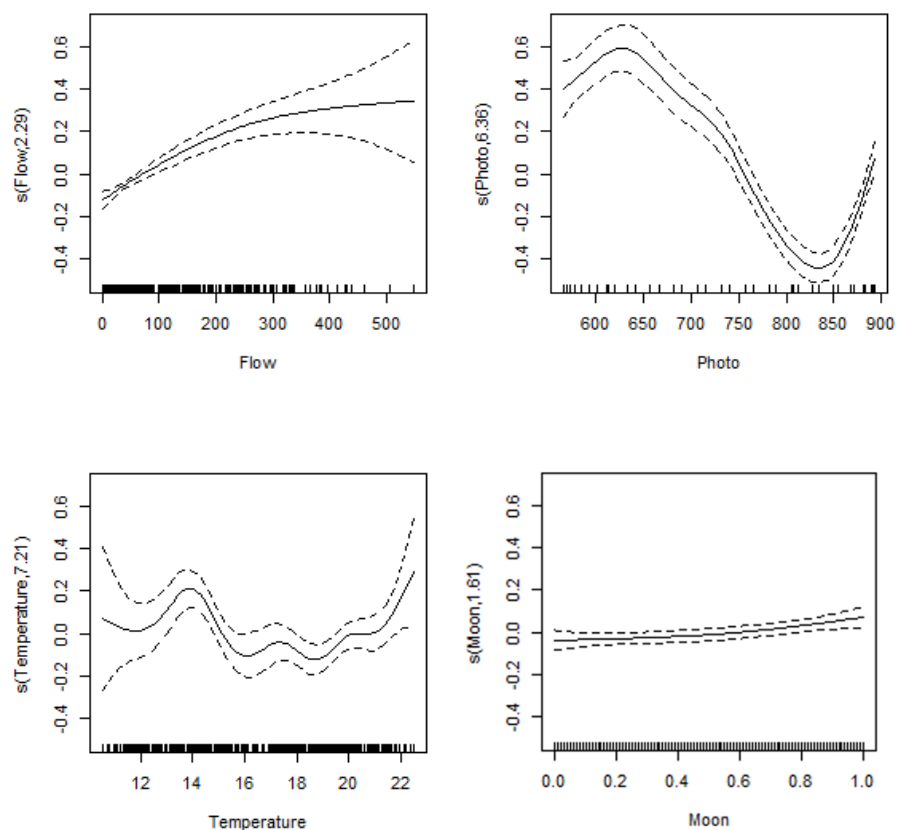


Figure 3.10 - Partial plots of the chosen depth use GAM model (model 10) revealing the correlations between the predictors and the depth use response variable.

Four Hurdle models were created during the process of finding the best explanatory model of the rate of activity outliers, *i.e.*, burst movements (Table 3.3). Due to the high level of correlation between the photoperiod and temperature variables ($\rho = 0.735$), two separate models were computed containing only one of these variables and the remaining set of predictors. The chosen Hurdle model has the lowest AIC and BIC and includes water flow, light period and photoperiod as significant explanatory variables on both binomial and count parts. The results of the selected model (Table 3.4) show that water flow has a positive effect on triggering burst movements (zero Hurdle part) but a negative correlation with the number of outliers' counts (count part). Photoperiod has a positive effect on both components. The *dawn* factor level (Light 1) was used as a reference level in the model so that the remaining levels can be compared to it. The model shows that extreme activity events are more likely to occur at dusk than at dawn and night-time but and more unlikely to occur at daytime, in this order. On the other hand, the frequency of outliers is maximum at dusk and decreases at night-time, dawn and daytime, in this order (Annex II, Figure II.5). The likelihood ratio test confirmed light period overall significance in explaining the rate of outliers. The rootogram validates the quality of the chosen model (Annex II, Figure II.6).

Table 3.3 – Selection process of the Hurdle model of the rate of *S. glanis* activity outliers (Y). Predictors tested for both count and zero Hurdle (binomial) parts of the Hurdle model are presented, as well as the distribution used for the count part – Negative Binomial (NB) and Poisson. The Akaike Information Criterion (AIC) and the Bayesian Information Criterion (BIC) each fitted model are also presented for each of the fitted models

Model ID	Outliers Hurdle Model Formula		Distribution	AIC	BIC
	Zero hurdle part	Count part			
1	Y ~ Flow* + Light + Temp	Flow + Light + Temp	NB	39425	39516
2	Y ~ Flow + Light + Temp	Flow + Light + Temp	Poisson	46388	46472
3 [†]	Y ~ Flow + Light + Photo	Flow + Light + Photo	NB	39195	39287
4	Y ~ Flow + Light + Photo	Flow + Light + Photo	Poisson	45264	45363

[†]Model selected as the best fitted.

*Non-significant variable for a 5% significance level.

Table 3.4 – Results of the selected two-part Hurdle model (model 3) of the rate of *S. glanis* activity outliers. Predictors and model intercept for each Hurdle component (zero Hurdle and count parts) are presented with respective coefficients (Coef), standard error (Std. Error), statistic test (z value) and p-value (p)

Zero hurdle model coefficients (binomial with logit link)				
Logit	Coef	Std. Error	z value	p
Flow	0.00038	0.00013	2.896	0.0038
Light2 (<i>daytime</i>)	-0.49828	0.10902	-4.570	0.0000
Light3 (<i>dusk</i>)	0.28022	0.15113	1.854	0.0637
Light4 (<i>night-time</i>)	-0.05788	0.11284	-0.513	0.6079
Photo	0.00719	0.00025	28.673	0.0000
(Intercept)	3.56832	0.20105	-17.748	0.0000
N=1794				
Count model coefficients (negative binomial with log link)				
NB	Coef	Std. Error	z value	p
Flow	-0.00019	0.00006	-2.898	0.0037
Light2 (<i>daytime</i>)	-0.08287	0.04432	-1.870	0.0615
Light3 (<i>dusk</i>)	0.49830	0.05551	8.977	0.0000
Light4 (<i>night-time</i>)	0.29755	0.04575	6.504	0.0000
Photo	0.00126	0.00012	10.946	0.0000
(Intercept)	-3.69553	0.09950	-37.140	0.0000
N= 6752				

4. Discussion

This study presents the first work that used tags with sensors to monitor *S. glanis* activity and depth use behaviours with a robust sample of fish in its invaded range. Using the latest technology in acoustic biotelemetry with transmitters equipped with 3D-accelerometer and pressure sensors, new and detailed insight into the activity and depth use patterns of this catfish were obtained. This study is also the first to compare longitudinal space use and movement behaviour between adult and juvenile *S. glanis* over an annual cycle in a single locality, in a non-native area. By combining the longitudinal and vertical (collected by the pressure sensors) space use, a comprehensive view of adult catfish habitat use throughout the year was obtained and compared to its activity.

The presented results indicate that adult *S. glanis* use considerably larger areas across the year than juveniles. Moreover, a temporal increase in area used was observed from colder to warmer months in adult fish, while this increase was not identified in juveniles. In adult fish, space use varied seasonally with a tendency for the use of specific reservoir sections throughout the year. *Silurus glanis* activity also varied considerably along the year, with adult fish more active in summer and late spring. Activity levels were higher at night and maximum at dusk relatively to the day period. Considerable seasonal variations were found in the vertical usage of the reservoir, with fish occupying deeper habitats during colder months and shallower habitats during warmer months. Circadian patterns on depth use were observed with different shapes along the year and with some interindividual variations. Water flow, water temperature, photoperiod and moonlight intensity were found to be significant drivers of catfish activity and depth use.

One of the main constraints in this work regarding the comparison of adult versus juvenile behaviour is related to the limited monitoring time of the juvenile fish. In addition to the shorter battery lifespan of the juveniles' transmitters (est. 6 months), a significant percentage of juveniles had shorter monitoring durations than expected which conditioned data acquisition. The relatively low spatial resolution of the receivers' array also constrains the identification of certain movement behaviours and space use patterns with higher definition. Moreover, the effects of water dissolved oxygen, considered as an important driver of catfish behaviour (Daněk *et al.*, 2014), were not analysed in this study, as the data was not available for the complete annual cycle on this reservoir. Despite these constrains, it was still possible to perform meaningful comparisons of space use between adults and juveniles and to obtain information about other ecologically important variables that drive its behaviour.

4.1 Longitudinal space use

Considering the used areas consistency between juvenile individuals and among the two monitoring periods of juvenile fish, during which adults had constantly larger monthly areas, it is reasonable to believe that the differences in behaviour found between adults and juveniles are ontogenic related and not due to the continuously shorter monitoring time of the juvenile group (maximum 8 months for juveniles and 16 months for adults). These results were consistent with Slavík *et al.* (2007) that observed that adults used larger areas than juveniles in their native range.

The juveniles present a consistency in the size of the used areas but, in the case of adults, the spatial use varied seasonally, with smaller used areas in autumn and winter and then a progressive increase until spring and summer, where used areas have the largest dimensions. These results differ from other studies that found that juvenile used areas size changes seasonally (Slavík *et al.*, 2007; Daněk *et al.*, 2016) and it is highly correlated with water temperature and water flow (Slavík *et al.*, 2007; Daněk *et al.*, 2016),

similarly to what happens with the adults. Smaller-scale seasonal space use variations of juveniles that cannot be captured due to the coarser spatial resolution of the receivers' array may explain these results.

A relation between the size of the used areas and the sections used by adult *S. glanis* in the study area seemed to occur. In colder months, between October and February, the size of the used areas decreases while *S. glanis* starts occupying more upstream areas. In previous studies, the decrease in the size of the used areas was regarded as a response to low temperatures, that reduce metabolism, and high flows (Slavík *et al.*, 2007; Ferreira, 2019), to minimize energetic costs. Upstream sections, which are progressively more lotic, are likely to have better conditions perhaps for feeding, due to higher prey availability during that period of the year, or provide better refuge, or better environmental conditions. Given that these conditions are supplied, *S. glanis* prefers to defend energetically optimal areas rather than large areas, as it is energetically more profitable (Slavík, Horký and Závorka, 2014). Between September and December, three individuals have exited the study area upstream, perhaps in search of such conditions. These upstream migrations can extend over 10 kilometres in the Belver reservoir (Ferreira, 2019). In every case, all tagged fish have returned to the study area.

In periods of larger used areas (April to September), adults tend to extend their space use areas towards more downstream sections, including the 'Ribeira de Eiras' stream. It is presumed that the increase in used areas is mostly related to foraging and reproductive events. Given the physiological optimum of 25-27°C (Copp *et al.*, 2009), the higher water temperatures in this period rise the catfish's metabolism, increasing mobility (Slavík *et al.*, 2007). *Silurus glanis* feeding tends to increase in warmer seasons (Copp *et al.*, 2009), suggesting a higher foraging activity that may result in larger longitudinal movements.

Between April and May, some adults start using the 'Ribeira de Eiras' tributary more intensely until the end of summer, with up to half of the fish spending most of the daily time at this section. This is consistent with what was found by Ferreira (2019) in the same study area, supporting that the occupation of this shallower section is replicated annually by different individuals and suggests a potential spawning aggregation. *Silurus glanis* tends to prefer shallower areas where it builds its nests in the spawning season (Kuzishchin, Gruzdeva and Pavlov, 2018), which in Turkish reservoirs happens between early June to August (Alp, Kara and Büyükçapar, 2004), and when water reaches a minimum temperature of 18-22°C (Copp *et al.*, 2009). Such temperatures in the Belver reservoir occur at the beginning of May (Annex II, Figure II.4A), which correspond precisely to the time of arrival of adult *S. glanis* to Ribeira de Eiras. This tributary has maximum depths of around 4m but, for most of the area, the habitats are quite shallow, generally below 2.5m. Migrations related to reproduction, including migrations to find partners and spawning sites are a known catfish behaviour (Copp *et al.*, 2009). Other migrations to unidentified spawning areas within the study site are probable. Such migrations contribute surely to the increase of the used areas in the reproductive season, which can last some months (Alp, Kara and Büyükçapar, 2004) and with females capable of laying multiple batches of eggs (Zholdasova and Guseva cited in Copp *et al.*, 2009).

Six juvenile fish had much shorter detection periods than the six months expected. In such cases, assuming no technical issues with the transmitters or respective batteries, the logical explanation is fish recapture by fishermen or fish dispersal from the study area. Considering the receiver where the fish were last detected, it is presumed that four of the juveniles were recaptured (last detection at 'Mid1', 'Mid2' or 'Rib' section) and two have dispersed downstream, through the dam by an unidentified route (last detection at 'Dam' section). Downstream dispersal is a known *S. glanis* behaviour (Gago *et al.*, 2016) usually performed by juvenile individuals (Slavík *et al.*, 2007). Regardless of these two dispersal

events, the remaining juvenile fish consistently remained within the study area boundaries; and despite the migrations upstream, no dispersal events were recorded for the adult fish. These results confirm once again *S. glanis* site fidelity (Carol, Zamora and García-Berthou, 2007; Brevé *et al.*, 2014; Daněk *et al.*, 2014) and the propensity to disperse during the juvenile stage (Slavík *et al.*, 2007).

4.2 Depth use and activity

Significant seasonal differences in depth use and activity were detected. Circadian patterns on vertical movements and activity were also identified. A seasonal vertical displacement is found between spring and summer, and autumn and winter months. During colder seasons, *S. glanis* is found in deeper waters generally within the most upstream areas of the study site. Although deeper areas are available (up to 30m), the tagged *S. glanis* generally occupied intermediate depths of around 10m, probably close to the riverbank where they tend to be more abundant, at least during colder periods in perialpine lakes of northern Italy (Santis and Volta, 2021). The increase in depth of the used areas in these periods could also be triggered by a decrease in light availability and an increase in water flow, as the depth use model indicates. All adult tagged *S. glanis* in April and May used shallow depths, generally below 5 meters of depth, independently of which section the fish were located. Knowing that *S. glanis* prefers shallow waters to spawn, it is suggested that the observed shallow depths in these months largely reflect a reproductive behaviour. If this is true, besides the ‘Ribeira de Eiras’ stream, there are possibly other spawning grounds in the study area. In summer, a dualistic behaviour is observed: while some fish continued roaming in shallow waters throughout the day, others occupied considerable deep waters, at least in some periods of the day, with different interindividual circadian patterns in vertical migrations (Annex II, Figure II.1). The use of shallow waters and the ‘Ribeira de Eiras’ stream may indicate that *S. glanis* reproductive period in Belver reservoir could extend further into summer, as described by Alp, Kara and Büyükçapar (2004) in a Turkish reservoir. Shallow depths could also refer to a predominant forage behaviour in these areas. Nevertheless, the high flows registered in Belver reservoir for this season may trigger the search for deeper waters by some fish, perhaps to find refuge in deeper areas to save energy or due to an increase in the number of invertebrates in deeper areas during high flow conditions (Copp *et al.*, 2009), on which *S. glanis* feeds (Ferreira, Gago and Ribeiro, 2019).

