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Declaration of authorship of work /Declaração de autoria de trabalho

I declare that I am the author of this work, which is original and unpublished. The authors and works consulted are properly cited in the text and are included in the reference list.

Declaro ser a autora deste trabalho, que é original e inédito. Autores e trabalhos consultados estão devidamente citados no texto e constam da listagem de referências incluída.

(Inês Ribeiro)
2024

Abstract

Meagre *(Argyrosomus regius)* is one of Europe's largest coastal fish and a top predator. It supports both commercial and recreational fisheries and has a growing importance in aquaculture. However, this long-lived species is particularly vulnerable due to significant genetic fragmentation and limited spawning areas. In these areas, they aggregate and are exposed to intense fishing pressures. Understanding the ecology and behavior of this species is crucial not only for fisheries management but also for conservation efforts. We used pop-up satellite archival tags (PSATs), to infer the movement and ecology of meagre, in one of its spawning areas, the Gironde estuary in France. 20 fish were tagged with PSAT, with 15 providing data over sampling periods ranging from 9 to 176 days, with an average of 72.2 days. The data was collected from June until December 2022. The remaining five tags did not transmit data due to a malfunction. The results show a seasonal shift in vertical habitat use where fish utilize shallower warmer waters during summer and deeper cooler waters during the winter, as observed in previous studies in Southern Portugal. Mean depth usage ranged from 5.66 (±1.98 SD) to 17.68 (±9.17 SD) meters, and temperatures ranged from 12.6°C to 24.95°C. The range of depths used in winter was wider than in summer. The opposite was found regarding temperature, with a wider range used during summer, when the water is stratified, and narrower during winter, as the water mixes. No patterns in diel vertical movement were detected. The geolocation models showed that between June and August, the meagre remained inside the estuary or nearby to coastal waters. Since September, meagre began dispersing to more offshore areas, though always inside the Bay of Biscay.

Resumo

A Corvina, *Argyrosomus regius,* é um dos maiores peixes costeiros da Europa e um predador de topo, assumindo uma relevância significativa nos ecossistemas marinhos. Alvo tanto de pesca comercial como recreativa, a sua notoriedade em aquacultura tem vindo a aumentar devido a inúmeros fatores como o seu sabor, qualidade, rápido crescimento e grande porte. Atualmente, compreender a ecologia e os padrões de movimento de espécies alvo da pesca, reveste-se de extrema relevância. Especialmente da Corvina, dada a sua particular vulnerabilidade atribuível a características como a reprodução tardia, dependência de áreas costeiras para reprodução – onde os peixes formam agregações e enfrentam intensas pressões pesqueiras - e a fragmentação genética da espécie. Além disso, as suas áreas de desova são bastante limitadas. A Corvina reproduz-se principalmente em seis estuários e deltas no Atlântico e no Mar Mediterrâneo: Gironde (França), Tejo (Portugal), Guadalquivir (Espanha), Nilo (Egito), Menderes (Turquia) e no Banco de Arguim (Mauritânia). Conhecer os habitats essenciais para esta espécies e os respetivos padrões de migração torna-se crucial para a gestão e conservação deste peixe. Embora a Corvina seja amplamente estudada em ambiente de laboratório e em aquacultura, apenas cinco estudos foram realizados *in situ* utilizando biotelemetria, de forma a investigar tanto preferências térmicas como padrões de movimento. No entanto, nenhuma destas análises teve o estuário de Gironde como área de estudo.

No presente estudo, foram utilizadas pop-up satellite archival tags (PSATs), com o intuito de estudar o movimento horizontal e vertical das Corvinas, bem como suas preferências térmicas, no estuário do Gironde (França) e zonas adjacentes. Para o efeito, 20 peixes foram marcados com PSATs, dos quais 15 forneceram dados relativos à temperatura, profundidade e luminosidade ao longo dos períodos de amostragem, que variaram entre 9 e 176 dias - entre Junho e Dezembro 2022 - com uma média de 72.2 dias.

Os resultados mostraram uma mudança sazonal no uso do habitat vertical, no qual os peixes utilizam águas mais superficiais e quentes durante o verão e águas mais profundas e frias durante o inverno, corroborando estudos anteriores. A utilização média de profundidade variou entre 5.66 (±1.98 SD) e 17.68 (±9.17 SD) metros, e as temperaturas variaram entre

12.60°C e 24.95°C. A amplitude de utilização de profundidade durante o inverno foi maior do que no verão e o oposto foi verificado em relação à temperatura, com uma amplitude maior durante o verão e menor durante o inverno. Relativamente a estas preferências verticais, é sugerido que a quebra da estratificação da coluna de água do Verão para o Inverno possa explicar, ou influenciar, esta alteração de habitats. No entanto, importa ressalvar que apenas um peixe forneceu informações para os meses de Novembro e Dezembro.

Embora a diferença entre a mediana de profundidade utilizada durante o dia e a noite, tenha sido de apenas 0.5 m, foi considerada estatisticamente significante, o que pode ser justificável devido a uma quantidade de amostra demasiado grande. Este resultado já foi observado noutros estudos para esta espécie em fase adulta. Ainda assim, contrastam com comportamentos de Corvinas juvenis e de outras espécies da família Sciaenidae, que tendem a ter comportamentos distintos do dia para a noite.

Com o intuito de inferir sobre os padrões de migração horizontal, foram utilizados modelos de geolocalização que fizeram uso de dados de temperatura, profundidade e intensidade de luz para estimar a localização das Corvinas. Além disso, implementámos uma abordagem inovadora ao integrar os resultados da análise de Continuous Wavelet Transform (CWT) em nos modelos de geolocalização, limitando as localizações dos animais ao estuário, sempre que sinais de ciclos de mudanças de temperatura de 12 horas fossem detetados. A incorporação desta informação nos nossos modelos assegurou a obtenção de previsões significativamente mais precisas.

Com os resultados obtidos, foi-nos ainda possível constatar que, entre junho e agosto, os indivíduos marcados permaneceram dentro do estuário em águas costeiras, e que após setembro, houve uma dispersão para áreas mais offshore, embora sempre dentro da Baía da Biscaia. As razões subjacentes a esta migração e à utilização, por parte das Corvinas, de áreas mais profundas durante o Inverno não foram ainda completamente elucidadas, ainda que tenham sido já propostas algumas hipóteses. São exemplo: a preferência de estar junto ao fundo do mar, como é característico de uma espécie demersal, o que justifica que a profundidade aumente quando migra para áreas mais offshore; e o fato da migração para áreas mais offshores ser uma resposta para evitar predadores ou mesmo uma alteração do tipo de presas que os impele a predar em áreas com maior profundidade.

Globalmente, o presente estudo contribuiu para uma melhor compreensão da população de Corvinas no estuário de Gironde, o que pode ser muito benéfico para a gestão e conservação desta espécie. A determinação dos locais e períodos de agrupamentos destes animais pode ser utilizado para restringir áreas de pesca ou para planeamento espacial marinho. Apesar da amostragem limitada, os resultados obtidos foram coincidentes outros estudos para esta espécie, realizados na Península Ibérica. Em trabalhos futuros, e tendo em vista uma maior robustez das conclusões obtidas, seria recomendável a utilização de uma amostra de maiores dimensões bem como de um período de amostragem mais longo, abrangendo um ou mais anos, a fim de compreender melhor o movimento das Corvinas durante o inverno. Adicionalmente, o recurso a uma dupla marcação, com marcas de satélite e acústicas, permitiria assegurar uma significativa melhoria dos modelos de geolocalização. Por último, um maior conhecimento sobre as eventuais mudanças na alimentação desta espécie entre os períodos de verão e inverno, poderá mostrar-se vantajoso para fundamentar as hipotéticas razões para as suas alterações sazonais de habitat.

Keywords

Sciaenidae, predatory fish, Biotelemetry, PSAT, Movement ecology, Bay of Biscay.

Sciaenidae, Biotelemetria, PSAT, Movimento, Baía da Biscaia

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List of Abbreviations, Acronyms, and Symbols

PSATs - Pop-up Satellite Archival Tags

TL – Total Length

TAD - Time-at-Depth TAD

TAT - Time-at Temperature

PDT- Profile of Depth and Temperature

DVM - Diel Vertical Movement

SST – Sea Surface Temperature

HMM - Hidden Markov Models

General Introduction

Contextualization

The movement of a species plays a crucial role in its ecology (Heylen & Nachtsheim, 2018). For conservation planners, considering those movements can be a great challenge, and understanding where, when, and why species move is undoubtedly helpful (Runge et al., 2014). By pinpointing feeding grounds, nursery habitats, and aggregation sites as well as spatiotemporal overlaps with identified threats and human activities, we can get insights to develop more effective and flexible spatial management and conservation strategies (Allen & Singh, 2016; Cagnacci et al., 2010). Even though marine protected areas offer potential for conservation gains (Agardy, 1994), studies continue to show that management actions focused on only one area may be insufficient for effectively conserving more mobile species, as they fail to account for these horizontal movements (Allen & Singh, 2016; Runge et al., 2014; Thirgood et al., 2004).

Vertical movements may result from fish optimizing their locomotion to minimize energy costs while seeking food, avoiding predators, and remaining within their physiological limits for temperature and oxygen levels (Andrzejaczek et al., 2019). Understanding an organism's vertical space utilization and thermal envelopes can reveal its diet and trophic level, as these factors define its environmental niche and, consequently, the organisms it preys upon, is preyed upon by, or compete with (Piccolo et al., 2007). Such understanding, particularly in the case of ecologically important species, such as higher levels predators, is pivotal for understanding the dynamics of entire ecosystems.

Estuaries and the case of Gironde Estuary

Estuaries are ecotones, playing vital roles in the functioning of different fish species and, therefore, constitute a fundamental area of research. These highly dynamic and productive environments support abundant biodiversity due to their mix of fresh and marine water characteristics (Lobry et al., 2003; Methven et al., 2001). Fish assemblages are very diverse and composed of true estuarine, amphihaline, or euryhaline species (Elliott &

Dewailly, 1995; Lobry et al., 2003; Methven et al., 2001). Different species use these key habitats during different phases of their life cycle and for various reasons, like reproduction, feeding, growth, or physiological preparation for migration (Lobry et al., 2003).

The Gironde estuary (Figure 1.2) is a 20-60 km long estuary located in southwestern France. It begins downstream of the Bec d'Ambés, at the confluence of the Garonne and the Dordogne rivers (Lobry et al., 2003; Zhan Hua et al., 1994). Two-thirds of the estuary's water comes from the Garonne (Allen, et al. 1974). The two rivers combined drain a basin amount of 71,000 km^2 and have an annual flow of approximately 500 m^3 per second(A. M. Allen & Singh, 2016; Deborde et al., 2007; Savoye et al., 2012; Sottolichio & Castaing, 1999). This mixed to well-mixed estuary is the largest in Western Europe, reaching 635 km^2 at high tide (Kraepiel et al. 1997; Rochard et al. 2001). There are two navigation channels: on the right side, a natural one with depths between 4 to 20 m, and on the left, an artificial one with depths between 7 to 30 m (Taverny et al., 2002). The water depth in the estuary varies significantly, starting at 3 meters near the shelf in the upper estuary and reaching up to 26 meters in the lower estuary. On average, the depth at mid-tide is about 8 meters (Taverny et al., 2002). There are two falling tides and two rising tides each day that last about 6.2 h (Taverny et al., 2002) with a tidal range of 1.5 to 5.0 meters (Kraepiel et al. 1997; Rochard et al. 2001). The water residence time ranges from 20 to 90 days, while particles remain for a long period in the system, for approximately five years (Kraepiel et al. 1997; Savoye et al. 2012). Its bottom is composed of a mixture of sand in the lower and deeper sectors, and mud in the upper and shallower sectors of the estuary, where the turbidity can be as high as 1 g L^{-1} near the surface and 10 g L $^{-1}$ in the bottom (Taverny et al., 2002). The water temperature ranges from 6°C in January to 26°C in July. It follows a gradient of temperature from the ocean to the river that inverts twice a year (during spring and fall) (Maurice, 1993). Coastal water is warmer than the river in winter, while the river is warmer than coastal water in summer. Salinity also follows a gradient, which is highly variable according to the river flow and strength of the tide, and the gradient starts in the mouth at 33 ‰ and reaches upstream of Bordeaux with 0.3 ‰. The freshwater estuary extends 70 km upstream (Deborde et al., 2007). Recent studies carried out in the Gironde estuary reported an increase in water temperature and an extended seawater intrusion associated with global changes, which led to a significant increase in the juvenile density of several marine species (Pasquaud et al., 2012).