A circadian pattern on the vertical habitat use was observed for most of the year and all tagged adult catfish. Between December and March, *S. glanis* performed clear daily vertical movements, from deeper depths during the day to shallower depths at night. Considering the nocturnal activity increase in the corresponding months, it is possible that the night movements to shallower depths are associated with foraging behaviour after a more stationary period during the day, presumably in areas closer to the river bank (Carol, Zamora and García-Berthou, 2007). Catfish spatial displacement patterns between resting and foraging areas have been described in Central Europe and North America (Daugherty and Sutton, 2005; Carol, Zamora and García-Berthou, 2007; Kadye and Booth, 2013). Between April and May, this species generally occupies shallower habitats (<5m) during the entire day, probably corresponding to *S. glanis* presence in spawning sites, as previously suggested. In summer, the only clear vertical movement pattern is observed in August, where there is a tendency for staying at shallower depths during the day. In August, the activity levels are also higher during the night, suggesting *S. glanis* tend to rest in shallower areas, contrary to what happens in winter months.

Significant seasonal differences in activity levels were observed. The activity results obtained with the accelerometer sensors are partly convergent with the existing information on activity based on fish longitudinal movements as a proxy. *Silurus glanis* was highly active in summer corresponding to what was described by Slavík *et al.* (2007), and Daněk *et al.* (2016) for juvenile fish in Central Europe.

However, in Belver reservoir, the tagged fish were fairly active during spring and winter, contrary to what was found by Slavík *et al.* (2007) and Daněk *et al.* (2016), respectively. In such studies, the consideration of longitudinal movements as a proxy of activity levels may not reflect the actual activity of the fish. For instance, activity related to short movements within small areas or vertical movements will not be measured and activity levels will be underestimated. In colder months at Belver reservoir, it was found that although activity decreases, it is not greatly different from the rest of the year, even though the used areas are smaller. This indicates that even when *S. glanis* occupies smaller areas, they tend to stay active, probably by making more intensive use of the available resources, longitudinally and vertically. Since in Belver reservoir water temperatures never reaches the low values of Central Europe rivers (<8°C), it is possible that *S. glanis* can stay active even in colder seasons, but still reducing the area used. An additional explanation for the considerable high levels of activity in the winter months, and especially between December and January, is an increase in directional movement due to water flow rise, as the explicative model reveals a positive relationship between flow and activity, also found in Daněk *et al.* (2016) for juvenile fish. The reduced water flow in autumn may explain the minimum activity levels in this season.

In warmer months, higher activity levels correspond to an increase in water temperature, as it approaches *S. glanis* physiological optimum of 25-27 °C (Copp *et al.*, 2009). The activity model confirms this positive relationship between water temperature and activity, as previously observed (Slavík *et al.*, 2007; Daněk *et al.*, 2016). The highest activity levels registered in August 2019 and May 2020 match, indeed, the water temperature maximum (~23°C). The increase in metabolism in these seasons results in higher foraging and prey consumption (Copp *et al.*, 2009) which may explain the high activity levels. Movement related to reproduction may as well be a factor contributing to this increase. Although there is a modest seasonal positive correlation between the size of the used areas with the activity levels, a clear monthly correlation is not found.

Silurus glanis displayed a constant circadian pattern of activity, with a remarkable activity peak at dusk and higher nocturnal activity, as depicted by Carol *et al.* (2007) for a catfish population in Ebro River, Spain, and a smaller peak at dawn was also identified between October and December. Such activity peaks match the diel vertical movements, as mentioned earlier, and could be linked to foraging behaviour (Carol, Zamora and García-Berthou, 2007). The explicative model on *S. glanis* extreme activity reveals that burst movements, most likely related to foraging and predation events, are predominantly crepuscular, indicating that *S. glanis* tends to hunt in such day periods. The diel values clearly show that even in autumn and winter, activity rarely ceases completely, and when it does it occurs during the day at deeper depths, presumably when *S. glanis* is stationary next to the river bottom in lentic areas with dense vegetation, tree trunks or large stones (Carol, Zamora and García-Berthou, 2007). The activity increase during the night may be also related to an increase in the longitudinal movements during this day period.

5. Final remarks

The European catfish (*Silurus glanis*) is a non-native species to Iberian waters with an invasive character. Due to its big dimensions, high fecundity and predatory potential (Copp *et al.*, 2009; McKnight *et al.*, 2017; Vejřík *et al.*, 2017; Cucherousset *et al.*, 2018; Ferreira, Gago and Ribeiro, 2019), this catfish has a significant impact on freshwater ecosystems in which it is introduced. The most concerning impact relates to the pressure it places on native and even on migratory species, as they constitute a big share of this catfish's diet in the Tagus River (Ferreira, Gago and Ribeiro, 2019). This pressure is of most concern when endangered species such as the European eel (*Anguilla anguilla*, L., 1758) or the sea lamprey (*Petromyzon marinus*, L., 1758) are involved. If allowed to spread further into other Tagus tributaries, *S. glanis* may as well impact other endangered species, such as the critically endangered Lisbon-arched-mouth-nase (*Iberochondrostoma olisiponense*, Gante, Santos and Alves, 2007) (Verissimo *et al.*, 2018) and the Iberian barbel (*Luciobarbus comizo*, Steindachner, 1864) (Antunes, Cobo and Araújo, 2015). Thus, it is recommended that measures aiming at *S. glanis* control should be put into practice as soon as possible.

Firstly, it is highly recommended that Portuguese competent organizations and authorities (e.g., the Portuguese Environmental Agency – APA, and the Portuguese Institute for Nature and Forests Conservation - ICNF) promote actions to avoid *S. glanis* dispersal into other reservoirs and hydrographic basins. *Silurus glanis* presence in Portugal is only confirmed in the Tagus basin but some citizen science data already evidence its presence in the Douro River (Martelo *et al.*, 2021). Recreational anglers are the main vector of *S. glanis* dispersal into non-native waters and spread of the species within the Iberian Peninsula (Gago *et al.*, 2016; Cucherousset *et al.*, 2018) and so it is advised that awareness actions alongside these fishermen regarding the impacts of this species' introduction should be done. If the anglers learn that the catfish is a serious threat to native communities and can also impact the general abundance of other species in rivers and streams that they enjoy fishing, they may be persuaded on stopping the translocation of individuals to other rivers and basins.

Secondly, since the *S. glanis* Tagus population is well-established and thriving (Ribeiro, F. and Quintella, B., unpublished data), it is of most importance that population control actions are executed. It is at this point that the work here presented is important. Understanding the ecology and behavioural patterns of an invasive species is the elementary step for developing or improving strategies for population control. The findings of this study will hopefully help to increase the spatial/temporal effectiveness of removal actions, maximizing the capture of individuals. Considering the observed patterns, it is proposed that removal efforts in Tagus River should focus on spring and summer (particularly at the end of April, in May and in August) and, for maximal effectiveness, nets and/or longlines should be placed perpendicularly to the riverbank during the day for catching the fish in late afternoon and night when *S. glanis* is more active and performs larger horizontal movements. In such seasons, the fishing instruments should aim for the first third of the water column (in Belver reservoir within the first 5-10 meters of depth).

Moreover, in Belver reservoir, the migration of individuals to the 'Ribeira de Eiras' stream, which begins by the end of April, constitutes an excellent opportunity for catching a larger number of fish, both in Tagus stretch as well as in the stream. Potential spawning sites where *S. glanis* aggregates should be identified, typically shallower and still water areas (<5 meters of depth), and the fishing effort should be enhanced next to those areas. Considering the behavioural patterns of *S. glanis* in the Belver reservoir are representative of the behaviour of the fish in other Tagus reservoir with run-off-the-river dams like 'Cedilho' or 'Fratel' dams, the same capture strategy should apply in these reservoirs.

Other telemetry studies have helped the control and even the eradication of invasive freshwater fish species, with special success in fish species that perform aggregations, as in the case of *S. glanis*, through mass removal of individuals (Crossin *et al.*, 2017). Vejřík *et al.* (2019) presented hook lines as a particularly efficient way of removing large numbers of individuals, estimating that 20 individual fishermen could reduce populations of this fish to 10% of their original size in one fishing season using this method. It is also financially and physically less demanding than, for instance, electrofishing. The help and experience of professional fishermen in this process is extremely valuable and so it is also important to enlighten and convince them about the potential danger *S. glanis* poses to the fish communities, namely to their high-value fish (mostly migratory species).

Live fish bait appears to be an effective and selective bait for catching adult catfish in hook lines in native waters, especially when using predatory fish. Juvenile catfish, on the other hand, are more easily caught using invertebrates, which are less selective (Vejřík, personal communication). In Lower Tagus, however, one of *S. glanis* preferent prey is the red swamp crayfish (*Procambarus clarkii*, Girard, 1852) (Ferreira, Gago and Ribeiro, 2019), so the two taxa should be tested as catfish live bait in hook lines for future removal actions.

In the future, it would be important to develop studies assessing the gonad maturation levels along the year to confirm *S. glanis* reproductive period in the Tagus basin. With the Judas fish technique (Bajer, Chizinski and Sorensen, 2011), the tracking of some tagged fish could identify the catfish spawning and aggregations sites, in order to allocate the removal efforts for such sites for better removal effectiveness. For the same reason, and because behavioural patterns may differ from lentic to lotic environments, activity and depth use patterns should also be assessed for the lotic portions of the Tagus basin, which are the areas that accommodate the endangered diadromous fish that this catfish predaes and the areas of co-occurrence with the critically endangered Lisbon-arched-mouth-nase. To improve the spatial resolution on the catfish location, which in this study constrained the identification of certain movement behaviours and space use patterns, a receiver triangulation method could be used, although a considerably higher number of receivers would be required.