The Gironde flows into the Bay of Biscay. This bay has two shelves, the Armorican and the Plateau des Landes. The latter is limited by the "Gouf du Cap Breton" and the "Cap Ferret Canyon," a large depression divided into upper (< 500 m), middle (500–1500 m), and lower (> 2000 m) canyon sections. (Cremer, Weber, and Jouanneau 1999; Durrieu De Madron et al. 1999; Koutsikopoulos and Le Cann 1996; Schmidt et al. 2014). The water masses in the upper layers, from 100 to 600 meters deep, exhibit characteristics similar to the ones of the North Atlantic Central Water, with temperatures ranging between 10.5 and 12.0°C and salinity levels from 35.45 to 35.00 ‰ (Koutsikopoulos and Le Cann 1996). This area has supported numerous fisheries and continues to be highly exploited (Pascal, 2009), and one of the targets of these fisheries is meagre.

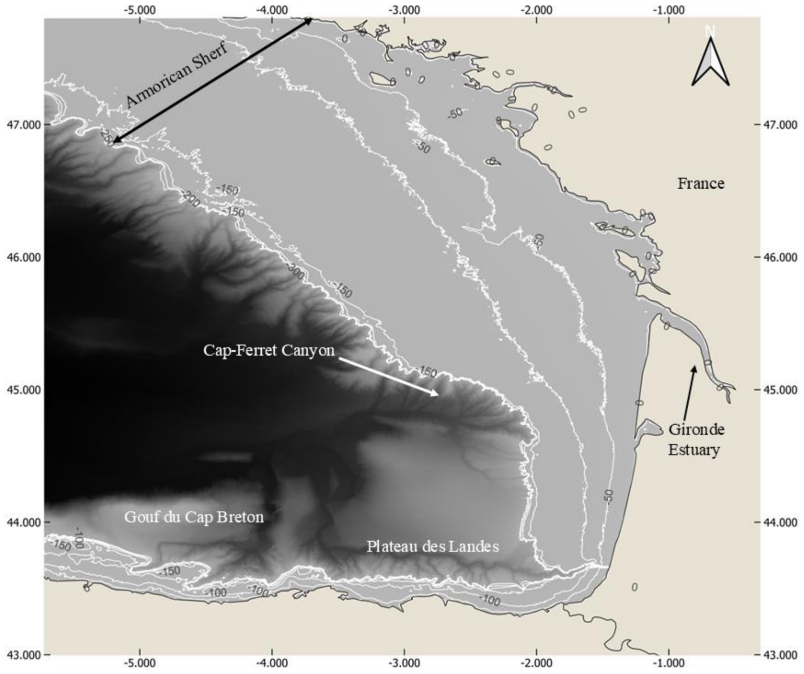


Figure 1.2 – The main areas of Bay of Biscay, France

The meagre: *Argyrosomus regius*

The meagre, *Argyrosomus regius,* stands as one of Europe's largest coastal bony fish, reaching over 230 cm in total length, weighing over 100kg, and reaching a maximum of 42 years of age (González-Quirós et al., 2011; Hubans et al., 2017; L. Quéméner, 2002; Lazo & Holt, 2010; Otero et al., 2013). It belongs to the Sciaenidae family, commonly known as drums or croakers, and it occurs in the eastern Atlantic, the Mediterranean, the western Black Sea, and recently, the Red Sea due to an invasion through the Suez Canal (Haffray, et al., 2012). They reproduce in the eastern Atlantic and Mediterranean Sea, primarily in large estuaries and deltas such as the Gironde (France), Tejo (Portugal), Guadalquivir (Spain), Nile (Egypt), Menderes (Turkey), and Banc D'Arguin (Mauritania). (Haffray, Malha, Ould, et al. 2012). Spawning commonly occurs in shallow waters inside estuaries and salt marshes, where the larval and early juvenile develop (González-Quirós et al., 2011). The planktonic eggs hatch within 48h, and the larvae start to develop in these shallow waters, which usually exceed 20ºC (Cinzia, 2012). By the end of summer, the one-year-old juveniles migrate to coastal areas, where they stay for the next two to three years. After this period, they move towards deeper and cooler offshore feeding grounds, remaining there until they reach reproductive maturity (Cinzia, 2012; Duncan et al., 2013b; Haffray, Malha, Ould Taleb Sidi, et al., 2012; Prista & et al., 2008). At that stage - around six years, measuring approximately 60 cm for males and over 80 cm for females - they return to shallow coastal areas to spawn during summer, with water temperatures varying from 13ºC to 23ºC (Morales-Nin et al. 2012; Winkler et al., 2023; Sourget & Biais, 2009). This migration starts in April or May and lasts until the end of June in European areas. After reproducing, they return to offshore areas where they spend the autumn and winter months presumably feeding (Abecasis et al., 2024; Gandra et al., 2024). It has been suggested that water temperature is a critical element in determining the migration and reproduction timing in meagre, and this seasonal migration might be triggered by warming sea temperatures in the boreal spring (Garel et al., 2024). During these migrations, the longest individual annual movements were recorded for a coastal teleost, exceeding over 2000 km. The maximum depths recorded during this study ranged from 64 m to 125 m, while temperatures varied from 13.1ºC to 24.9ºC (Gandra et al., 2024). According to the same authors, this species undergoes shifts in depth use, during the seasonal migrations, but does not display a significant change in depth use during the day and night (Gandra et al., 2024; Winkler et al., 2023). Therefore, this fish is thought to have a high diet plasticity and adaptability in foraging (Gandra et al., 2024). The meagre is mostly piscivorous with a diet dominated by fish, such as anchovy, sardines, pout, and whiting. To a lesser extent, it consumes cephalopods. Cannibalism also constitutes a non-negligible part of the diet, amounting to more than 5% of the ingested biomass (Hubans et al., 2017).

The relevance of studying the Meagre

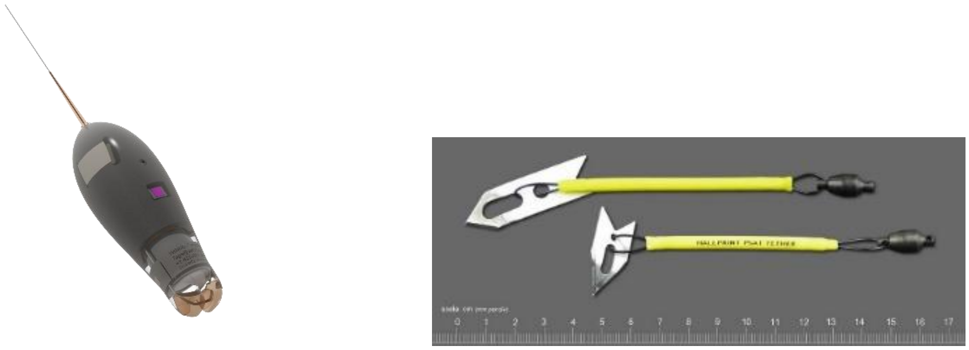
Even though this species is listed as Least Concerned by the International Union for Conservation (IUCN), it is known to have late first reproduction, (Pollard and Bizsel 2020), and to be highly dependent on coastal and estuarine areas, that are more anthropogenically impacted (Rilov et al., 2020). They aggregate for reproduction, which makes them both more accessible to fishers, and vulnerable to exploitation. Additionally, their breeding locations are very limited and dispersed, which also contributes to their susceptibility to local extinction, as has already occurred in the Balearic Islands (western Mediterranean Sea), where they were abundant only a few decades ago (Gil et al., 2014; Morales-Nin et al., 2012). The genetic fragmentation and differentiation between the Atlantic and Mediterranean populations also add to their vulnerability, especially in the context of climate change, where shallow areas of low latitude are more prone to environmental changes (Abecasis et al., 2024; Almeida et al., 2022; M.Gil et al., 2014; Haffray, et al., 2012). Moreover, large predators like meagre assume a critical role in the ecosystem. They regulate species abundance, distribution, and diversity by controlling prey densities and increasing competition (Sergio et al. 2006). The decline of top predators can lead to trophic downgrading, significantly impacting marine ecosystem structure and dynamics (Estes et al. 2011; Sergio et al. 2006). Even though there is intense research on meagre in captivity for aquaculture (Arechavala-Lopez et al., 2015), there is still a lot to unveil about the spatial ecology of this species in the wild.

Most studies on this species in its habitat now rely on biotelemetry, with five studies conducted on the thermal habitat preferences and movement patterns of the meagre in the Iberian Peninsula (Abecasis et al., 2024; Gandra et al., 2024; Garel et al., 2024; Winkler et al., 2023). However, it is important to note that these telemetry studies are mostly concentrated in the same geographic area and involve largely the same individuals. In contrast, earlier studies, of other populations, depended on otolith microchemical analysis and fisheries-dependent data (e.g. Morales-Nin et al., 2012; Quero & Vayne, 1985), methods that can be influenced by fish catchability and sampling efforts, leading to indirect evidence of migrations.

Given meagre's vulnerability to exploitation, its increasing importance to fisheries, and its key role in the ecosystem, there is an urgent need for more *in situ* research on this species. A deeper understanding of its ecology is essential for conserving the species and the ecosystem's health and supporting sustainable fisheries that benefit human populations. Therefore, recognizing and understanding key habitats for these fish is very important. In this study, we used satellite telemetry to infer the depth, temperature, and movement patterns of meagre around one of their main spawning grounds, the Gironde estuary (France). We used data visualization techniques and an inferential modelling framework to better understand their spatial ecology.

Telemetry and pop-up satellite archival tags

Water is a significant barrier to obtaining spatial ecology knowledge (Bradford et al., 2011). However, the urgent need to understand this crucial part of the animal's ecology, combined with rapid technological advancements over the past several decades, led to the creation of suitable electronic tracking devices that are now available to monitor animals in these challenging environments (Allen & Singh, 2016; Bradford et al., 2011; Hussey et al., 2015; Tomkiewicz et al., 2010). Satellite and acoustic transmitters play a crucial role in this advancement. Innovations in miniaturization, battery technology, and software and hardware development potentiated both tracking and characterization of the horizontal and vertical movements of individual organisms, populations, and entire communities across extensive spatial scales, ranging from meters to tens of thousands of kilometers (Hussey et al., 2015). Additionally, these tags can also provide information about the physiology of the animals and the environment where they live, for instance, temperature, light, conductivity, and many other variables, can be monitored simultaneously with these transmitters (Hussey et al., 2015; Hays et al., 2016). Pop-up satellite archival tags (PSATs) are tags that record, summarize, and archive data that is then transmitted via satellite. They consist of an Argos transmitter and sensors that record external physical variables (such as depth, light, and temperature), as well as tri-axial acceleration, which can be used to infer animal movements and geographical distributions. The tag is attached to the animal by a tether (Figure 1.1 B) and a corrodible attachment link that connects the transmitter with the tether (WildlifeComputers 2019). The deployment period is previously set so that the tag can release itself from the animal. Once it reaches the surface, the tag transmits the summarized data to Argos satellites (Hussey et al., 2015; WildlifeComputers 2019; M.S. Coyne & B.J. Godley, 2005). In addition, the tag provides its location information to facilitate the recovery. In such cases, we have access to the full raw data (WildlifeComputers 2019).



A B

Figure 1.1 A – Pop-up Archival Satellite Tag. **B -** Tether that will attach the tag to the animal. (WildlifeComputers, 2019)

These tags have been used in various animals, mainly mammals, followed by reptiles, teleost fish, elasmobranchs, and others, mostly for tracking large-scale open ocean movements (Hussey et al., 2015). Nevertheless, tracking animals in coastal areas is crucial due to the significant ecological importance of these regions and their high exposure to anthropogenic pressures (e.g. estuaries).

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Insights on meagre (*Argyrosomus regius*) spatial ecology around the Gironde estuary based on satellite telemetry

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Abstract

Argyrosomus regius, one of Europe's largest coastal fish and a top predator, plays an important role in both commercial and recreational fisheries and is becoming increasingly important in aquaculture. Yet, this species is particularly vulnerable due to its high genetic fragmentation, late first reproduction, and limited, coastal, and highly anthropogenic-impacted spawning areas. Therefore, understanding the ecology and behavior of this species is crucial, for fisheries management and conservation efforts. We used pop-up satellite archival tags (PSATs), to infer the horizontal movement, depth, and temperature preferences of meagre, in one of its main spawning areas, the Gironde estuary, in France. 20 fish were tagged, with 15 providing data over sampling periods ranging from 9 to 176 days, with an average of 72.2 days. The data was collected from June to December 2022. Our results show a seasonal shift in vertical and horizontal habitat use, where fish utilize shallower warmer waters during summer and deeper cooler waters during the winter. The mean depth usage ranged from 5.66 (±1.98 SD) to 17.68 (±9.17 SD) meters, and temperatures ranged between 12.6°C and 24.95°C. Depth utilization range during winter was wider than in summer and the opposite was found regarding temperature, with a wider range during summer, and narrower during winter. This can be related to the stratification of the water during summer. The mean depth used during the day (11.0 meters) was very similar to the one found during the night (11.5 meters). The horizontal movement predictions showed that between June and August, meagre remained inside the estuary or in nearby coastal waters. After September

meagre began dispersing to more offshore areas, though always inside the Bay of Biscay. We suggested that studies with larger sample sizes and longer monitoring periods should be carried out, as well as diet analysis, to detect any feeding preference change during seasons, that might explain the observed movement patterns.

Introduction

A species' movement plays a crucial role in its ecology (Heylen & Nachtsheim, 2018). Understanding horizontal migrations and their durations can reveal several important habitats for the species, such as nursery areas, feeding grounds, or other aggregation sites. Additionally, recognizing spatiotemporal overlaps with identified threats and human activities is of great importance for the development of more effective and flexible spatial management strategies, and for improving conservation efforts (Abecasis et al., 2024; Allen & Singh, 2016; Cagnacci et al., 2010). Additionally, comprehending vertical movements in the water column, allows us to gain insights into the animals' diets and trophic levels, as it outlines their environmental niche (Piccolo et al., 2007). Over the past decades, technological advancements led to the creation of suitable electronic tracking devices, like pop-up satellite archival tags (PSATs) that provide information about animals' environment – including, temperature, salinity, and depth - that can be translated into their movement (Hussey et al., 2015; Hays et al., 2016). These tags allow scientists to track individual organisms, populations, or even entire communities across different spatial and temporal scales (Hussey et al., 2015).

Studying the movement of animals around areas like estuaries can be particularly important due to their ecological significance. These ecotones play vital roles in different phases of several animals' life cycles and for various reasons, such as reproduction, feeding, growth, or physiological preparation for migration (Lobry et al., 2003). Additionally, due to the increasing influence of anthropogenic pressures and the heightened susceptibility to environmental changes caused by climate change, we must work to preserve and understand these sensitive and important areas and their biodiversity (Gil et al., 2014; Haffray et al., 2012).

The meagre, *Argyrosomus regius,* stands as one of Europe's largest coastal bony fish, reaching over 230 cm in total length, weighing over 100kg, and reaching a maximum of 42 years of age (González-Quirós et al., 2011; Hubans et al., 2017; L.; Otero et al., 2013). It reaches reproductive maturity around 6 years,at a size larger than 60 centimeters for males and larger than 80 centimeters for females (Sourget & Biais, 2009). This fish belongs to the Sciaenidae family, commonly known as drums or croakers, and it occurs in the eastern Atlantic, the Mediterranean, the western Black Sea, and recently, the Red Sea due to an invasion through the Suez Canal (Haffray, et al., 2012). Meagre is highly dependent on coastal systems, as they reproduce within large estuaries and deltas, in the eastern Atlantic and Mediterranean Sea (Haffray, et al. 2012). Adults live in deeper areas, where they most likely feed (Morales-Nin et al. 2012), and migrate to coastal areas for spawning, from April or May to the end of June (in European areas), where temperatures vary from 13ºC to 23ºC(González-Quirós et al., 2011). After spawning, meagre returns to offshore areas where they spend the autumn and winter months (Abecasis et al., 2024; Gandra et al., 2024). This predatory fish has gained increasing importance for humans. It supports significant recreational and commercial fisheries, both large and small scale, in the Atlantic and Mediterranean(González-Quirós et al., 2011). Furthermore, its promising growth potential and general commercial acceptance led to significant interest in developing its aquaculture (Duncan et al., 2013; Gil et al., 2014; Ortega, 2007). Research on meagre has been carried out in both aquaculture settings (Arechavala-Lopez et al., 2015) and in wild populations using otolith microchemical analysis and fisheries-dependent data (e.g. Morales-Nin et al., 2012; Quero & Vayne, 1985). However, these traditional methods are often influenced by fish catchability and sampling efforts, leading to indirect evidence of migration patterns. More recently, biotelemetry has been established as a valuable tool for studying the thermal habitat preferences and movement patterns of meagre. Five telemetry studies have been conducted along the Portuguese coast (Abecasis et al., 2024; Gandra et al., 2024; Garel et al., 2024; Winkler et al., 2023), marking significant progress. However, similar studies on other meagre populations are still lacking, and the existing studies are concentrated in the same geographic area, occasionally involving the same individuals.

The Gironde Estuary, in France, is one of the six areas where meagre is known to reproduce, alongside Tejo (Portugal) and Guadalquivir (Spain) estuaries, the Banc d'Arguin

(Mauritania) and the Nile (Egypt) and Menderes (Turkey) deltas (Haffray et al., 2012). The Gironde estuary (Figure 1.1) is a mixed to well-mixed estuary, that begins downstream of the Bec d'Ambés at the confluence of the Garonne and the Dordogne rivers and extends for 20-60km until the Bay of Biscay (Lobry et al., 2003; Zhan Hua et al., 1994). It is the largest in Western Europe, reaching 635 km2 at high tide (Kraepiel et al. 1997; Rochard et al. 2001). The water depth varies significantly, ranging from 3 meters near the shelf in the upper estuary to up to 26 meters in the lower estuary, with an average depth of approximately eight meters at mid-tide (Taverny et al., 2002). The water temperature ranges from 6°C in January to 26°C in July and follows a gradient of temperature from the ocean to the river, that inverts twice a year (during spring and fall) (Maurice, 1993). Recent studies have reported an increase in water temperature and an extended seawater intrusion associated with global changes, and these changes led to a significant increase in juvenile density of several marine species like *Engraulis encrasicolus, Sprattus sprattus, Dicentrarchus labrax, Solea solea*, *Merlangius merlangus* and *Argyrosomus regius* (Pasquaud et al., 2012).

Information on the movement patterns of meagre in and around the Gironde estuary are very limited. Considering meagre’s vulnerability to exploitation, its growing importance to fisheries, and its critical role in the ecosystem, it is crucial to study this species in one of its most important spawning areas. Therefore, in this study, we used satellite telemetry to infer the depth, temperature, and movement patterns of adult meagre, around one of their main spawning grounds, the Gironde estuary. We used data visualization and an inferential modelling framework to better understand their spatial ecology.

Materials and Methodology

Meagre capture and tagging

Individual meagre were captured at the entrance of the Gironde estuary of France (45°32.31' latitude, 0°59.90' longitude) (Fig 2.1) on four different days in June 2022. Fish were caught using longline baited with sardines. This passive fishing technique can be adapted for targeting specific species through changes in materials, lengths, bait, and deployment strategies (Watson & Kerstetter, 2006). The operations were carried out onboard a commercial fishing boat using their standard methods.

Fish were individually brought aboard the vessel, where their Total Length (TL) was measured with a flexible measuring tape. The weight was estimated using a length/weight equation, where the intercept, that is specific to the organism is 9.058×10^{-6}, and the proportion in which the weight increases with the length is 2.993 (Weiller et al. unpublished data). Only fish with sizes larger than 100cm TL were selected for tagging to ensure that all individuals had reached sexual maturity (Sourget & Biais, 2009).

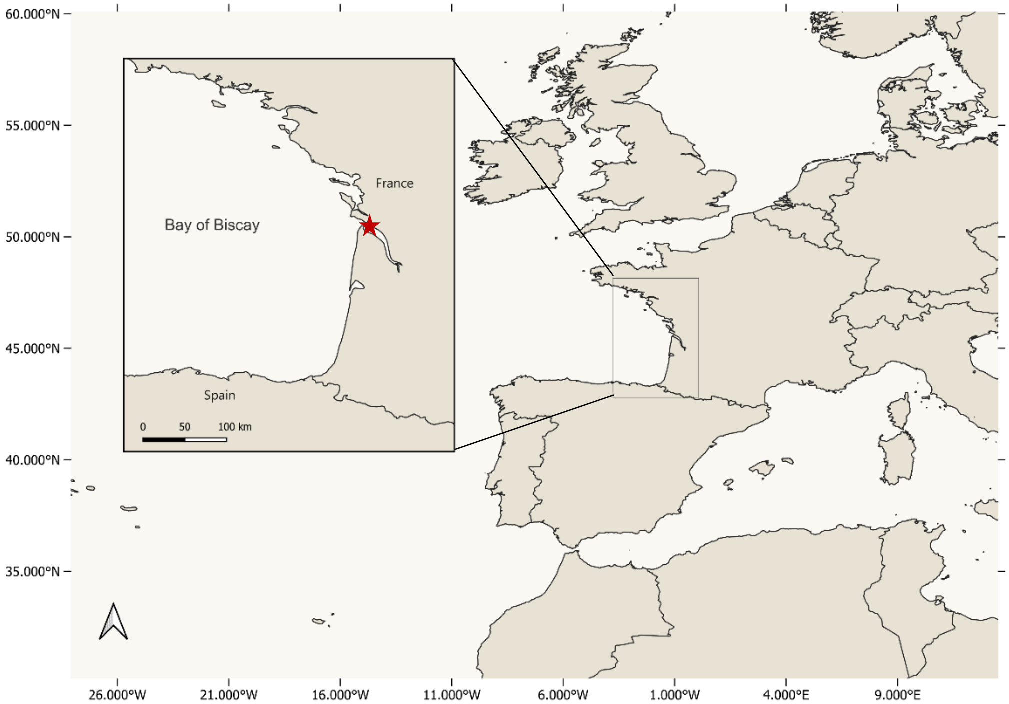


Figure. 2.1 Map of the study area, Bay of Biscay and Gironde Estuary. Red star represents the tagging site.

For a tagging, each fish was placed on a soft stretcher with running seawater through the gills for oxygenation. Their eyes were covered with a wet cloth to reduce stress, while a small incision was made at the base of the first dorsal fin where the tag was inserted. A titanium anchor was connected to the pop-up satellite archival tag (MiniPAT, Wildlife Computers, WA, USA) with a coated steel cable. The tag was darted into the dorsal musculature so that it would be anchored between the pterygiophores. To decrease drag on the anchor, a swivel was added and to minimize the tag's movement, a secondary anchor point was established. This anchor featured a steel cable loop, loosely fitted around the tag's body, and was embedded into the dorsal muscle, aligned longitudinally with the primary anchor (Figure 2.2). Tagging procedures were approved by the Animal Welfare Committee of the Centro de Ciências do Mar (CCMAR - ORBEA).

Figure 2.2. - MiniPAT tag anchored to the dorsal musculature of meagre, *Argyrosomus regius.* The secondary anchor with yellow Steel cable loop attached.

The tags were programmed to archive temperature, pressure (depth), light level, acceleration (Ax, Ay, and Az), every five seconds (sampling rate), for deployment period of 300 days. Additionally, duty cycling settings were programmed to generate Argos messages intermittently for both time series and summary data. For the data regarding Time-at-Depth (TAD) and Time-at Temperature (TAT) summary histograms, Profile of Depth and Temperature (PDT), and mixing layer data were summarized using a six-hour period. The time series interval for depth and temperature was set to a 10-minute interval. The duty cycling is used to reduce the total number of messages and to extend the deployment period (Wildlife Computers, 2019).

The tags transmitted the summary data through Argos Satellite constellation, after getting detached from the fish. When the tags were physically recovered, the complete records were obtained.

Table 2.1. Deployment summary, showing fish ID, MiniPAT serial number, fish total length (TL; in cm), estimated weight (W; in kg), tagging date, pop-up date, and number of days attached and relative time of attachment. The asterisk denotes the tags that were physically recovered.

Fish ID	MiniPAT SN	Fish TL (cm)	Fish W (kg)	Tagging date	Pop-up date	Days attached
1*	20P1368	131	19.68	2022-06-13	2022-07-01	19 (6%)
2	20P1451	120	15.14	2022-06-13	2022-08-26	75 (25%)
3*	20P1461	115	13.33	2022-06-13	2022-07-02	20 (7%)
4	20P1721	114	12.98	2022-06-13	No Transmission	NA
5	20P1374	118	14.39	2022-06-14	2022-10-15	123 (41%)
6	20P1392	106	10.44	2022-06-14	2022-07-03	20 (7%)
7	20P1723	120	15.14	2022-06-14	No Transmission	NA
8*	20P1786	106	10.44	2022-06-14	2022-06-22	9 (3%)
9*	20P1816	111	11.99	2022-06-14	2022-08-13	61 (20%)
10*	20P1473	106	10.44	2022-06-17	2022-10-10	115 (38%)
11	20P1563	116	13.68	2022-06-17	2022-07-13	27 (9%)
12*	20P1651	107	10.74	2022-06-17	2022-08-09	54 (18%)
13	20P1665	101	9.04	2022-06-17	No Transmission	NA
14	20P1689	118	14.39	2022-06-17	2022-07-30	43 (14%)
15*	20P1320	122	15.90	2022-06-18	2022-12-11	176 (59%)
16	20P1406	107	10.74	2022-06-18	No Transmission	NA
17	20P1458	106	10.44	2022-06-18	2022-11-17	148 (49%)
18*	20P1529	104	9.86	2022-06-18	2022-08-20	63 (21%)
19	20P1687	126	17.52	2022-06-18	No Transmission	NA
20*	20P1690	111	11.99	2022-06-18	2022-10-26	130 (43%)

Data management and analysis

The transmitted data and the archived data (from recovered tags) were decoded using the manufacturer's proprietary program DAP and analyzed with R in R Studio. Additionally, data from recovered tags was first observed in the Wildlife Computers' Instrument Helper software. Archived data were preferred over summary time series data (obtained from satellites) due to their higher resolution and more comprehensive coverage.