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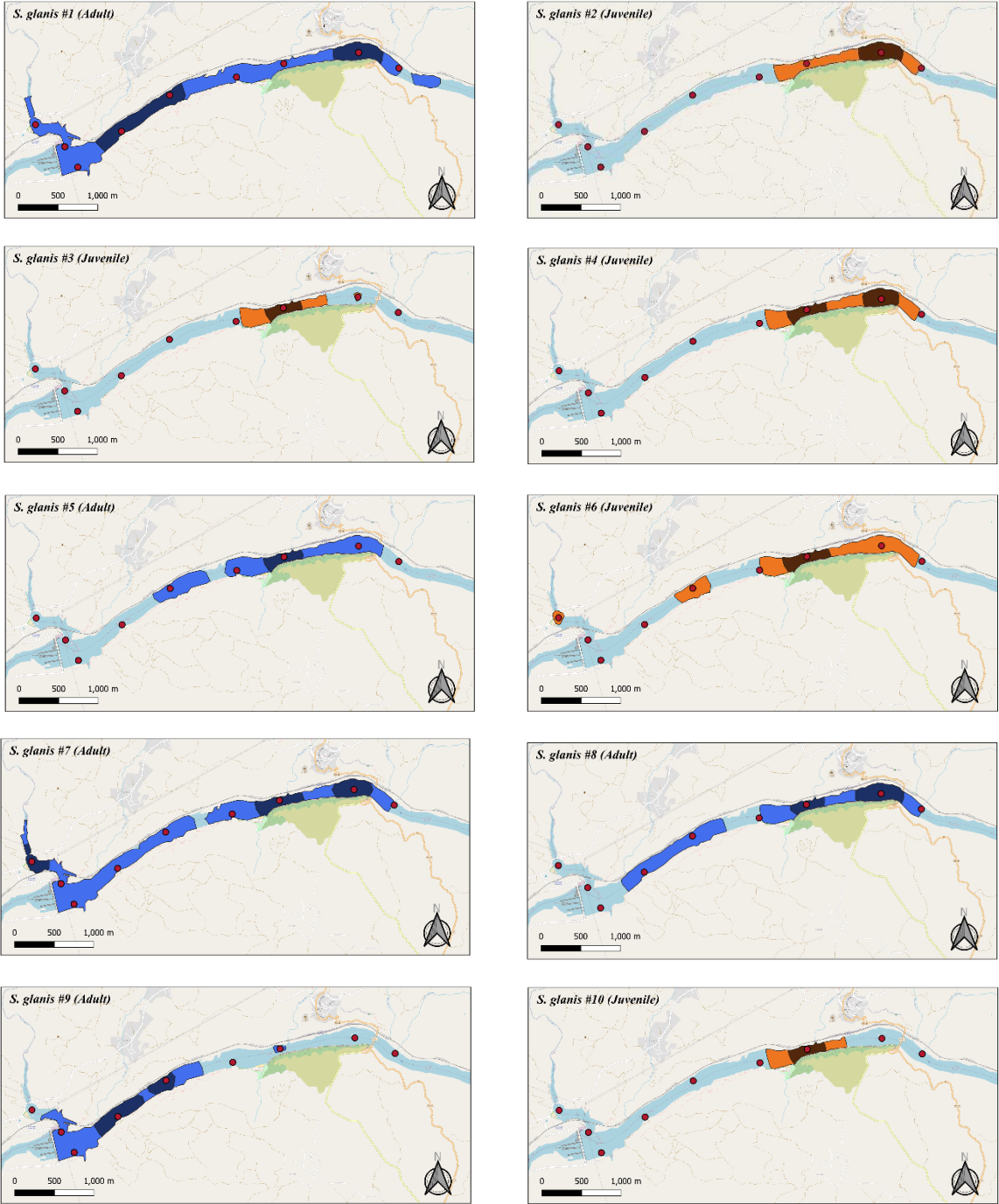
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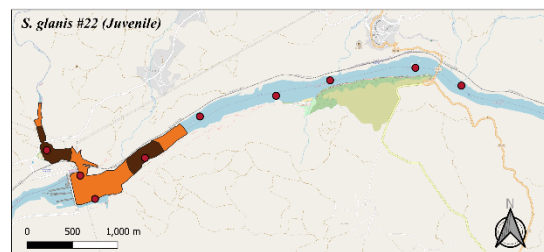
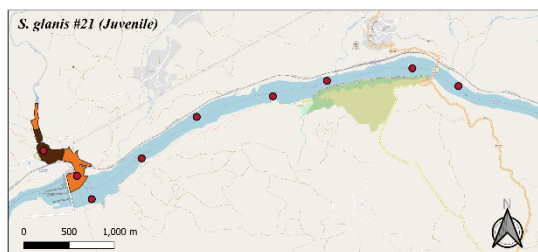
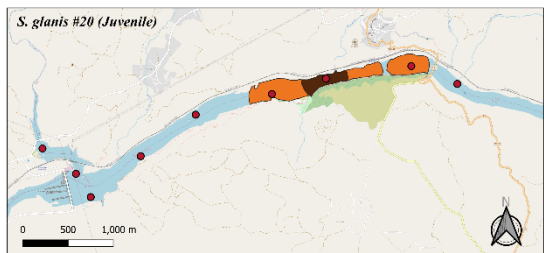
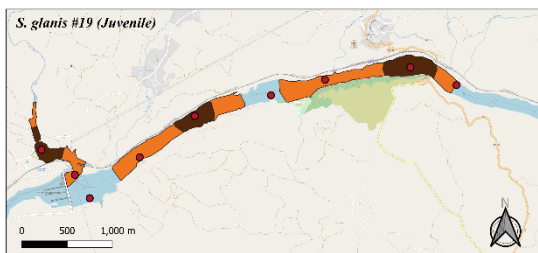
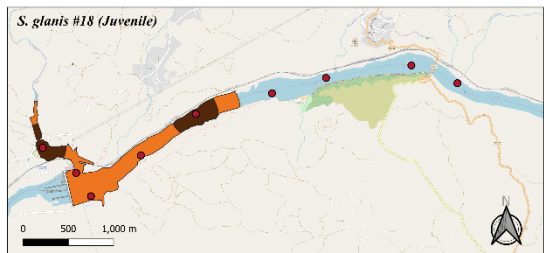
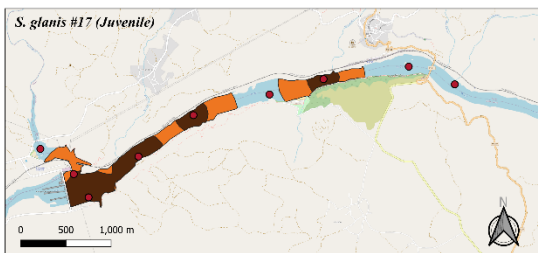
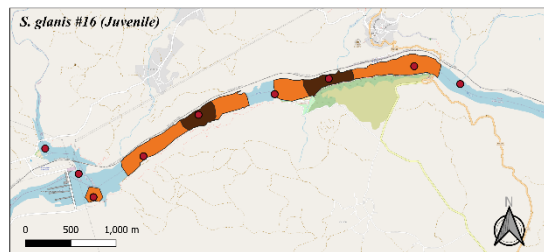
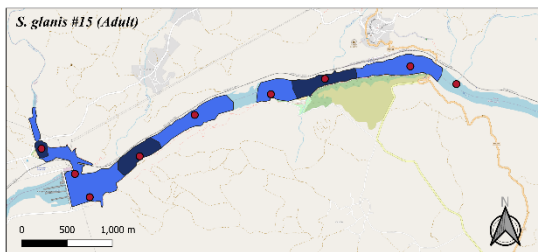
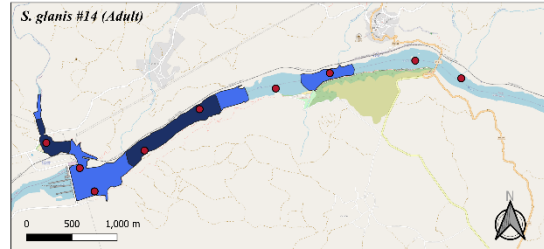
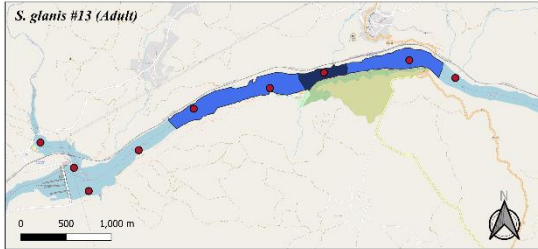
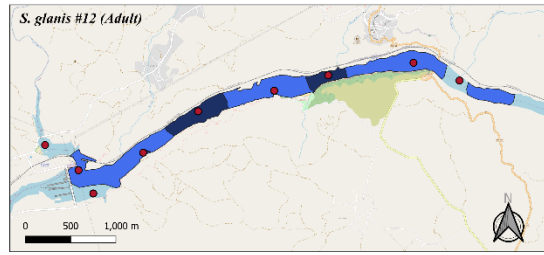
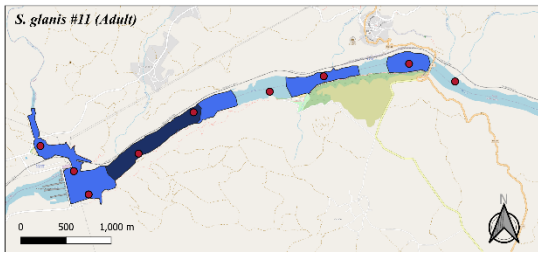
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Annex I

This annex contains supplementary material about the tagged *Silurus glanis* longitudinal space use and movement behaviour.



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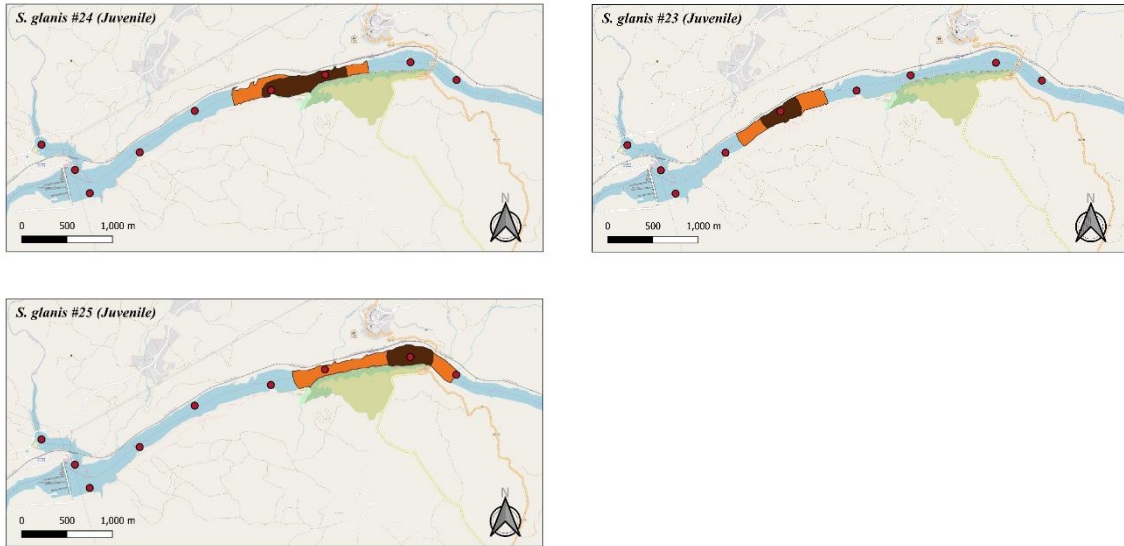
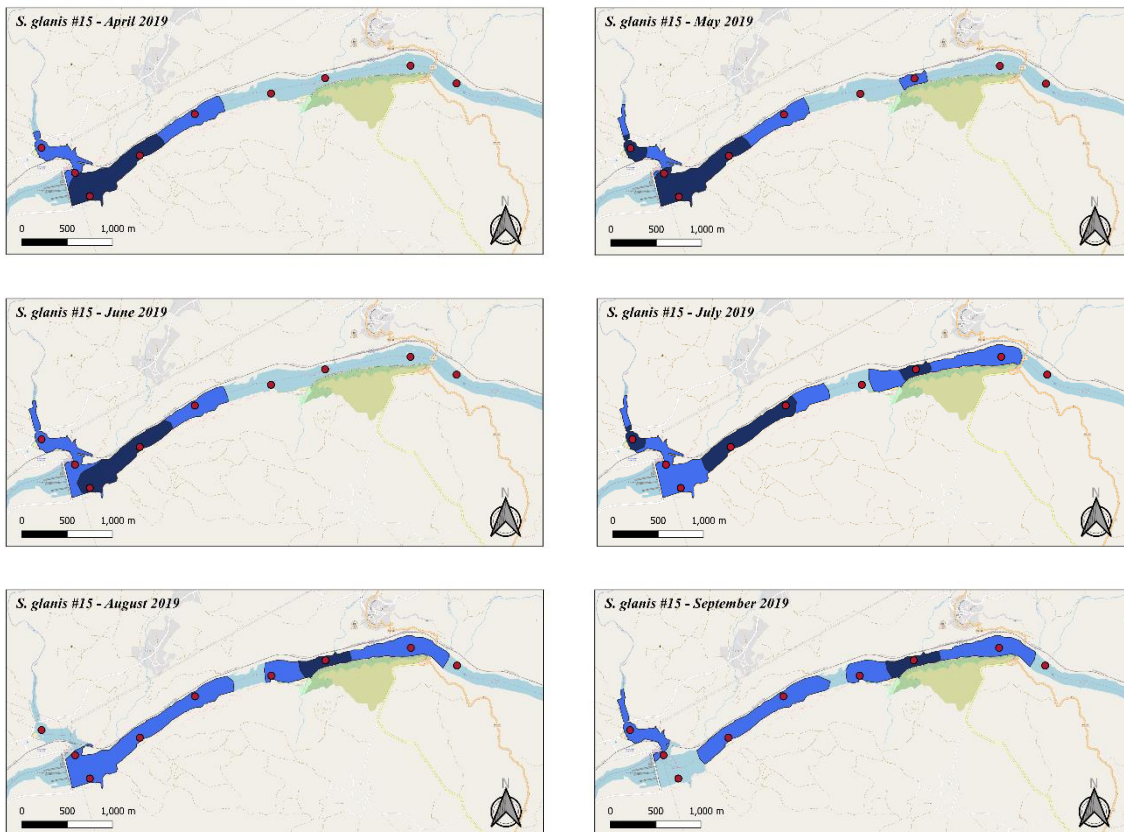


Figure I.1 – Distribution of the tagged *S. glanis* vital areas for the entire monitored period. Lighter colors represent the BRB95 areas and darker colors the BRB50 areas. For the adult fish, these areas represent the home-range and core-range, respectively, since the detection period for every fish (except individual #14) corresponds to almost or more than one year cycle. The red dots correspond to the receiver stations.



(Figure continues in the next page)