The archived data included measurements from the period when the tag was floating, after premature detachment from the fish. Therefore, the last relevant record was used to determine the pop-up date, and to calculate the tag attachment duration. All records made at the surface were excluded from the analysis. Additionally, due to the short sampling period, meagre #8 was excluded from the continuous wavelet transform analysis and geolocation models.

Depth, temperature and diel phases

Depth and temperature data from all fish were plotted to visually examine possible temporal (seasonal) patterns and vertical distribution. Box plots of changes in depth and temperature use over the months were made (Supp figure 3.1 and 3.2). The results were statistically analyzed using a Kruskal-Wallis test. Additionally, a monthly depth-temperature plot was made per individual and for all animals. To do so, the maximum depth to the nearest multiple of 10, and the density of depth and temperature data were estimated. Afterward, the overall monthly depth and temperature ranges could be calculated. We also explored the effect of the diel phase on vertical habitat use (Supp figure 3.3). The *sunriset* function from the package *suntools* was used to associate each diel phase - day or night - to every record. To assess the diving profile during each diel period, box plots of depth were plotted with the *Rcmdr* package (Fo, 2017) using the data from all fish and for each individual separately. As the data was non-normally distributed and the variances between variables were different, the differences in depth use between diel phases throughout all the data were assessed through a two-sample Wilcoxon non-parametric test.

Continuous wavelet transform

To better understand the periodic changes in temperature and depth utilization during the sampling periods, a continuous wavelet transform (CWT) analysis was performed using the R package *wavScalogram* (Bolós et al., 2017). This analysis was made to infer meagre's positions inside or outside of the estuary, with the aim of using this information to later on improve the accuracy of the geolocation models. Cyclical changes in temperature in a 12-hour period correspond to tidal cycles, suggesting that the meagre was inside the estuary. Due to gaps in the data transmitted via satellite, only the data obtained from the recovered tags (Fish #1, #9, #10, #15, #18, and #20) was analyzed. In the CWT analysis, the data of depth and temperature was separated into 5-minute time bins and compared with a Morlet mother wavelength. The coefficient of similarity between our data and the mother wavelength was calculated using the function "*cwt_wst"*. The results were plotted to observe when these patterns were detected, and what was the periodicity.

Geolocation

To analyze the horizontal habitat use, the movements of all the individuals were reconstructed. The trajectories were predicted using Hidden Markov models (HMMs), implemented through the "*HMMoce*"(Braun et al., 2018) package, which was modified by Gandra et al., (2024). The HMMoce package was modified, as it was developed mainly for oceanic pelagic species. To improve the accuracy of the trajectories, the tagging and pop-up locations were used to restrict the likelihood distributions, as well as the information obtained on the CWTs analysis: whenever a clear 12-hour temperature change periodicity signal was observed, a location within the estuary was incorporated into the trajectory prediction model, constraining the likelihood distribution for that specific day.

This state-space-based framework compares in-situ variables collected by the tag against high-resolution (HR) environmental datasets or oceanographic models. This comparison creates likelihood layers that range from 0 to 1. Values close to 1 are assigned to areas where the data collected by the tags closely match those predicted by the HR environmental datasets/oceanographic models. The datasets collected by the tags, used to estimate the geolocation trajectories were light levels, SST, depth-temperature profiles, MinMax depths, and lastly, GPE2 files, which are light-based longitude probabilities, obtained through the tag manufacturer GPE2 software. The HR environmental datasets or oceanographic models used to create the SST likelihoods were the Multi-scale Ultra-high Resolution (MUR) SST Analysis dataset from NOAA. For the temperature-at-depth likelihoods, we used the Hybrid Coordinate Ocean Model (HyCOM), while the bathymetry likelihoods were obtained from the EMOdnet bathymetry dataset. After obtaining all the likelihoods, we combined the different layers one by one and used an algorithm to figure out the distribution of each time point. We picked the best model for each meagre using the

Akaike's Information Criterion (AIC) method to find their most likely location each day (Table 2.2).

Results

Of a total of 20 meagre tagged, 15 transmitted data. The number of days in which the tag was attached was shorter than the initial programmed deployment period for all individuals, achieving an average of 72.2 days, corresponding to 24% of the programmed deployment period (300 days). Only four tags (20%) remained attached for 43% of the programmed deployment. The minimum number of days attached was 9 and the maximum 176 days (Table 2.1). Additionally, in some cases, data packages were not fully transmitted, resulting in gaps in data such as missing days or records of either temperature or depth, which is recurrent in this type of study.

Nine (45%) tags were retrieved, and the full archived data was extracted. These tags were recovered by fishermen (recreational and commercial) or beach goers. Among the 15 tags that provided data, the proportion of environmental information used to estimate geolocation likelihoods varied (Table 2.2). Light-based position estimates were available for a median of 23% of the deployment days (ranging from 0% to 80%). Sea Surface Temperature (SST) data was available for a median of 40% of the deployment days (ranging from 3% to 96%). Depth-temperature profile data was available for a median of 35% of the deployment days (ranging from 1% to 62%), while maximum depth profiles were available for a median of 100% of the deployment days (ranging from 10% to 100%).

Regarding vertical movement, the maximum depth recorded varied between 16.60 (#6) and 141.50 meters (#15), and the mean maximum depth between all individuals was 42.92 meters (±28.84 SD). Temperatures ranged between 12.60ºC (#15) and 24.95ºC (#12) (Table 2.2), averaging 19.93 ºC (±2.05 SD). When we compared all depth data used during each diel phase, statistically significant differences were observed (Wilcoxon Test: W= 11826755572307, p-value < 2.2e-16) (Supp figure 3.3) with the median of depth used during the day being 11.0 meters and during night 11.5 meters. The box plots for each fish did not show any specific pattern of depth use shift during day and night (Supp figure 3.4).

Regarding depth and temperature utilization over the sampling period, there were statistically significant differences in depth utilization over the months (Kruskal-Wallis test: χ^2 = 2,419 df = 6, p-value < 2.2e-16), and the same was observed for the temperature (Kruskal-Wallis test: χ^2 = 2,838,742, df = 6, p-value < 2.2e-16) (Supp figure 3.2 and 3.5). The results revealed that during spring and summer months, from June to September, the fish predominantly occupied shallower waters, with median depths of 10.5, 10.5, 11.0, and 13.0 meters, respectively. On the contrary, during the autumn and winter months, from October to December, the fish utilized deeper waters, with median depths of 14.5, 26.0, and 41.0 meters. An inverted trend was observed regarding temperature. From summer to winter, the temperatures used decreased, with median values of 19.20, 19.45, 19.40, 19.25, 16.70, 15.65, and 16.40°C from June to December, respectively. (Figure 2.2). (Supp figure 3.5)

The results from the CWTs revealed cyclical patterns of temperature change in all fish during some of the days (Figure 2.4) and the results for depth analysis did not show any signals (Supp figure 3.8). Regarding the temperature analysis, meagre #1, #3, #9, #10, #12, #15, and #18 exhibited only a distinct 12-hour period pattern, while meagre #3 and #20 also showed patterns corresponding to a 24-hour period over different days (table 2.2; figure 2.4). In meagre with shorter sampling periods, such as #1, and #3, consistent 12-hour patterns were observed, though the signal strength varied. The same happened for meager #18, even though it had a larger sampling period. For meagre #9, strong temperature periodicity was evident in June, but no signals were detected in early July. From mid-July to the end of August, only weak signals were observed. Meagre #10 and #15, showed 12-hour periodic patterns from the beginning of the sampling period until the beginning of August. Lastly, meagre #20 had weak 12-hour signals from June to early August, and 24-hour signals during the rest of August. No significant signals were detected in September and October. Notably, all robust 12-hour patterns across all individuals occurred between June and early August.

Table 2.2 : Summary data for *Argyrosomus regius* tagged with satellite transmitters (MiniPATs). The columns for Light, SST, PDT, and Depth indicate the percentage of deployment days with light-based location estimates, sea surface temperature data, depth-temperature profiles, and maximum depths, respectively. The Observation Likelihoods column lists the data streams used to reconstruct the most probable track for each animal: L - light-based longitude, S - sea surface temperature, O - integrated Ocean Heat Content, B - bathymetry. IDs marked with an asterisk denote tags that were physically recovered. Estuary Days – Number of days where the CWT's results showed that each meagre was inside of the estuary.

Fish #	Mean Depth ± SD (m)	Max Depht (m)	Mean Temp ± SD (ºC)	Min temp (ºC)	Max Temp (ºC)	Light	SST	PDT	Depths	Obs Likelihood	Estuary Days
1*	10.28 ± 2.07 *	43.0*	17.96 ±1.33 *	13.4*	19.8*	15 (79%)	8 (42%)	7 (37%)	19 (100%)	L S B	14
2	9.94 ± 2.55	35.0	19.33± 1.91	14.8	23.3	22 (31%)	62 (87%)	5 (7%)	35 (49%)	L O B	-
3*	10.52 ± 3.36*	32.8	18.44 ±0.96*	14.6*	20.1*	10 (59%)	10 (59%)	8 (47%)	17 (100%)	S O B	8
5	11.87 ±7.15	48.0	21.51 ± 1.96	13.8	27.3	7 (6%)	30 (26%)	4 (4%)	41 (36%)	L O B	-
6	10.46 ±4.35	16.5	20.74 ± 1.00	16.6	24.3	0 (0%)	10 (59%)	3 (18%)	17 (100%)	O B	-
8*	6.99 ±2.02 *	25.0*	21.78 ± 1.75 *	17.6*	24.5*	-	-	-	-	-	-
9*	14.00 ±6.54 *	41.0*	20.81 ± 3.14 *	17.0*	23.1*	8 (15%)	14 (26%)	33 (62%)	53 (100%)	L S B	11
10*	11.26 ± 3.48 *	49.5*	19.30 ± 1.87 *	14.1*	23.1*	90 (80%)	51 (45%)	62 (55%)	113 (100%)	L S B	24
11	5.91 ± 1.57	23.5	20.46 ± 0.78	16.6	23.3	0 (0%)	23 (96%)	4 (17%)	24 (100%)	O B	-
12*	5.66 ±1.98 *	32.5*	22.26 ± 1.27 *	16.5*	25.0*	5 (10%)	50 (98%)	25 (49%)	51 (100%)	S O B	2
14	12.87 ± 3.74	35.0	20.84 ± 0.98	18.0	23.5	4 (10%)	14 (33%)	9 (21%)	22 (52%)	L S B	-
15*	17.68 ± 9.17*	141.5	17.36 ± 1.53	12.6	21.4	114 (38%)	33 (11%)	101 (34%)	177 (59%)	S O B	39
17	15.12 ±7.84	48.0	18.68 ± 0.97	16.5	20.8	5 (3%)	5 (3%)	1 (1%)	15 (10%)	S O B	-
18*	11.44 ± 2.10*	38.0*	18.89 ± 1.69 *	14.2*	23.2*	19 (35%)	15 (27%)	19 (35%)	55 (100%)	L S B	25
20*	12.23 ± 4.17*	34.5*	19.04 ± 1.44 *	15.0*	22.6*	47 (42%)	43 (38%)	69 (61%)	113 (100%)	L S B	0
Average	11.08± 3.26	42.92±28.84	19.83±1.48	15.40±1.65	22.99±2.29						

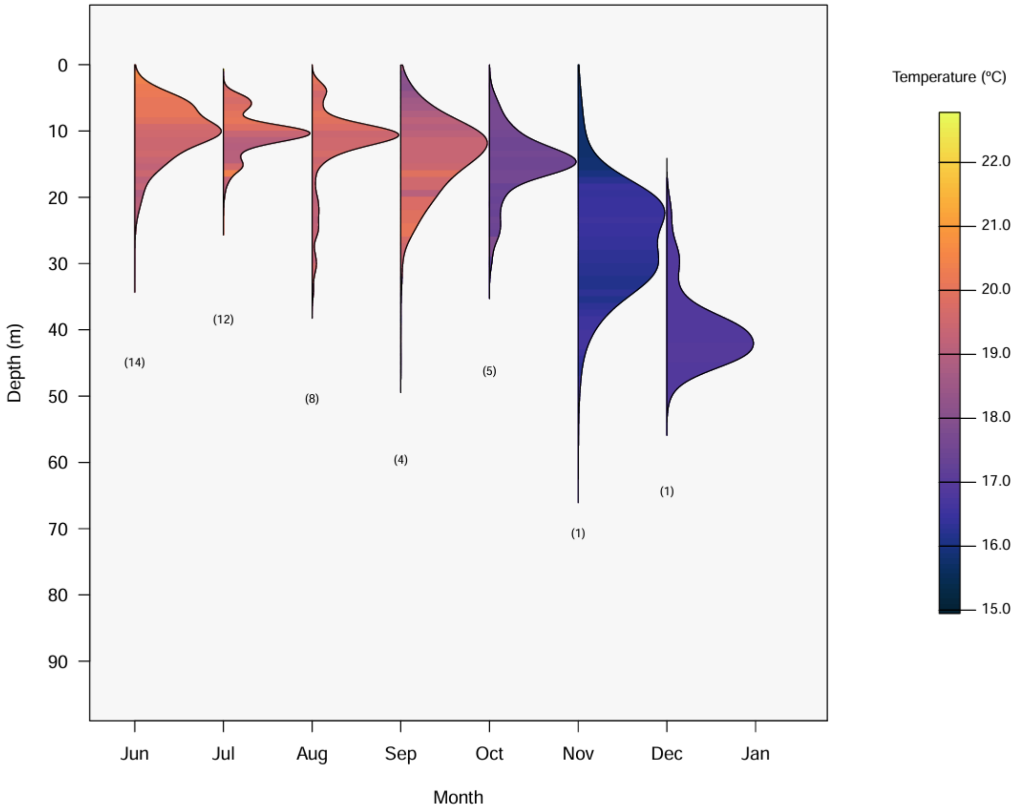


Figure 2.3 - Density of depth usage by month, color-coded by average temperature (1-m depth bins). The number of individuals with depth data in each month is shown in parentheses.