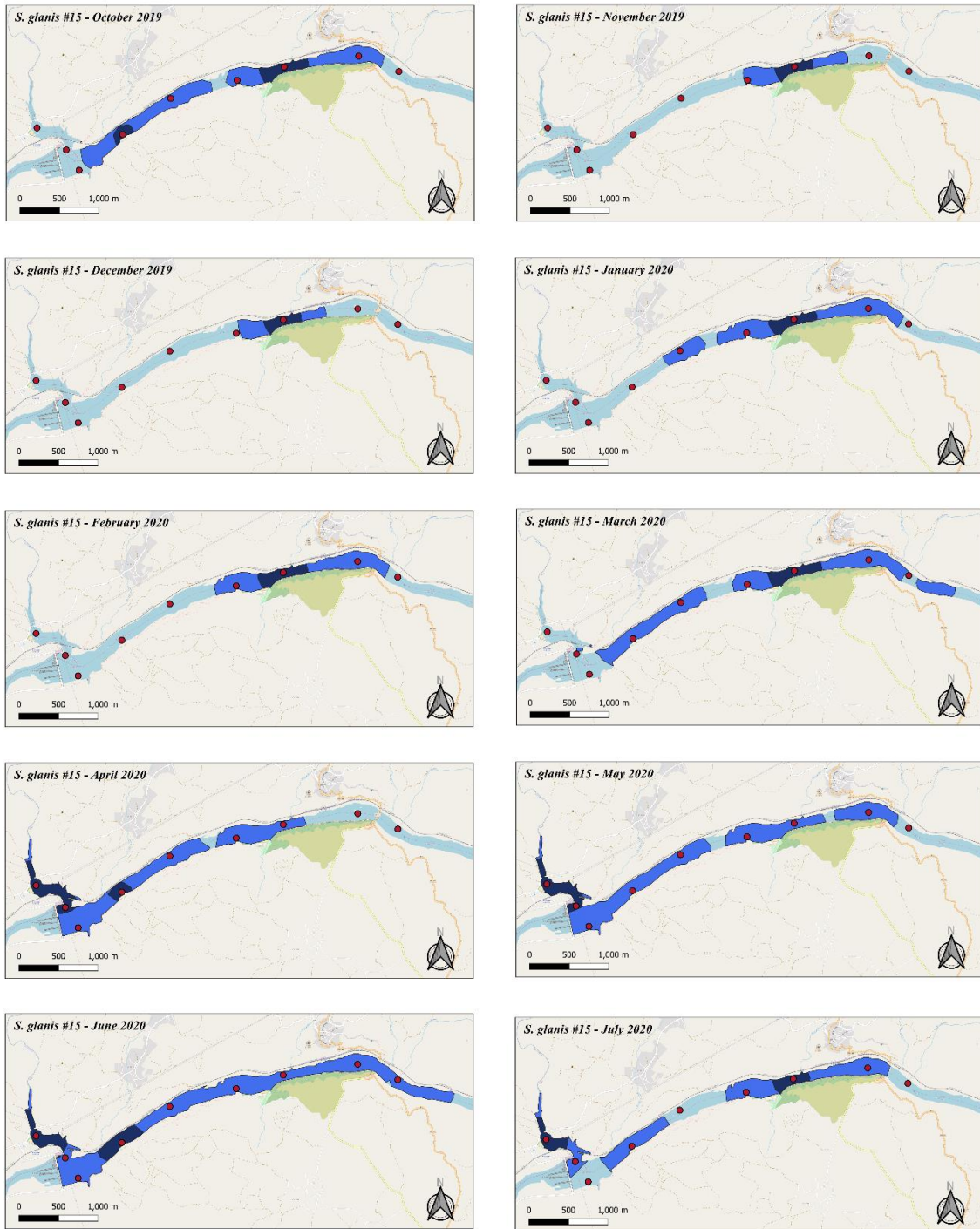
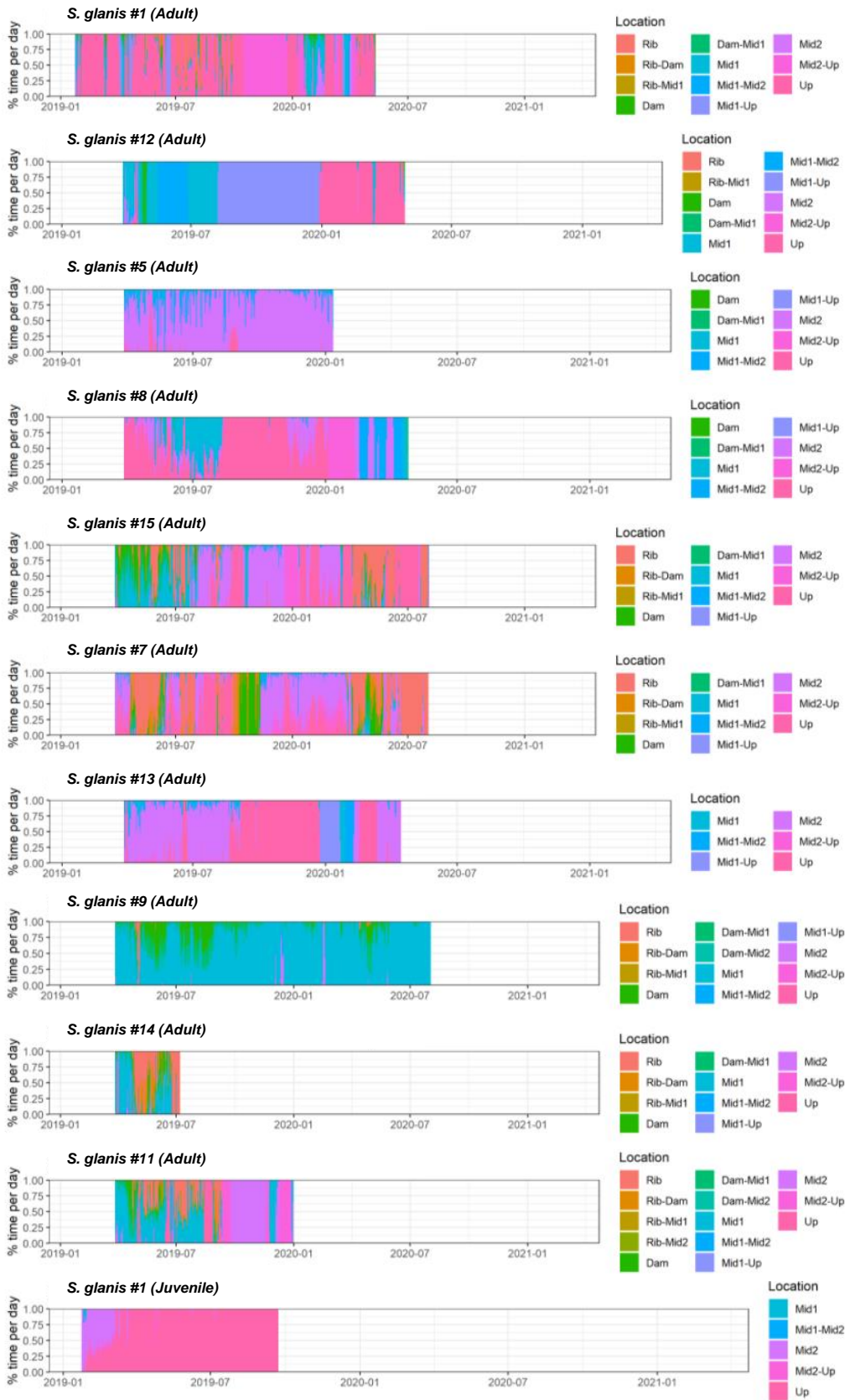
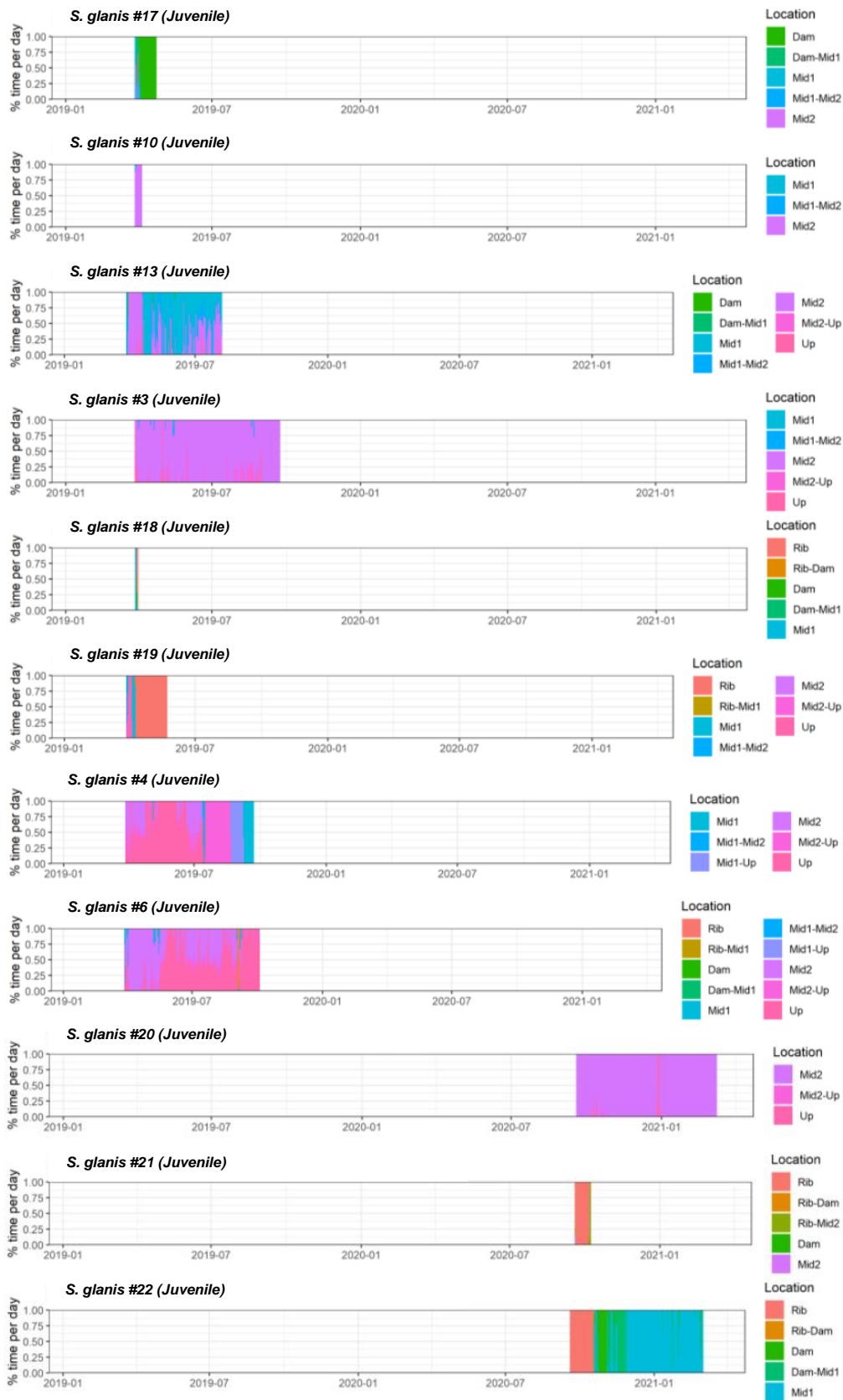


Figure I.2 – Monthly distribution of a tagged adult *S. glanis* (#15) vital areas, which was chosen as the best representation of the general annual behaviour of an adult *S. glanis* in the study area. Lighter colors represent the home-range areas (BRB95) and darker colors the core-range areas (BRB50). The red dots correspond to the receiver stations.



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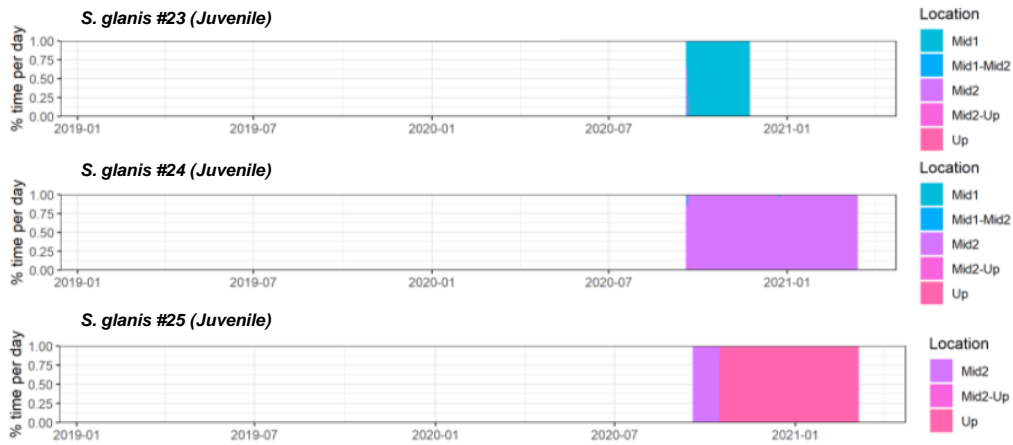
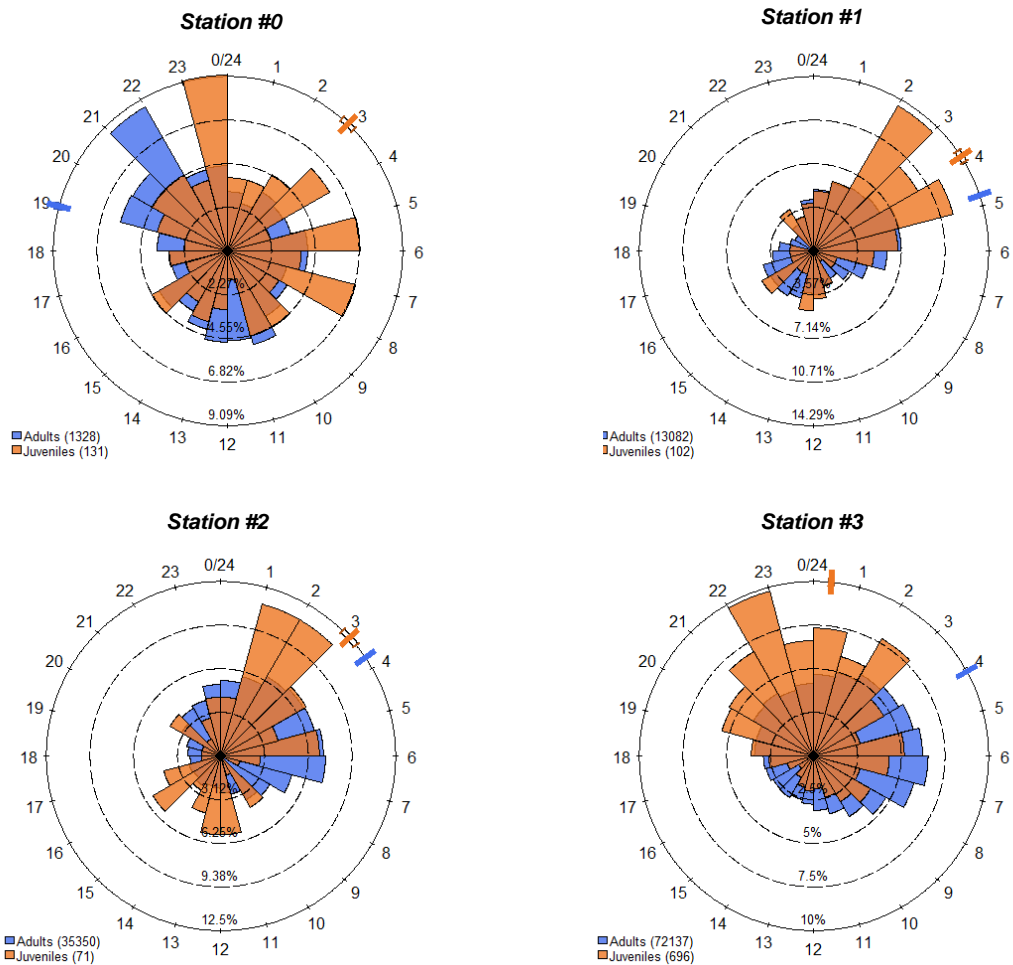


Figure I.3 – Actel individual residency plot showing the percentage of time the tagged *S. glanis* spent on each location per day. The locations include the Ribeira das Eiras tributary section ('Rib'), the dam section ('Dam'), the middle section 1 ('Mid1'), the middle section 2 ('Mid2'), the upstream section ('Up'), as well as the intermediate locations between sections (e.g., 'Rib-Dam'). These intermediate locations are generated when a tagged fish travels undetectably between sections or when is being simultaneously detected by two receivers of different sections. Occasionally, a fish (or at least the transmitter's signal) jumps over a section, creating non-adjacent intermediate sections (e.g., 'Rib-Mid1').



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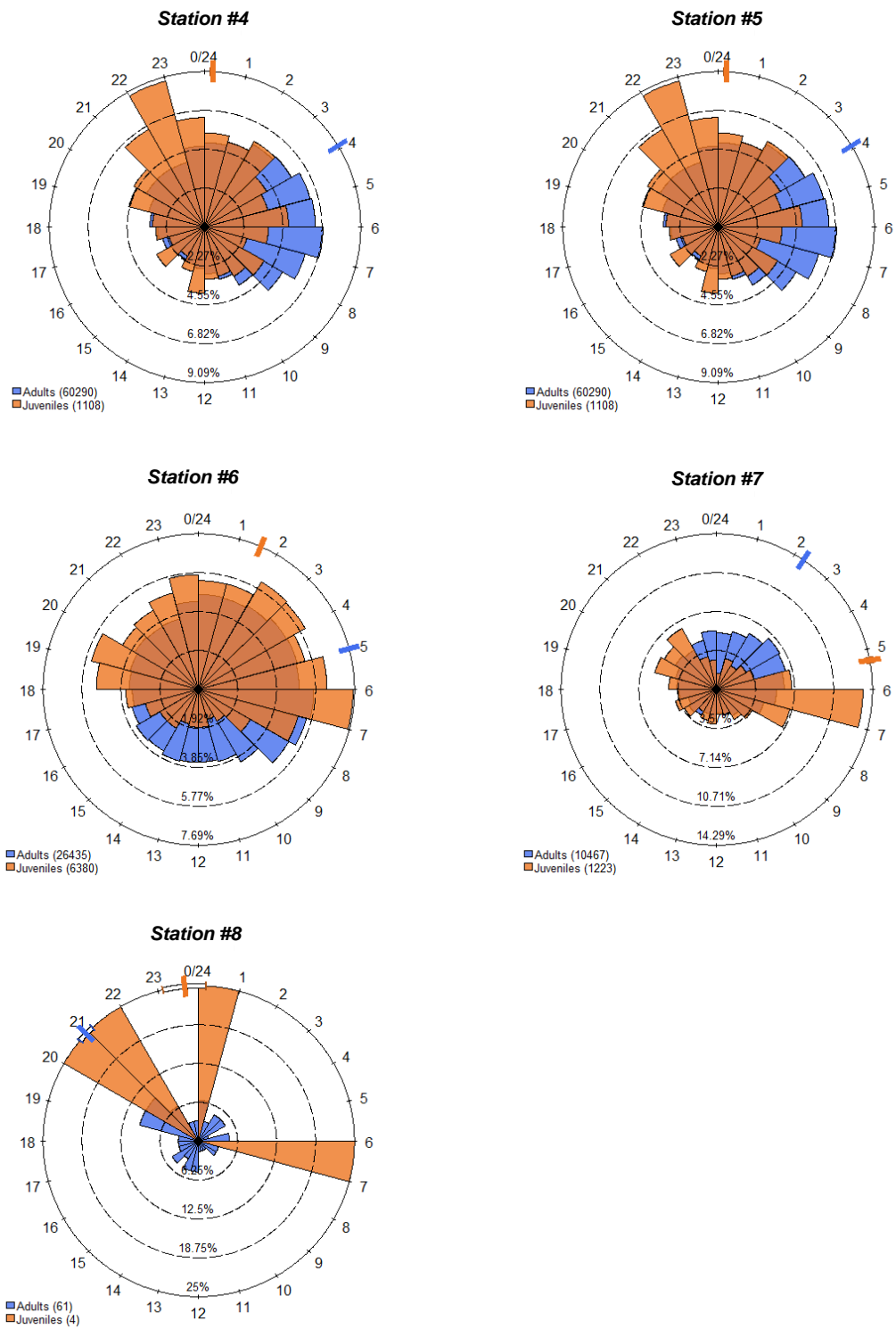
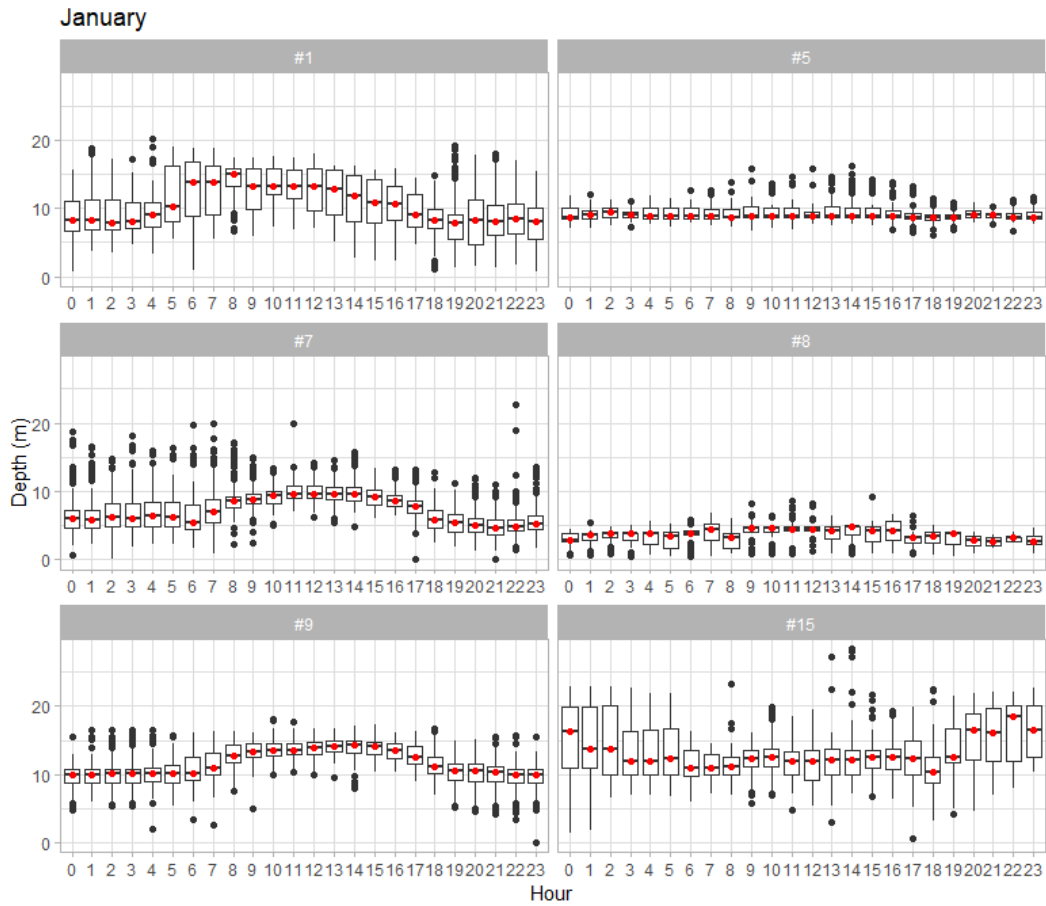


Figure I.4 – Circular plots showing the arrival times of each tagged *S. glanis* group (Adults and Juveniles) to each receiver station. The lines on the outer circle indicate the mean value for each group with the associated standard error. Each group’s bars sum to 100%. The number of events in each group is presented between brackets in the legend of each plot.

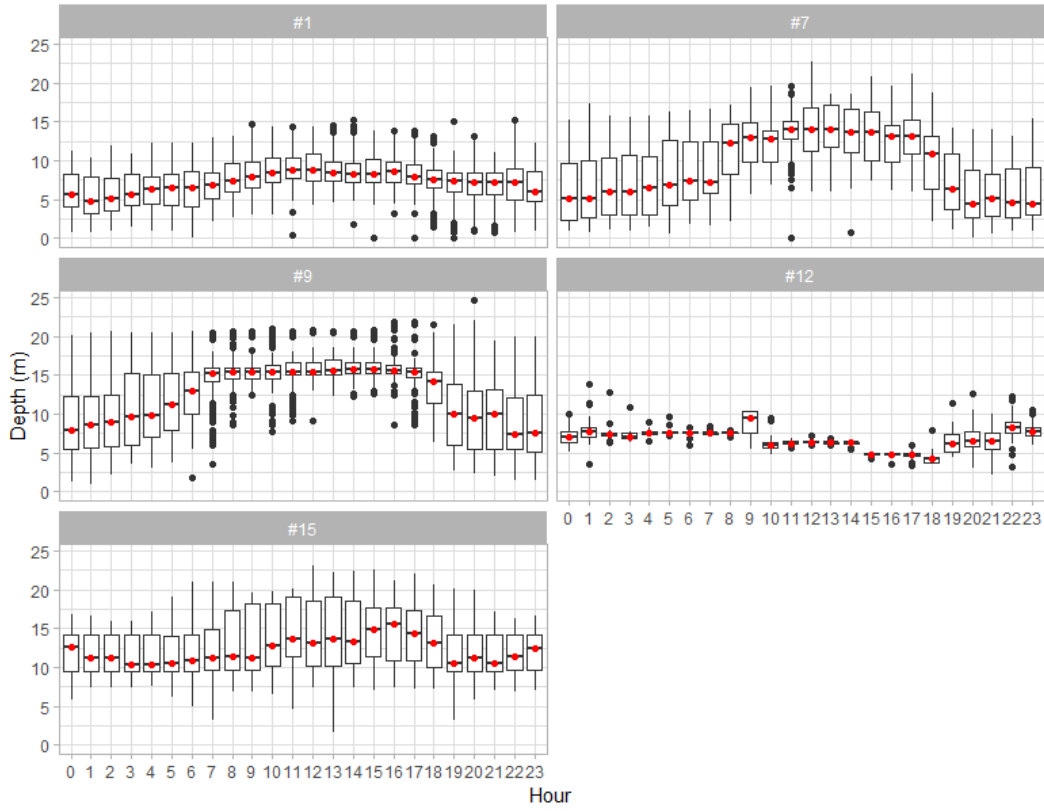
Annex II

This annex contains supplementary material about *Silurus glanis* depth use, model predictions and water temperature and flow information along the monitoring period.