Concerning horizontal movements, the reconstructed trajectories indicated activity both within and beyond the Gironde Estuary, but consistently within the Bay of Biscay (Figure 2.5). The models integrating information from the CWTs, restricting positions within the estuary whenever strong 12-hour period signals were observed, revealed that meagre #1 was the only individual that stayed mainly inside the estuary, although it had a very short sampling period of 19 days (during June). Meagre #15 and #17, which had the longest sampling periods of 176 and 148 days respectively, were the ones that migrated furthest from the shore. Fish #15 was detected close to the Cap Ferret canyon and, coincidentally, was the fish with the deepest recorded depth of 141.5 m. All other fish were predicted to remain in areas close to shore for most of the time, though their sampling periods were shorter. The general pattern observed started with an initial northward movement.

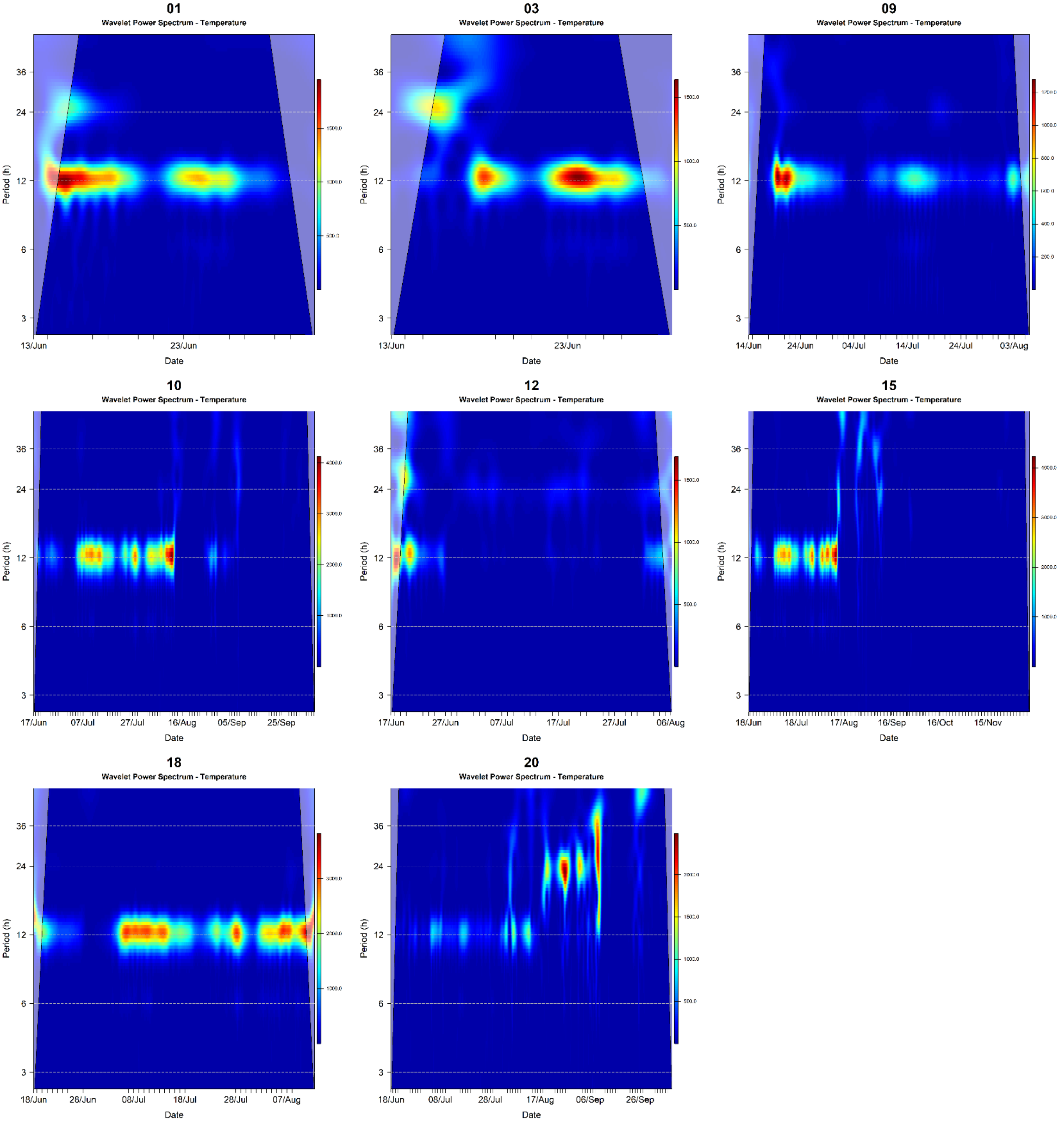
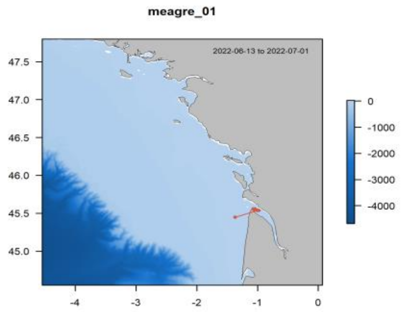
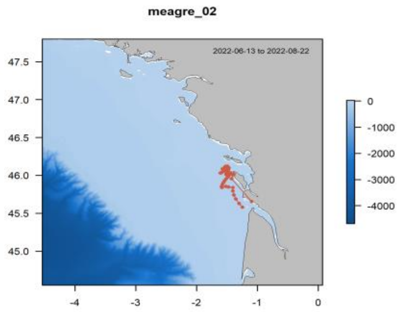
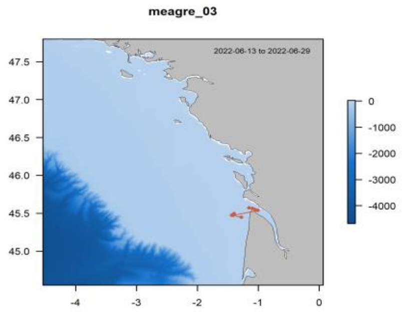
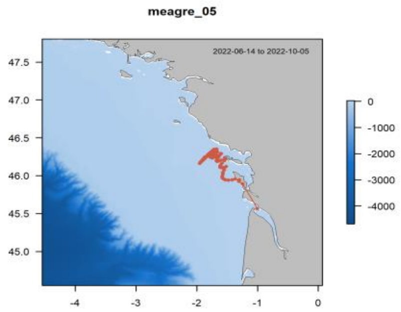


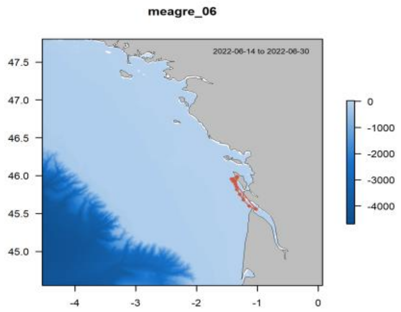
Figure 2.4 - Continuous wavelet transformations (CWTs) for temperature over the days. The x-axis represents the total days the tags were attached. The y-axis shows the frequency of cyclical patterns in hours. Patterns outside the cone of influence should not be interpreted. Wavelet power levels are represented by the colors, shown in the color ramp, from blue (low wavelet coefficient) to red (highest wavelet coefficient).

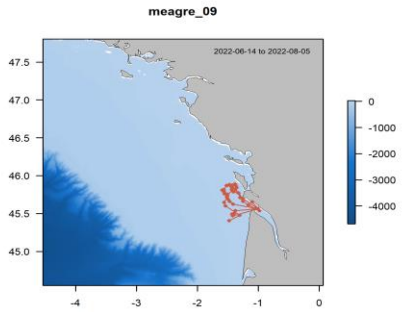

meagre_01
2022-06-13 to 2022-07-01
47.5
47.0
46.5
46.0
45.5
45.0
-4
-3
-2
-1
0
0
-1000
-2000
-3000
-4000

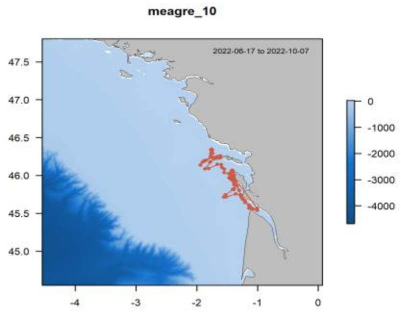

meagre_02
2022-06-13 to 2022-08-22

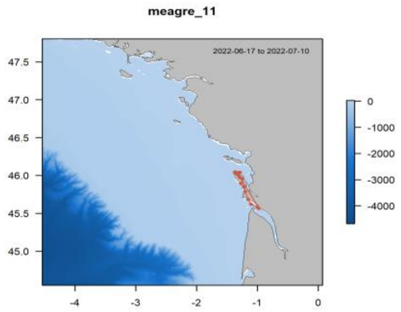

meagre_03
2022-06-13 to 2022-06-29

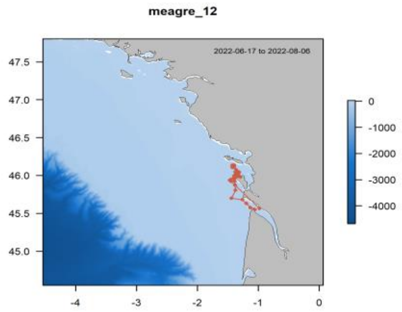

meagre_05
2022-06-14 to 2022-10-05

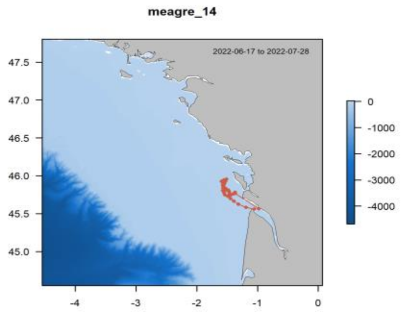

meagre_06
2022-06-14 to 2022-06-30

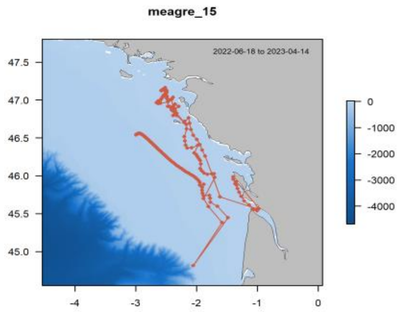

meagre_09
2022-06-14 to 2022-08-05

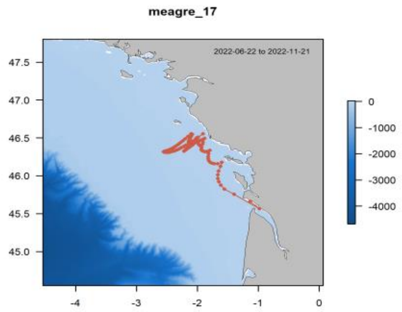

meagre_10
2022-06-17 to 2022-10-07

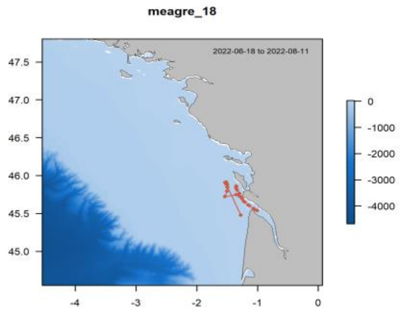

meagre_11
2022-06-17 to 2022-07-10


meagre_12
2022-06-17 to 2022-08-06


meagre_14
2022-06-17 to 2022-07-28


meagre_15
2022-06-18 to 2023-04-14


meagre_17
2022-06-22 to 2022-11-21


meagre_18
2022-06-18 to 2022-08-11

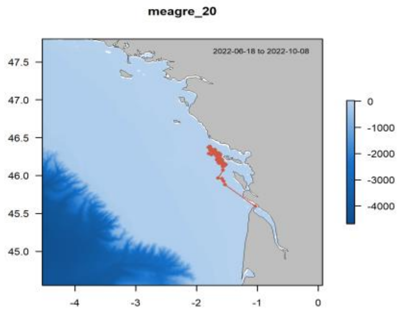

meagre_20
2022-06-18 to 2022-10-08

Figure. 2.5 – Continuous wavelet transformations (CWTs) for temperature over time. The x-axis represents the period during which the tags were attached, while the y-axis shows the frequency of cyclical patterns in hours. Patterns outside the cone of influence should not be interpreted.