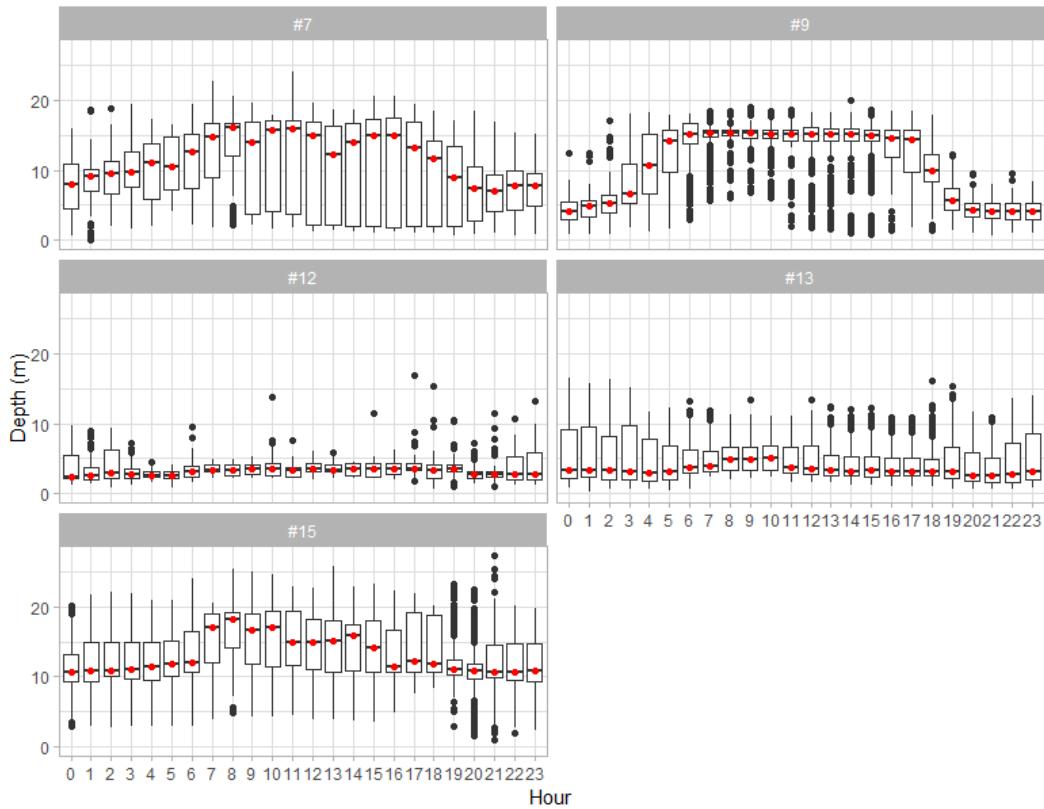


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February

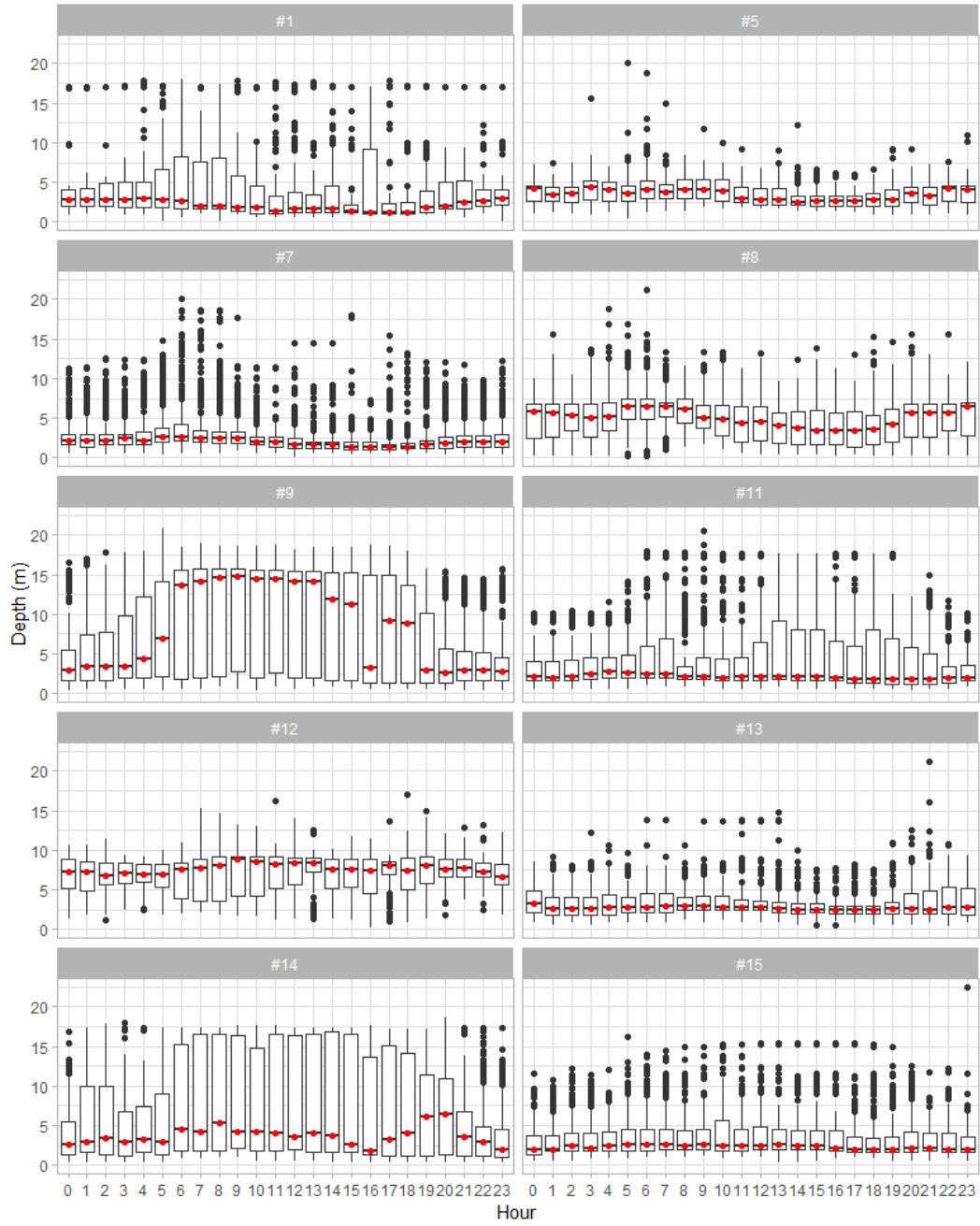


March



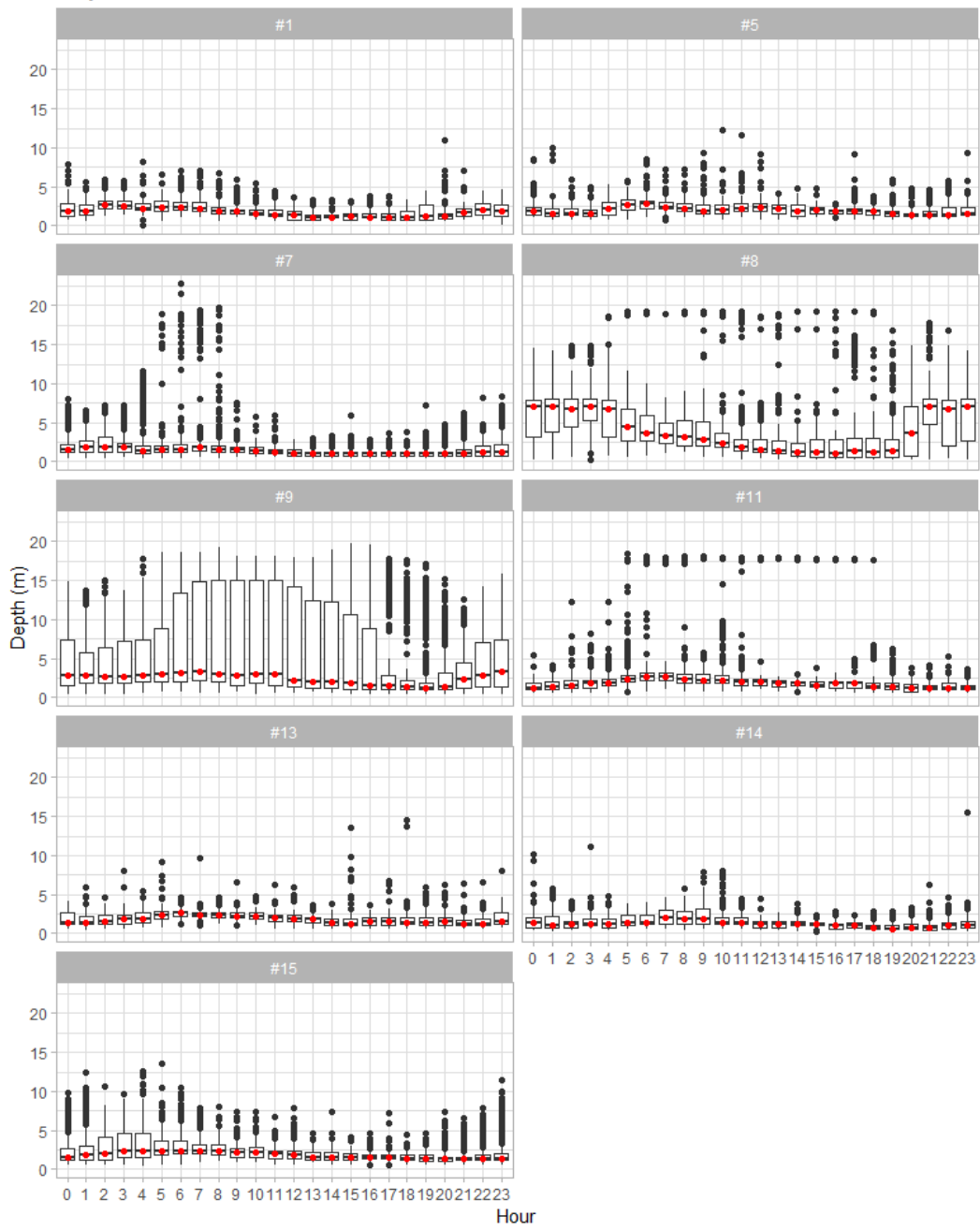
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April

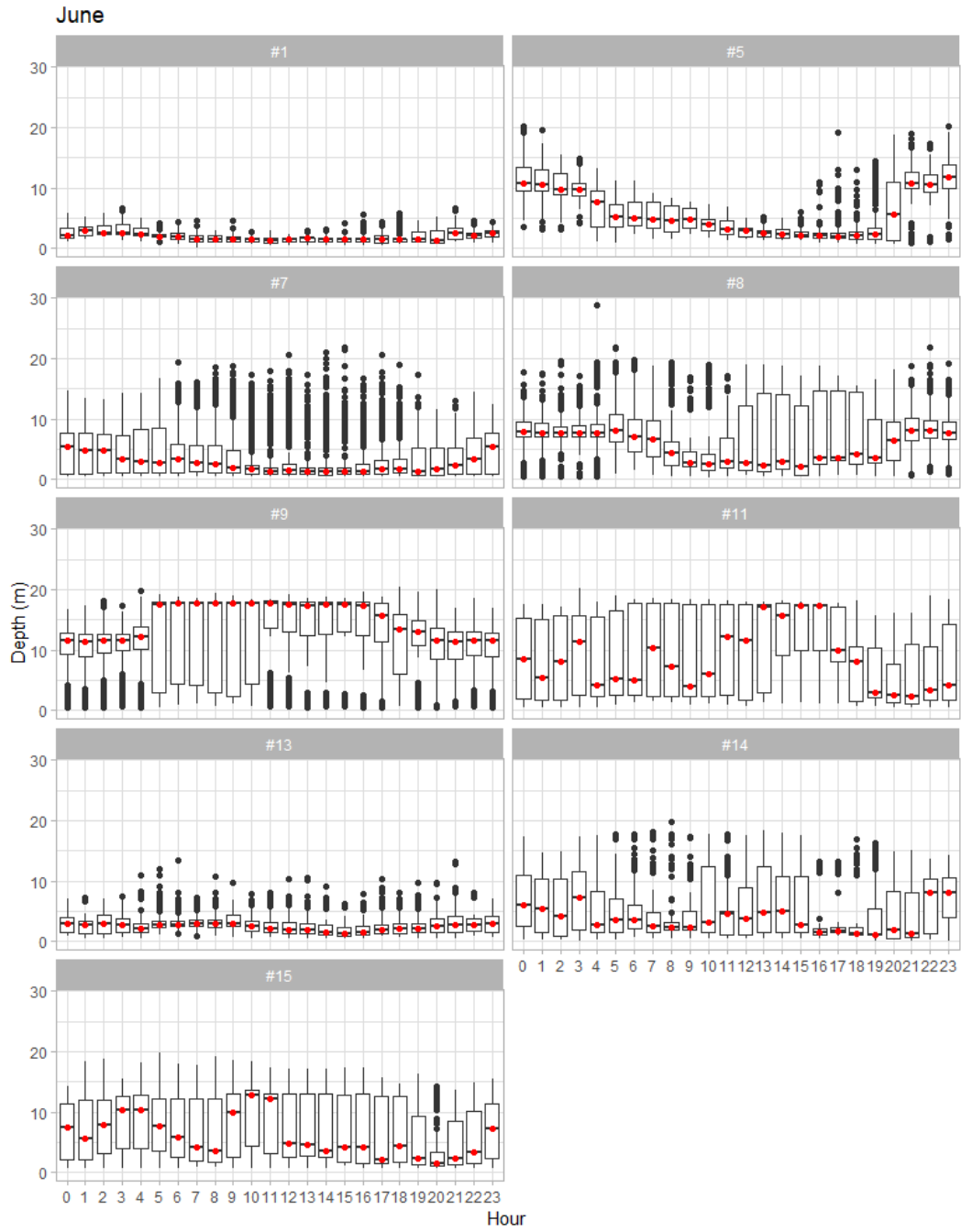


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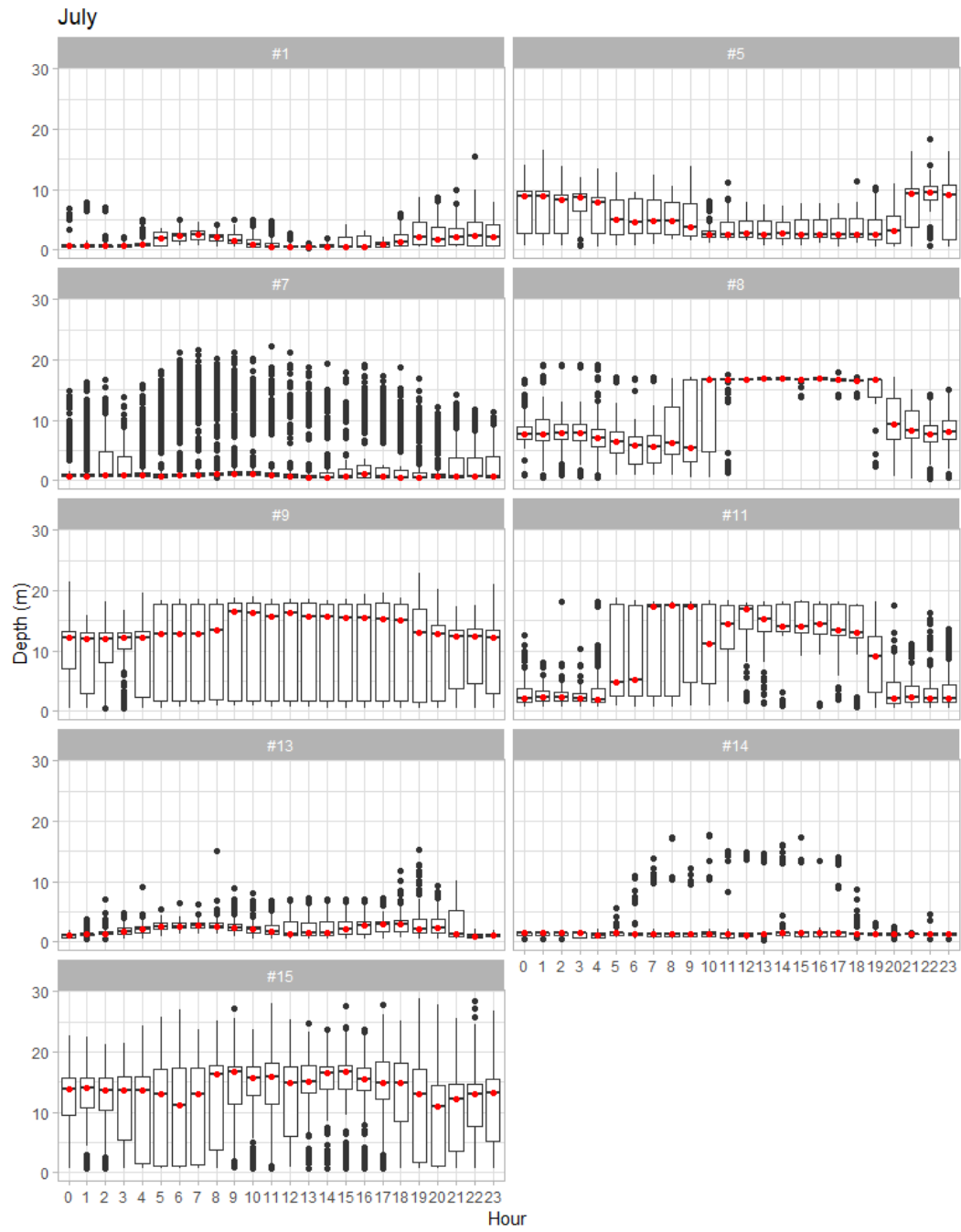
May



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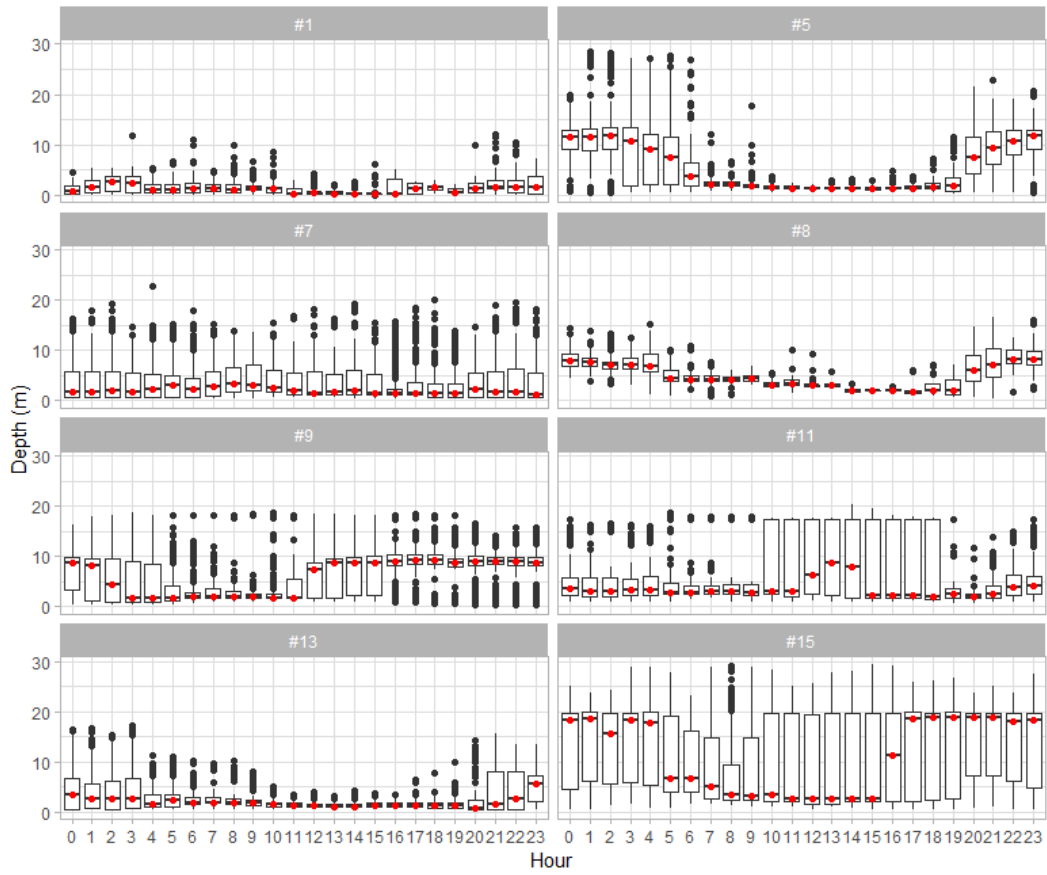


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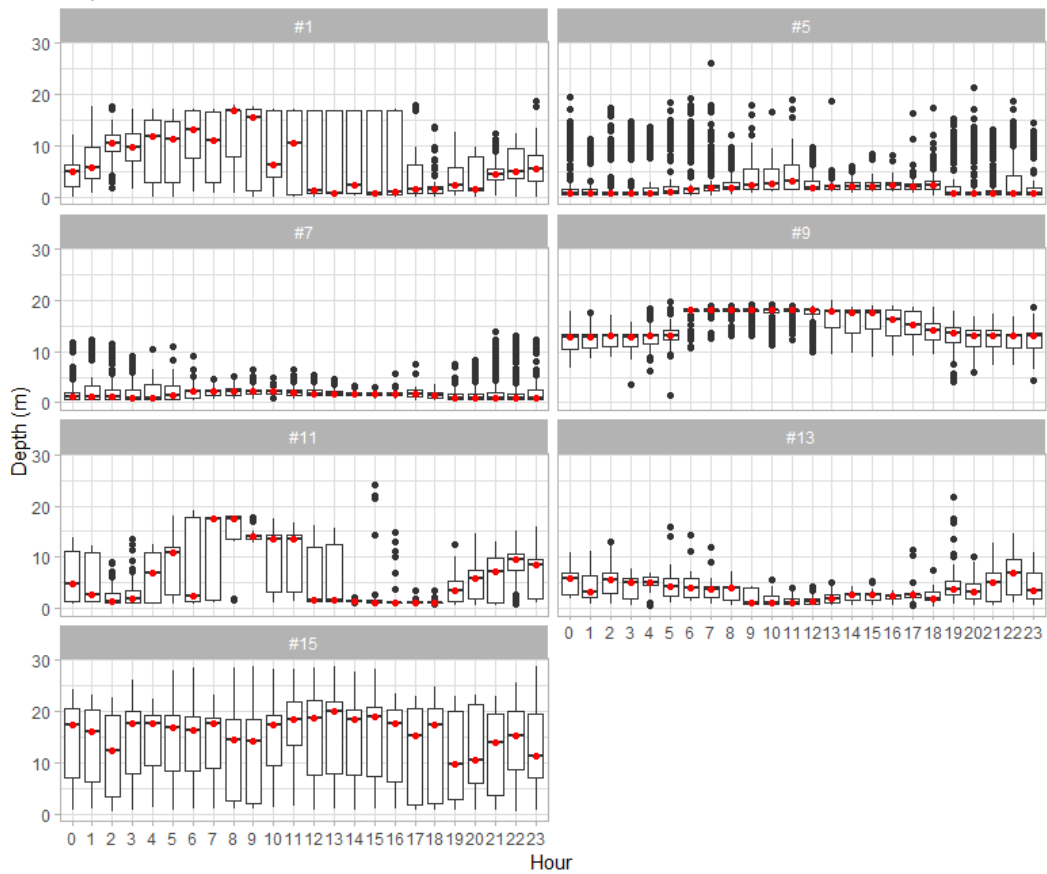


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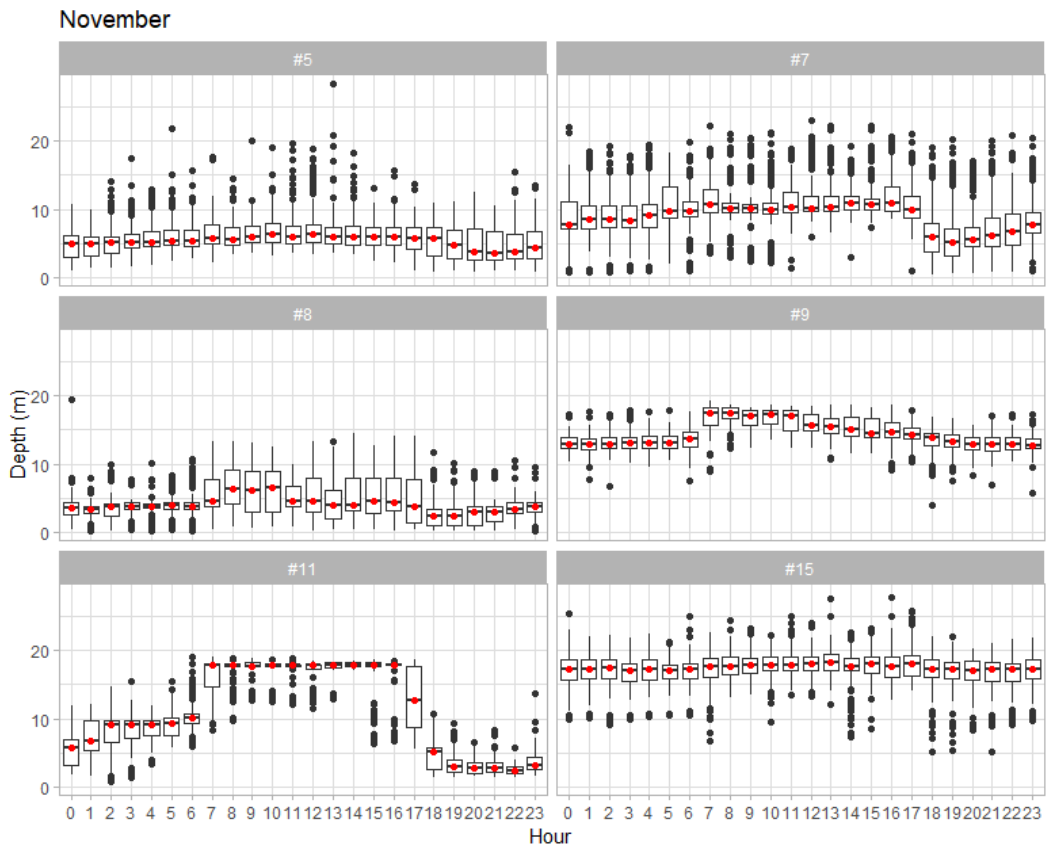
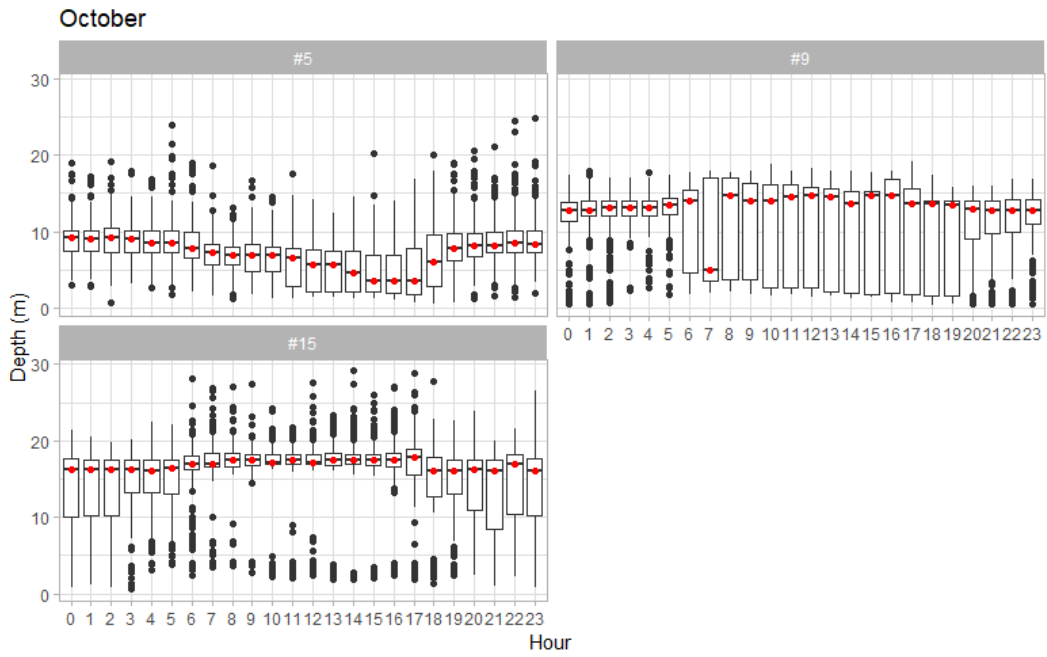
August



September



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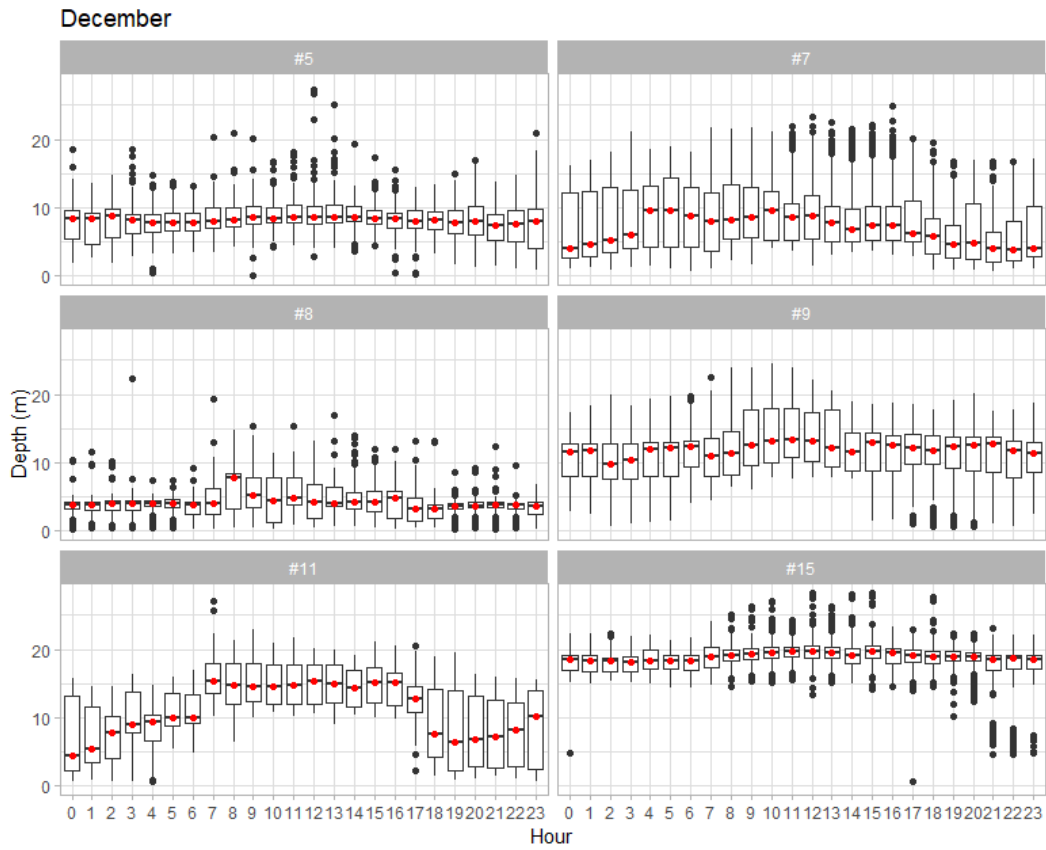


Figure II.1 – Depth use of each tagged *S. glanis* per month. Fish with insufficient monthly depth data were excluded from the panels sequence of the respective month.