Discussion

This study presents the first *in situ* assessment of horizontal movement, depth, and temperature preferences of meagre in and around the Gironde estuary. We analyzed data collected by pop-up satellite archival tags from June to December 2022, covering the spawning period (June to mid-July) (Lagardère & Mariani, 2006) and the subsequent migration to the sea (Morales-Nin et al., 2012a; Quero & Vayne, 1985), although the results are primarily weighted towards the summer and autumn months due to fewer data collected during the winter months. The short attachment period observed in all tags can be related to a problem with the tether, which got detached from the fish before it started to corrode. Additionally, premature releases may occur due to poor insertion, infection at the insertion site, increased drag from biofouling, entanglement, fish death, or if the tag is removed by a predator, social and sexual behaviors of the tagged individuals or a fisher upon capture (Musyl et al., 2011). This study implemented a novel approach by integrating CWT analysis results into the geolocation models. Since the results of depth measurements from CWTs did not show any cyclical signals, but the temperature measurements did, it suggests that the observed periodic signals are likely related to tidal cycles in the estuary: The 12-hour temperature cycle signals recorded correspond to tidal temperature fluctuations, indicating the fish's presence in an area significantly affected by these changes within the estuary. Incorporating this information into the models significantly improved prediction accuracy. This innovative approach of using temperature periodicities to infer fish location demonstrates the potential of CWT in analyzing PSAT data, highlighting its value in marine spatial ecology.

Vertical movements

The observed vertical use is in agreement with earlier findings that documented a seasonal shift in depth and temperature utilization (Abecasis et al., 2024; Gandra et al., 2024;

Garel et al., 2024; González-Quirós et al., 2011; L.; Winkler et al., 2023). Fish occupy shallower and warmer waters during summer (June to September) and move to deeper and cooler waters starting in October as winter approaches, which can be related to their known migration to deeper offshore areas (Abecasis et al., 2024; Gandra et al., 2024; Garel et al., 2024; Winkler et al., 2023). Given that the sampling period included seasonal changes and habitat shifts, we observed a significant range of maximum depths, from 16.6 meters to 141.5 meters, with an average maximum depth of 42.92 meters. Previous studies, conducted in 2018 and 2019 along the southern Portuguese coast, have documented meagre inhabiting depths of up to 125.0 m (Gandra et al., 2024; Winkler et al., 2023). In the Bay of Biscay, the depth is around 100 meters except in canyons, where it increases significantly. The greater depth recorded, by meagre #15, is likely due to its longer tracking period until December, which allowed it to move into deeper offshore areas and canyons. Although this is a unique occurrence in our data, meagre can reach depths of 200 meters in offshore shelf waters, though they usually stay between 15 and 100 meters.(Griffiths & Heemstra, 1995). Changes in water temperatures might trigger migration towards offshore areas, in the same way warming sea temperature in the boreal spring triggers migration to spawning(Garel et al., 2024; Quero & Vayne, 1985). The use of deeper waters, as meagre move to offshore areas during winter, may be linked to the behavior of their main prey, the anchovy (*Engraulis encrasicolus*), which stays near the bottom during the day (Tsagarakis et al., 2012). This could explain why meager are found at greater depths in these areas.

The average depth used was 13.99 meters, whereas the average maximum depth was 42.92 meters. This great difference arises from two issues. The sampling period does not cover all winter months - when meager uses deeper waters - and the early release of the majority of the tags before November, leaving only one fish to provide data for November and December. Therefore, the mean depths more accurately reflect meagre's depth preferences during the spawning season, as the majority of data was collected during this period, resulting in the shallower average depth. Consequently, all the maximum depths reflect the migration towards deeper offshore areas that occurred during October, and for fish #15 that extended until December.

During summer, the vertical habitat ranges were smaller when compared to winter. This likely results from meagre's spawning behavior and the habitat preference during this time, as they aggregate inside the estuary, where depths range from 3 to 26 meters (Taverny et al., 2002). As water temperatures drop in October, meagre begins to use deeper, cooler waters, with a broader range of depth utilization clearly observed during November (Figure 2.3). However, because only one tag provided data for the months of November and December, the movement of a single individual may not fully represent the population. These findings agree with previous studies on meagre depth preferences, which found that the species typically reside at depths of shallower than 30 meters during spring and summer and deeper during winter (Winkler et al., 2023). Additionally, it matches with results from the Australian *Argyrosomus japonicus* which also spends significantly more time at deeper depths (between 20.1 – 50.0m) in the autumn and shallower depths (2.1 – 10.0m) during the summer (Barnes et al., 2019).

The variations in depths throughout the year, are likely due to the horizontal movements and the changes in depth in the different locations, as meagre prefers to stay near the seafloor, consistent with its classification as a demersal species (Cropper et al., 2014). Meagres tend to feed opportunistically throughout the day, as a predator of both pelagic and demersal species, they rely on a wide range of food, ranging from clupeiformes to demersal fish and cephalopods (Hubans et al., 2017). Nevertheless, a shift in prey preference might occur, during different seasons, and could explain these migrations. Regarding diel vertical movement (DVM), even though the statistical analysis was significant, the median of depth utilization between day and night varied by 0.5 meters. These results might have happened due to a sample size too large. This happens because the standard error of the mean decreases with larger samples, making the test more sensitive, and resulting in several outliers. With a large enough sample, the test can detect differences that may not be significant from an ecological point of view but are statistically significant. Therefore, we can conclude that the DVM results align with previous research, and did not show any pattern regarding diel phases (Gandra et al., 2024; Winkler et al., 2023), and this can be explained by its opportunistic feeder characteristics.

The temperatures experienced by the tagged individuals were generally within their known range 13–28°C (Nousias et al., 2020). Recorded temperatures varied from 12.6°C to 27.3°C, with a mean of 18.9°C (± 2.1 SD), and showed an inverse relationship to depth patterns: a wider temperature range was observed during summer compared to winter. Research indicates that estuary temperature decreases from 26°C in September to 6°C in January (Maurice, 1993). In October, the fish inhabits approximately the same range of depths as during summer, even though the water temperature is colder in that month. With a decrease in temperature, the only remaining fish, meagre #15 migrated to deeper waters, suggesting sensitivity to temperature fluctuations. As hypothesized in previous studies, the results support that temperature is the most important factor in determining the timing of migration, and reproduction (González-Quirós et al., 2011; Quero & Vayne, 1985). Additionally, starting in spring and throughout summer, the water column stratifies due to continental water discharges, creating a wider range of temperatures at different depths due to south-westerly winds. These different temperatures are visible in figure 2.3, where a small variation of depth results in a great shift of temperature. When Azores Hight leaves the Iberian Peninsula and enters the Bay of Biscay, and these well-mixing poleward waters break the stratification, leading to more uniform temperatures throughout the column. (J. Gil, 2008). Additionally, during winter the water temperature inside the estuary tends to be colder than in coastal areas. During summer this trend inverts, and coastal areas become colder (Deborde et al., 2007). This can also be a reason for this migration towards coastal areas as winter approaches.

The limited use of colder waters during the winter months is likely due to meagre’s need to migrate much further south to access warmer waters. Moreover, in aquaculture studies meagre has been observed to reduce food intake rates when temperatures fall below 14ºC, lowering winter growth (Duncan et al., 2013). Due to the decrease in water temperatures during winter months and the mixing of the water column, it can be hypothesized that the migration towards deeper waters, which may not be significantly colder than the top layers, may serve as a predator avoidance mechanism or a shift in prey preference while maintaining the tendency to be close to the seafloor. Previous research has suggested that when meagre swim deeper during the winter season, they exhibit less high-activity periods, consequently decreasing the need to feed as often (Gandra et al., 2024), therefore a switch in feeding habits can explain this behavior. An analysis of the acceleration and overall activity of the individuals in this study can provide further clarification and potentially support Gandra et al., 2024 findings.

Horizontal movements and seasonal behaviour

Regarding geolocation, our results are in accordance with previous studies. It has been documented that this species begins its aggregations in the estuaries in April or May, spawns from June to August, and subsequently migrates towards offshore areas for winter periods (Gandra et al., 2024; Lagardère & Mariani, 2006; Quero & Vayne, 1985). The observed changes in depth align with the geolocation data, showing that the individuals initially inhabit the shallower waters of the Gironde estuary. Over time, they progressively migrate towards coastal areas and eventually move into deeper offshore regions. The meagre with shorter sampling periods (#1, #3, #6, and #11) remained inside of the estuary or very close to its mouth. The individuals with longer sampling periods (#2, #5, #10, #11, #12, #14, and #18) displayed a similar pattern, starting in the estuary, moving near the shore before swimming northward, but still close to the coastline. Meagre #9, however, stayed close to the mouth of the estuary throughout the entire duration of the sampling period, 61 days, between June and August. The tags that recorded data the longest (#15, #17 and #20) were the ones that moved farthest away from the coast. Notably, after initially moving north, fish #15 dispersed southern and more offshore. Geolocation predictions indicated horizontal movements near the Cap Ferret Canyon, specifically close to the upper canyon region (< 500 m) (Cremer, Weber, and Jouanneau 1999; Durrieu De Madron et al. 1999), this aligns with depth data, where detection at 141.5 meters deep was recorded, potentially explaining this result. During the period of this depth record, the range of vertical use was particularly wider, probably due to the greater availability of vertical habitat. Even though this record was a one-time event in our data, meager can inhabit these depths during their offshore periods, as observed by Winkler et al.(2023).

The reasons behind the habitat shift are still unclear, however, previous studies have suggested that, like many other fish, meagre moves to estuaries as a breeding strategy (Winkler et al., 2023), due to this ecosystem nursery characteristics (Pasquaud et al., 2012;

Taverny et al., 2002). Spawning in high-prey areas ensures resources not only during gamete production and courtship but also estuaries provide a highly productive, sheltered, shallow, and warmer environment for egg and larvae survival (Duncan et al., 2013; Gandra et al., 2024). Our findings might be consistent with the limited adult travel theory of genetic isolation put out by Abecasis et al., (2024), since most of our individuals remained near the estuary and coastal regions, none of them leaving the Bay of Biscay. However, our data was somewhat limited in terms of the sampling period, which prevents us from making inferences on this matter. Additionally, recent research showed that this species, studied off the coast of Portugal, exhibited some of the longest migrations ever recorded for a coastal species (Gandra et al., 2024).

Conclusion

This research provided new information regarding the *Argyrosomus regius* population from the Gironde estuary and supported findings from previous studies. The clear seasonal shift in depth and temperature already hypothesized through indirect data (Morales-Nin et al., 2012; Quero & Vayne, 1985) and recently observed during *in-situ* studies (Gandra et al., 2024; Winkler et al., 2023) was also observed here, as well as a horizontal movement from the estuary to offshore areas, after spawning aggregations (Gandra et al., 2024; Morales-Nin et al., 2012). The enhancement of geolocation models made by Gandra et al., 2024 along with the additional information obtained from the CWT results contributed to more accurate and coastal-species-appropriate predictions. These outperformed both the commonly-used GPE3 software (provided by the manufacturer) and the geolocation models that lacked CWT data. (Supp figure 3.6 and 3.7)

For future studies, an extent of the sampling period and an increase in the sample size would offer a clearer understanding of depth shifts and migrations throughout the year, as well as insights into potential spawning site fidelity (Gandra et al., 2024). Combining pop-up archival satellite transmitters with acoustic tags through double-tagging methods would enhance geolocation accuracy. Additionally, a more detailed investigation of seasonal feeding habits could help uncover the underlying reasons for these migrations.

Research on this species has become increasingly important. The meagre supports economically important fisheries which relate to the rising exploitation of these fish populations (González-Quirós et al., 2011). This species is already highly genetically fragmented, due to their limited and dispersed breeding areas (Abecasis et al., 2024; Haffray, et al., 2012; Almeida et al., 2022). Additionally, the meagre spawns in areas that are heavily affected by anthropogenic pressures, making their reproduction harder. All of these contribute to their vulnerability. As a high predator, they are essential in ecosystems, as they control the abundance of other species. Therefore, a thorough understanding of the species' ecology, movements, and feeding habits is essential to inform ecosystem management strategies. Equally important is investigating the impacts of temperature changes on this species' life history characteristics, like growth, reproduction, or movement patterns, and on important habitats such as feeding grounds and spawning areas, to address the challenges posed by climate change.

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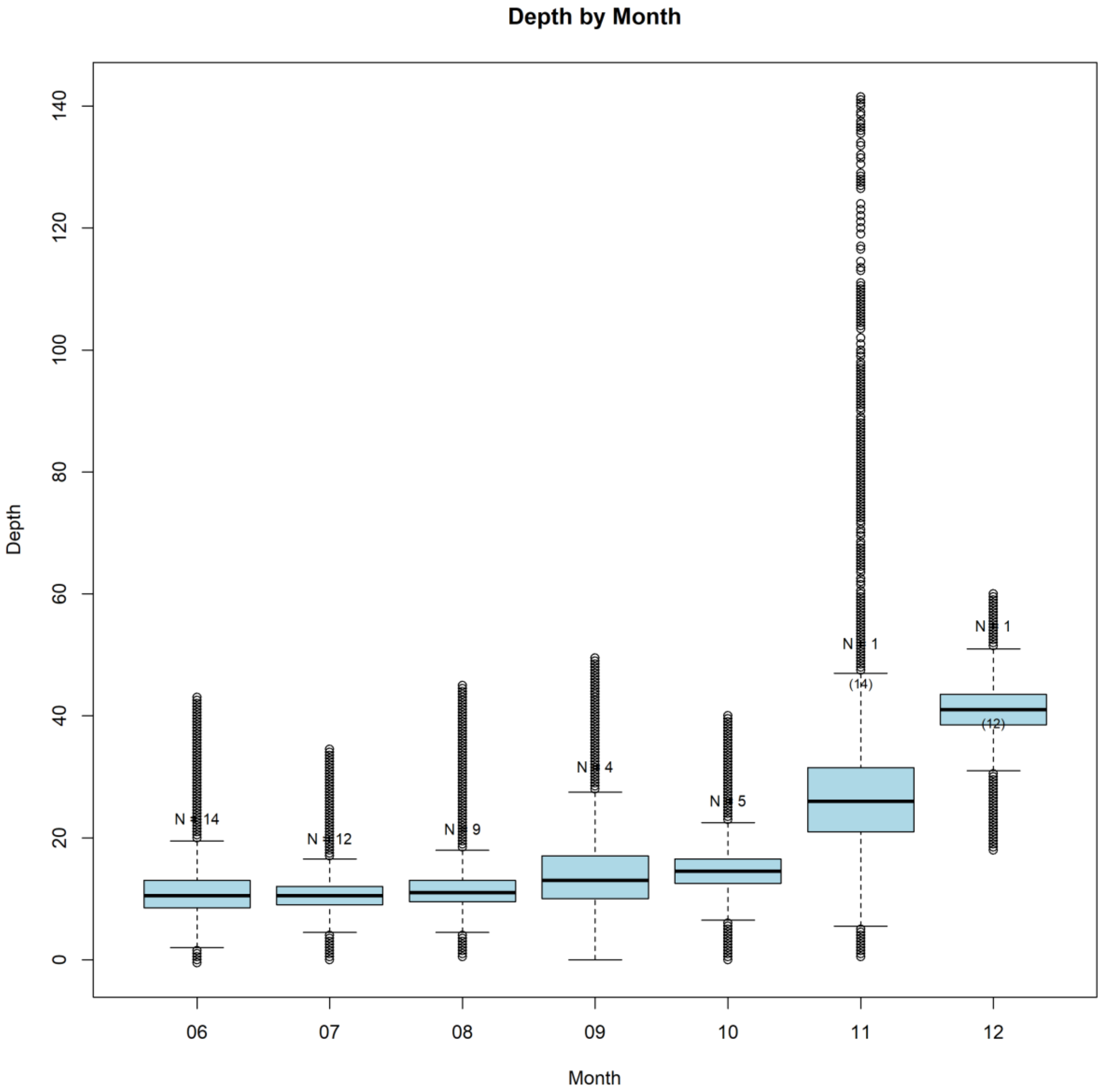
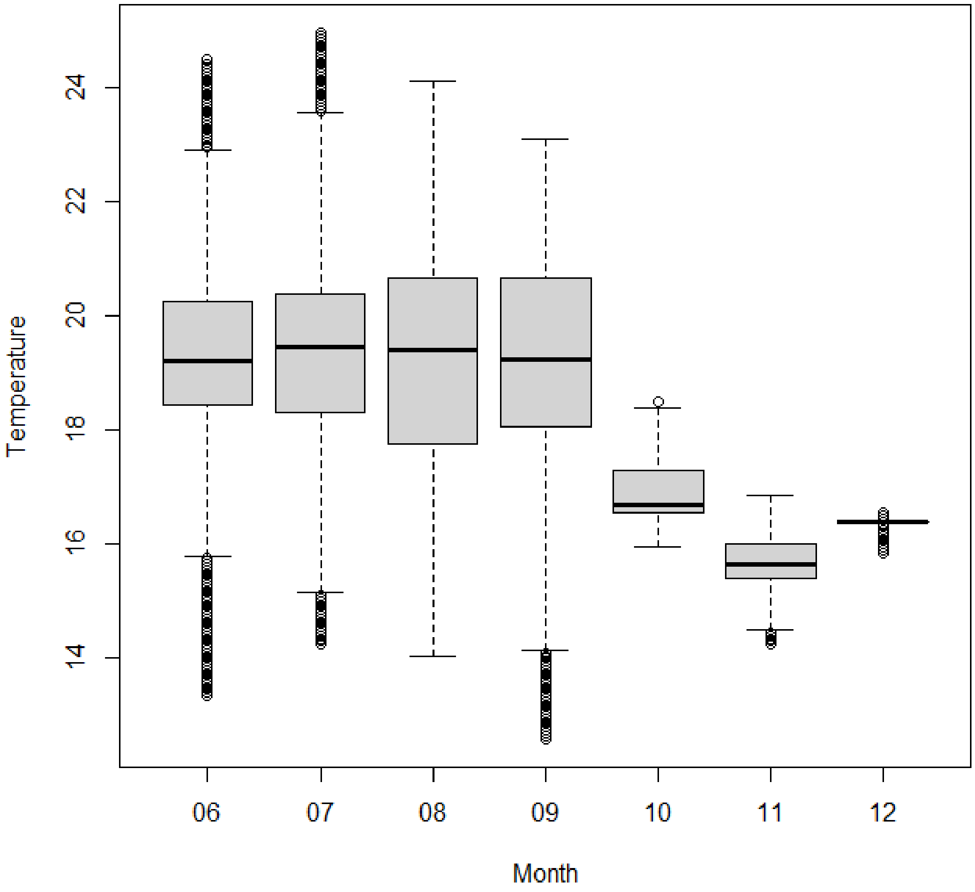
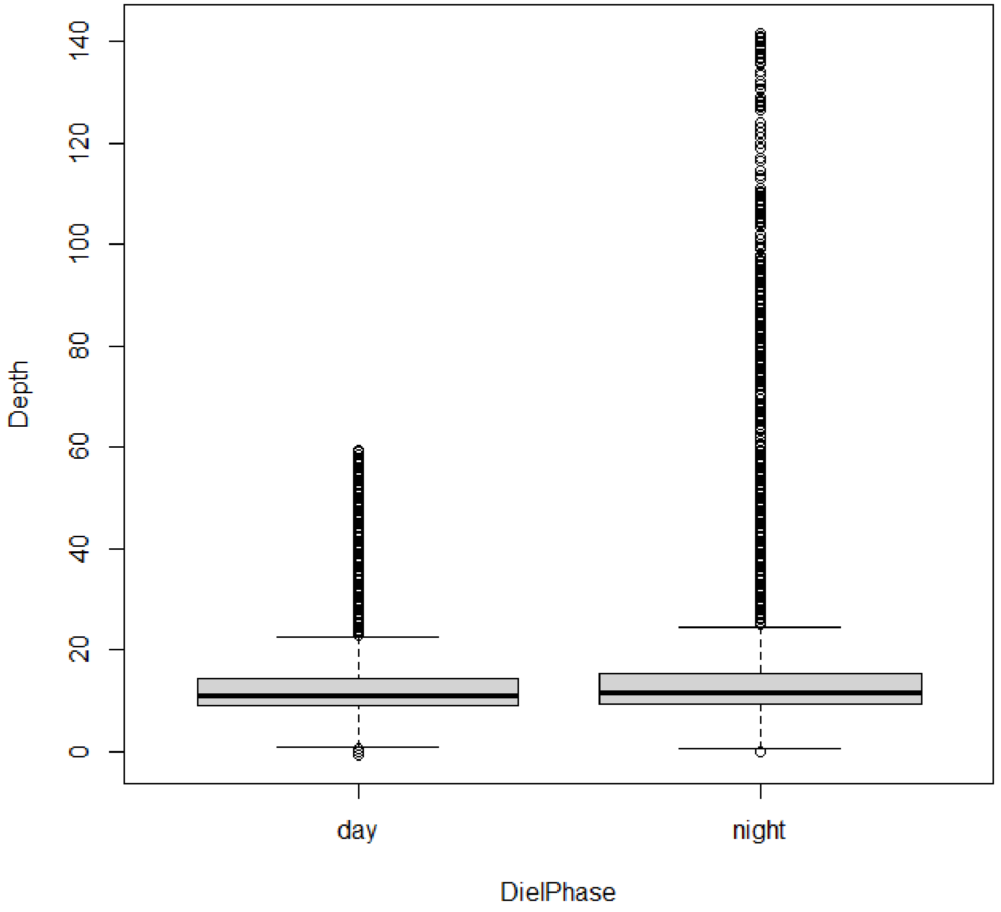
Appendix



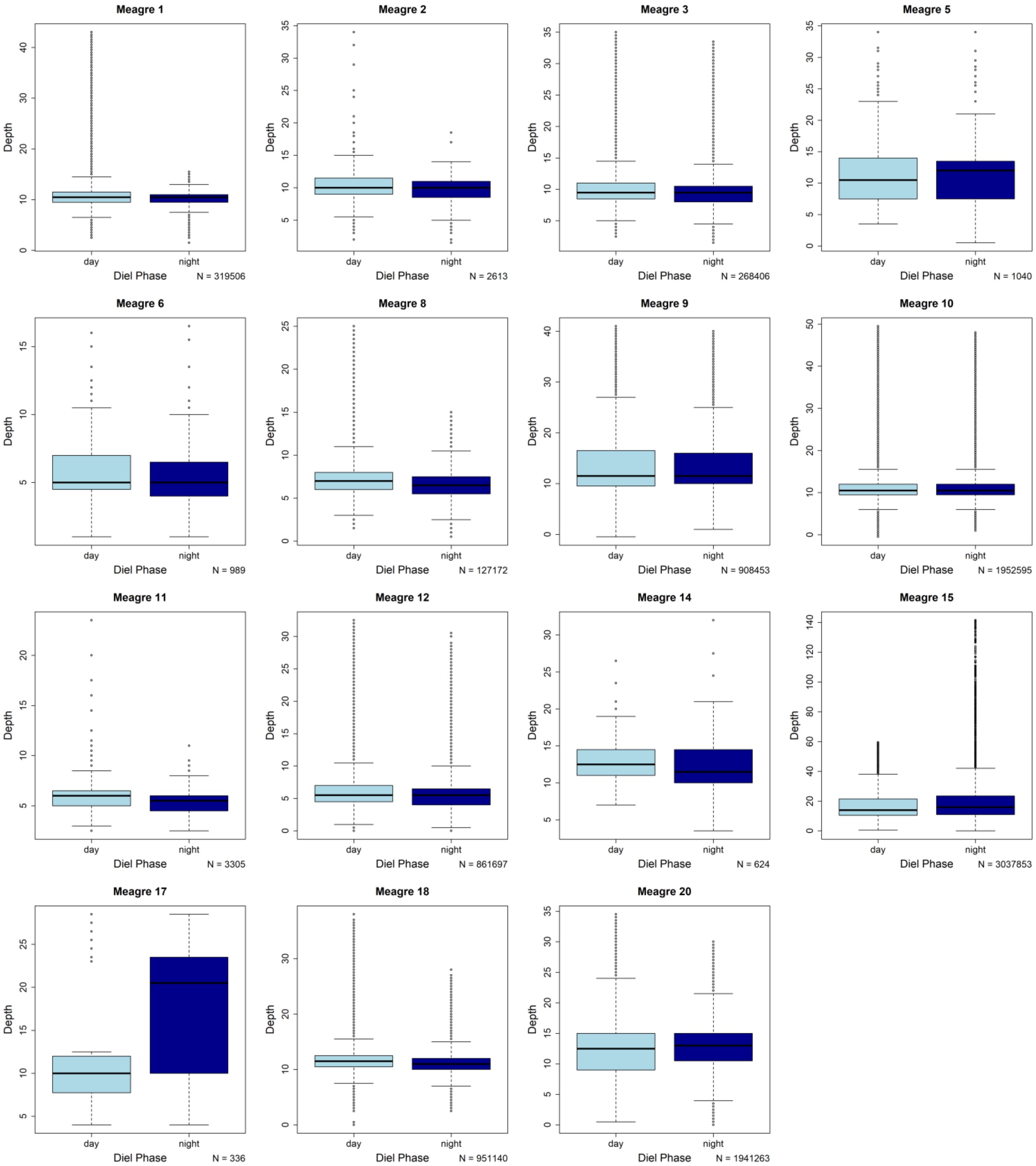
Supp figure 3.1- Monthly depth distributions recorded by pop-up satellite archival tags on sixteen *Argyrosomus regius*. Boxplots are structured with the median, the box represents the interquartile range (IQR), whiskers Extend to the smallest and largest values within 1.5 times the IQR from Q1 and Q3, respectively, and outliers represented by dots. X-axis is showing the month number from June (06) to December (12) , y-axis shows the depth in meters.