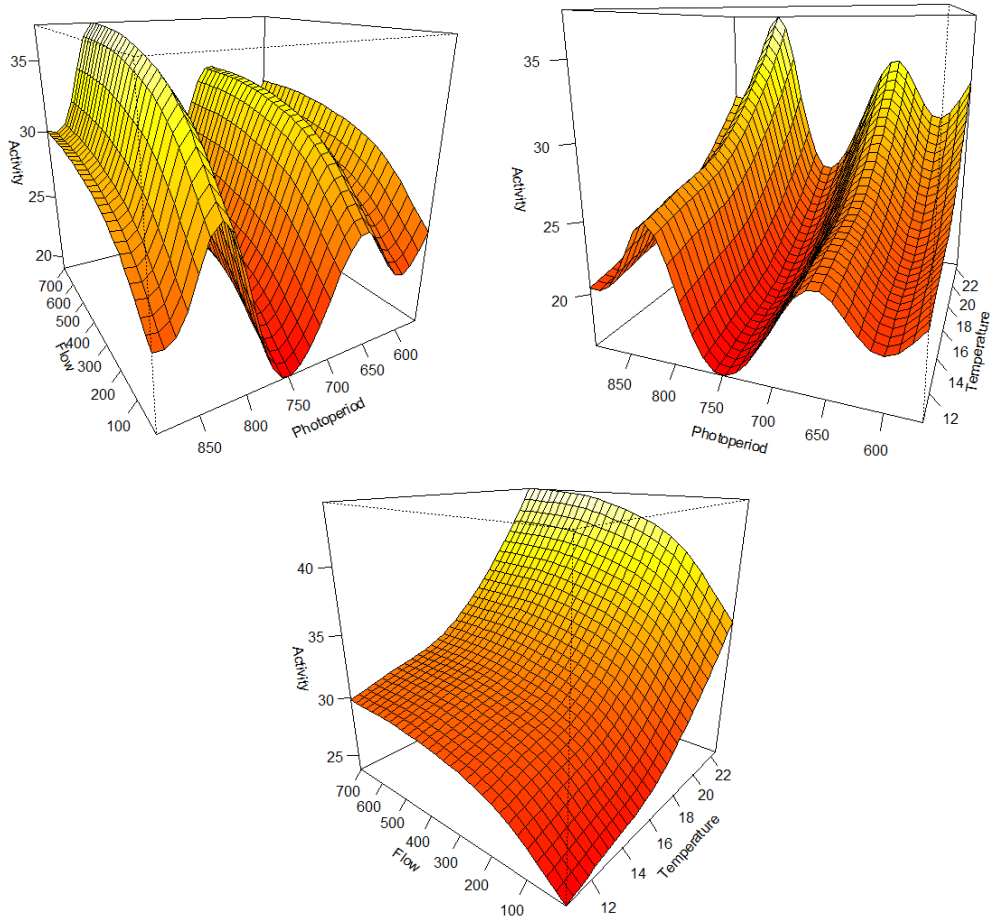


Figure II.2 – Perspective plots of the activity (m/s^2) GAM predictions (model 10) for the combination of the 3 main independent variables on the model: Flow (m^3/s), Photoperiod (min) and Temperature ($^{\circ}C$). The remaining variables omitted in each graph have their value fixed to the closest observed value to the median. The red color indicate minimum predicted values and white color maximum predicted values.

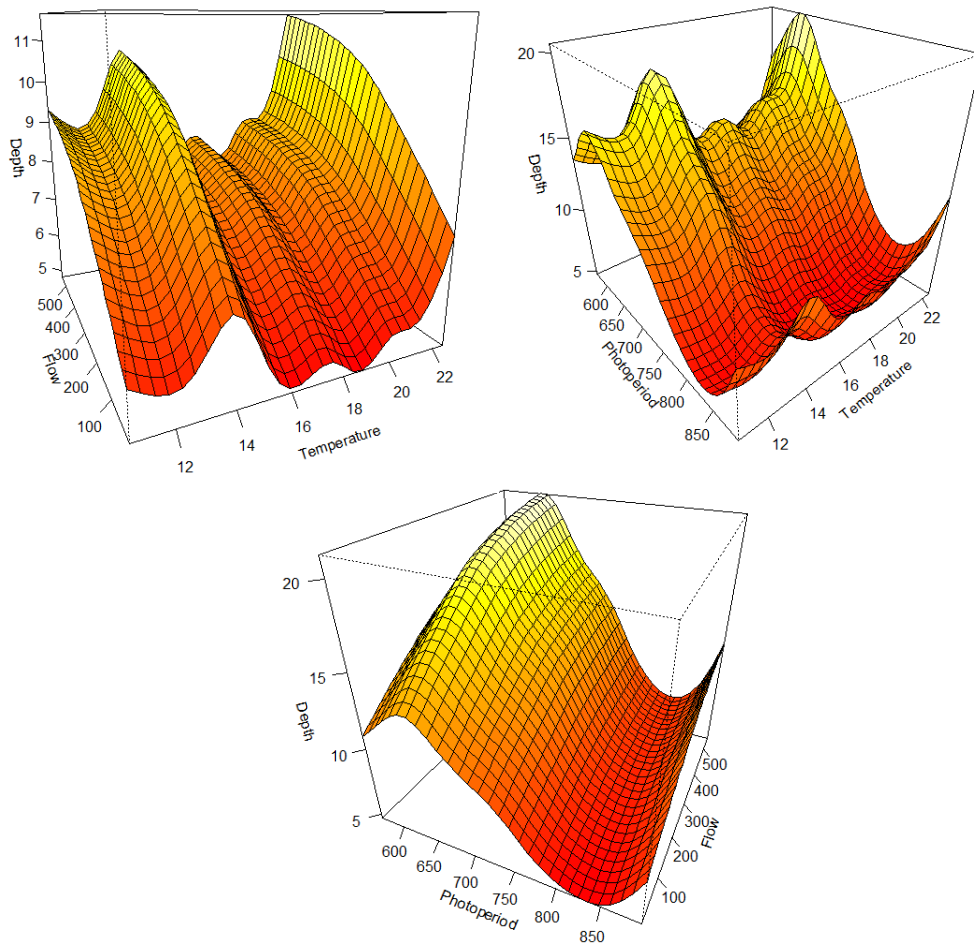


Figure II.3 – Perspective plots of the depth use (m) GAM predictions (model 10) for the combination of the 3 main independent variables on the model: Flow (m³/s), Photoperiod (min) and Temperature (°C). The remaining variables omitted in each graph have their value fixed to the closest observed value to the median. The red color indicate minimum predicted values and white color maximum predicted values.

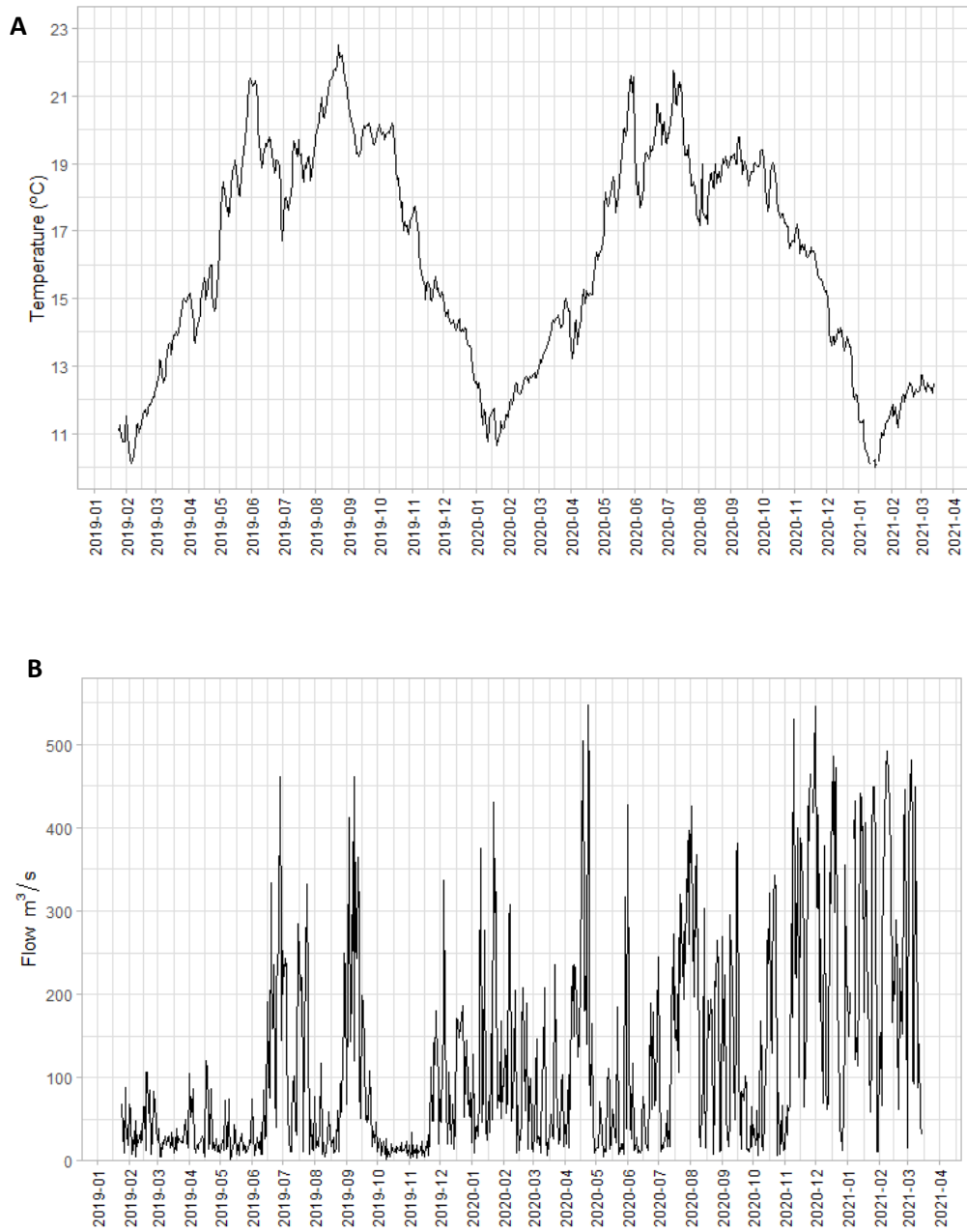


Figure II.4 – Daily average water temperature (A) and water flow (B) in Belver reservoir during the monitoring period.

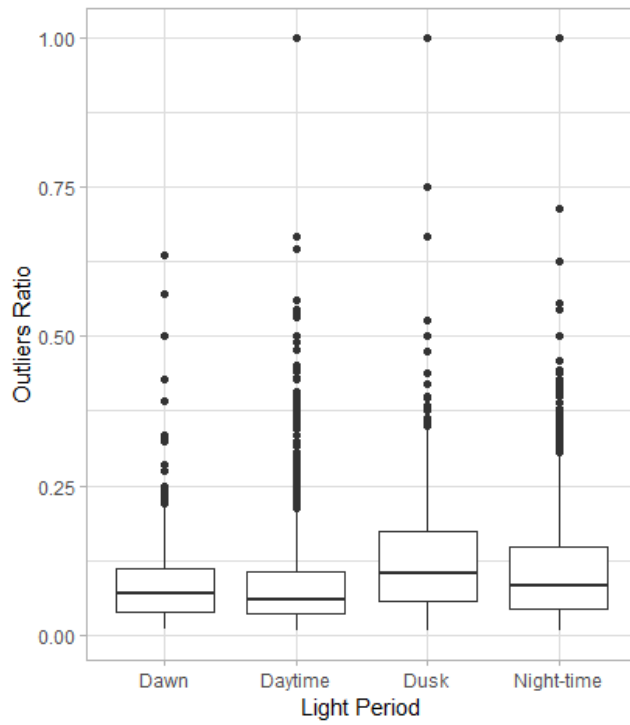


Figure II.5 – Outliers count ratio boxplots (n° outliers/ n° detections) with zeros excluded (count part only).

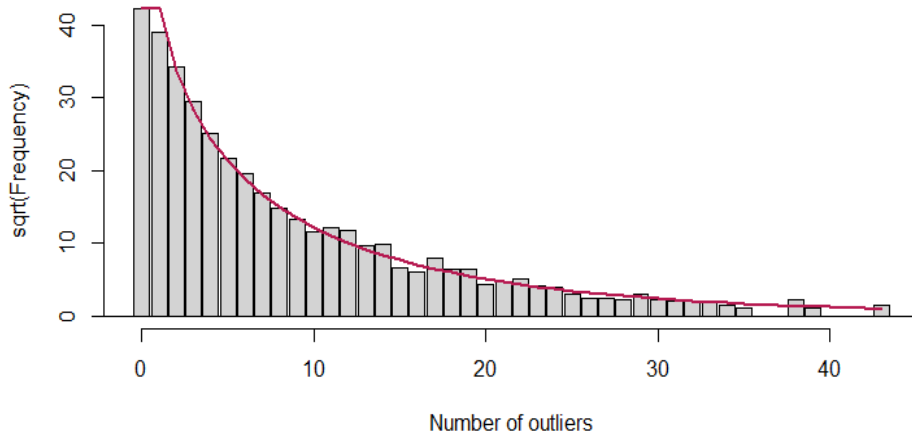


Figure II.6 – Rootogram showing the square-rooted frequencies of the number of outliers with the superimposed curve of the fitted Hurdle model (model 3).

Annex III

This annex contains the references of the installed R packages used in this work.

actel: Flávio, H. and Baktoft, H. (2021) ‘*actel*: Standardised analysis of acoustic telemetry data from animals moving through receiver arrays’. *Methods in Ecology and Evolution*, 12(1), pp. 196–203. doi: 10.1111/2041-210X.13503. R package version 1.2.1. <https://cran.r-project.org/web/packages/actel>

adehabitatHR and *adehabitatLT*: Calenge, C. (2006) ‘The package “*adehabitat*” for the R software: A tool for the analysis of space and habitat use by animals’. *Ecological Modelling*, 197(3–4), pp. 516–519. doi: 10.1016/J.ECOLMODEL.2006.03.017. R package versions 0.4.19 and 0.3.25. <https://cran.r-project.org/web/packages/adehabitatHR>

dplyr: Wickham, H. *et al.* (2021). ‘*dplyr*: A grammar of data manipulation’. R package version 1.0.7. <https://cran.r-project.org/web/packages/dplyr/>

dunn.test: Dinno, A. (2017). ‘*dunn.test*: Dunn's test of multiple comparisons using rank sums’. R package version 1.3.5. <https://cran.r-project.org/web/packages/dunn.test/>

ggplot2: Wickham, H. (2016). ‘*ggplot2*: Elegant graphics for data analysis’. *Springer-Verlag New York*. R package version 3.3.5. <https://cran.r-project.org/web/packages/ggplot2/>

lmtest: Zeileis, A. and Hothorn, T. (2002). ‘Diagnostic checking in regression relationships’. *R News*, 2(3), 7–10. R package version 0.9-39. <https://cran.r-project.org/web/packages/lmtest>

lubridate: Grolemund G, Wickham H (2011). ‘Dates and times made easy with *lubridate*’. *Journal of Statistical Software*, 40(3), 1–25. doi:10.18637/jss.v040.i03. R package version 1.8.0. <https://cran.r-project.org/web/packages/lubridate/>

mgcv: Wood, S. N. (2017) *Generalized additive models: An introduction with R*. 2nd Edition. Boca Raton: Chapman and Hall/CRC. doi: 10.1201/9781315370279. R package version 1.8-36. <https://cran.r-project.org/web/packages/mgcv/>

pscl: Jackman S (2020). ‘*pscl*: Classes and methods for R developed in the Political Science Computational Laboratory’. United States Studies Centre, University of Sydney, Sydney, New South Wales, Australia. R package version 1.5.5. <https://cran.r-project.org/web/packages/pscl>