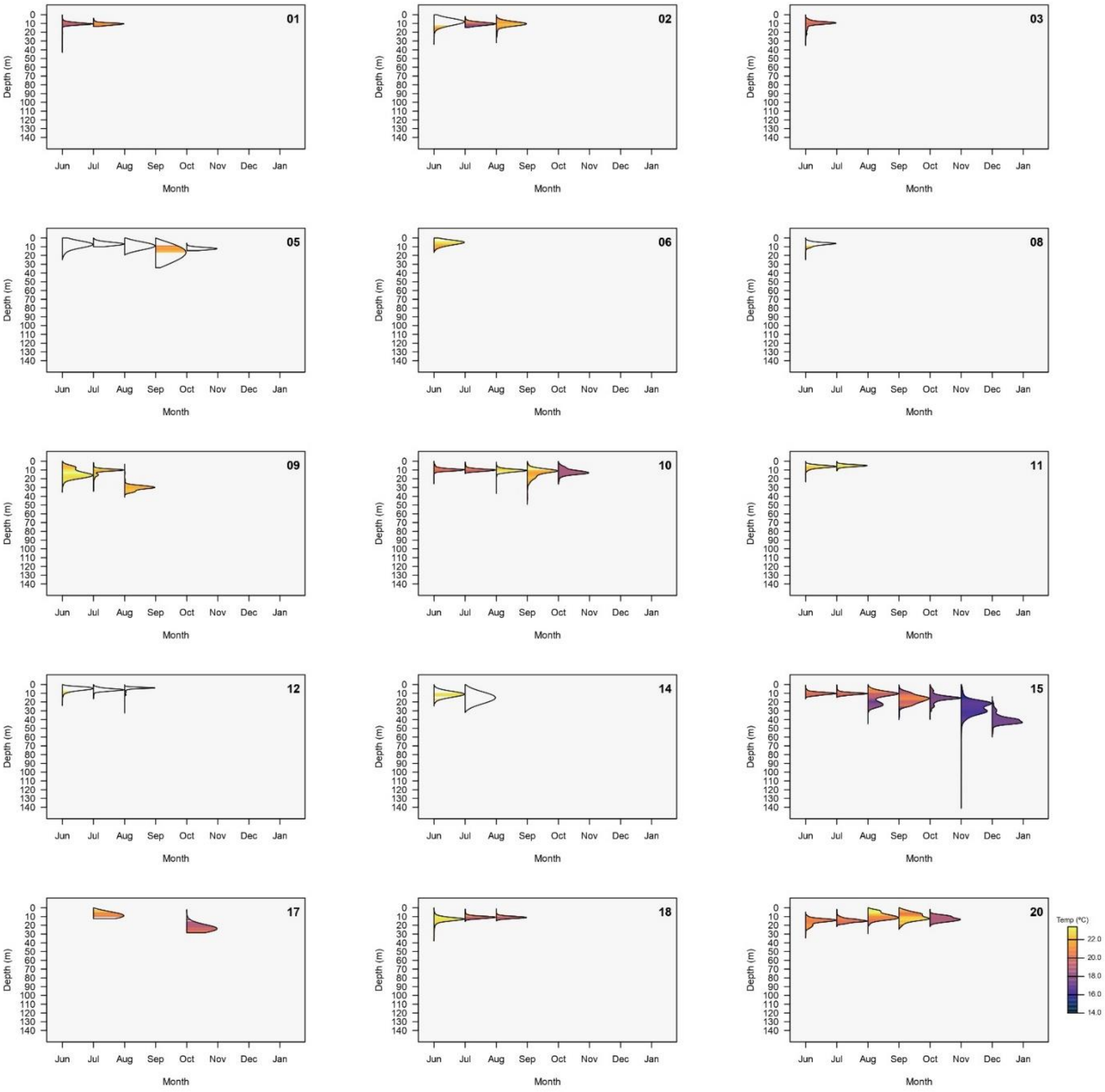
Supp figure 3.2 - Monthly temperature distributions recorded by pop-up satellite archival tags on sixteen *Argyrosomus regius*. Boxplots are structured with the median, the box represents the interquartile range (IQR), whiskers Extend to the smallest and largest values within 1.5 times the IQR from Q1 and Q3, respectively and outliers represented by dots. X-axis is showing the month number from June (06) to December (12) , y-axis shows the temperature in ºC.



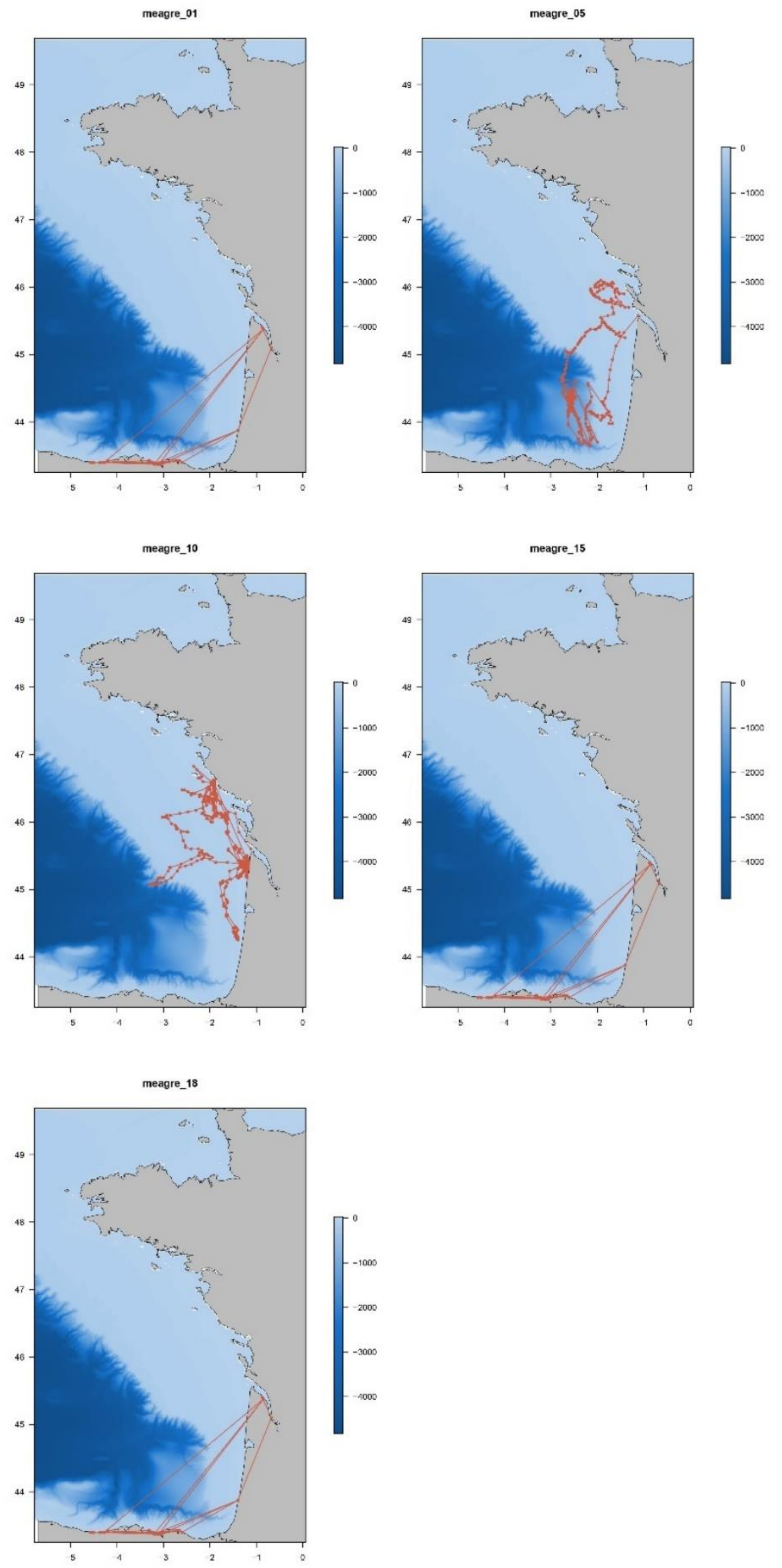
Supp figure 3.3 – Diel depth distributions recorded by pop-up satellite archival tags on sixteen *Argyrosomus regius*. Boxplots are structured with the median, the box represents the interquartile range (IQR), whiskers Extend to the smallest and largest values within 1.5 times the IQR from Q1 and Q3, respectively and outliers represented by dots. X-axis is the diel phase (day and night), y-axis shows the depth in meters.



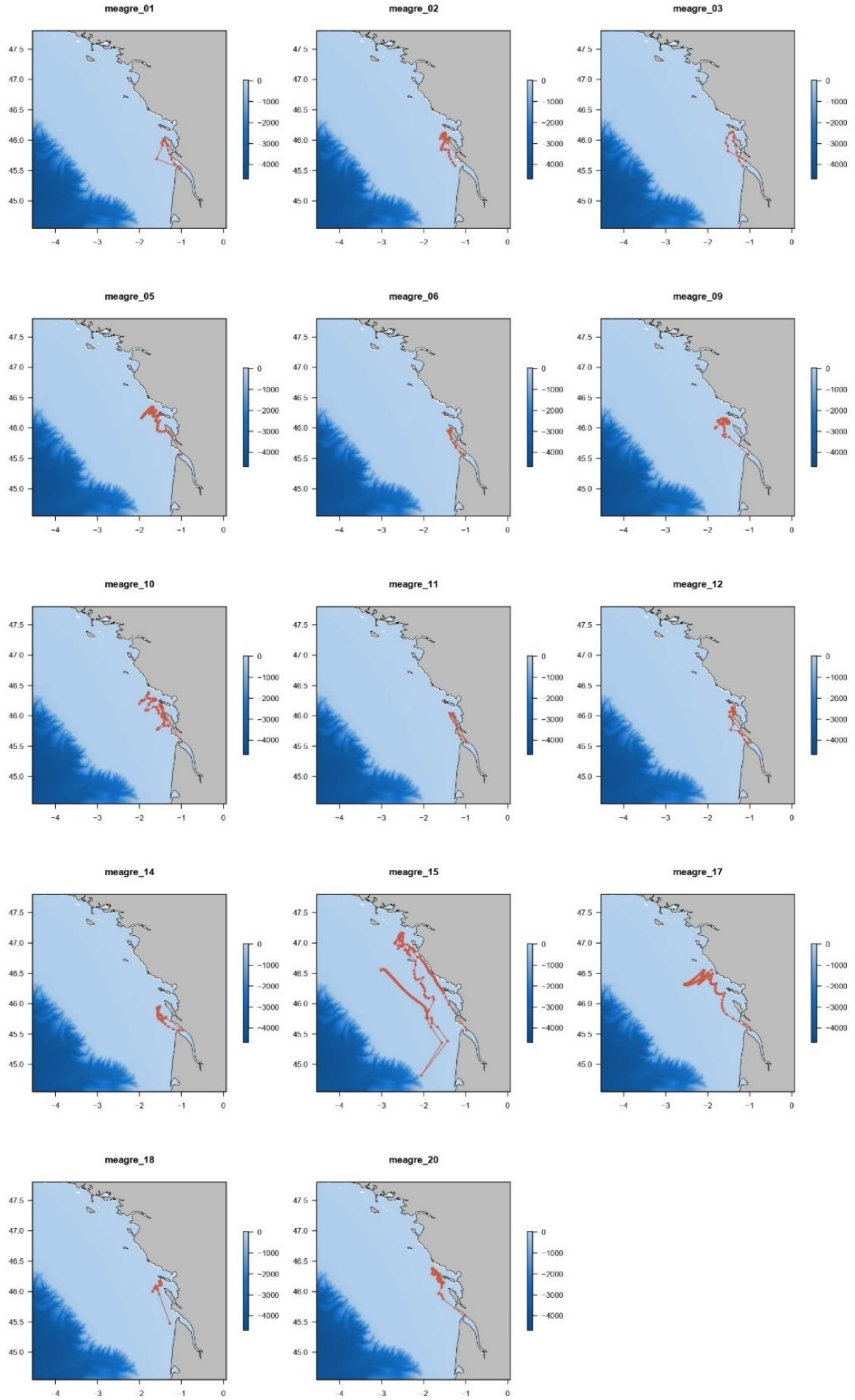
Supp Figure 3.4 – Box plot of intraspecific variability of depth use during each diel phase. X-axis shows the diel phase, y-axis the depth. On the bottom right is showed the number of data used for the plots.



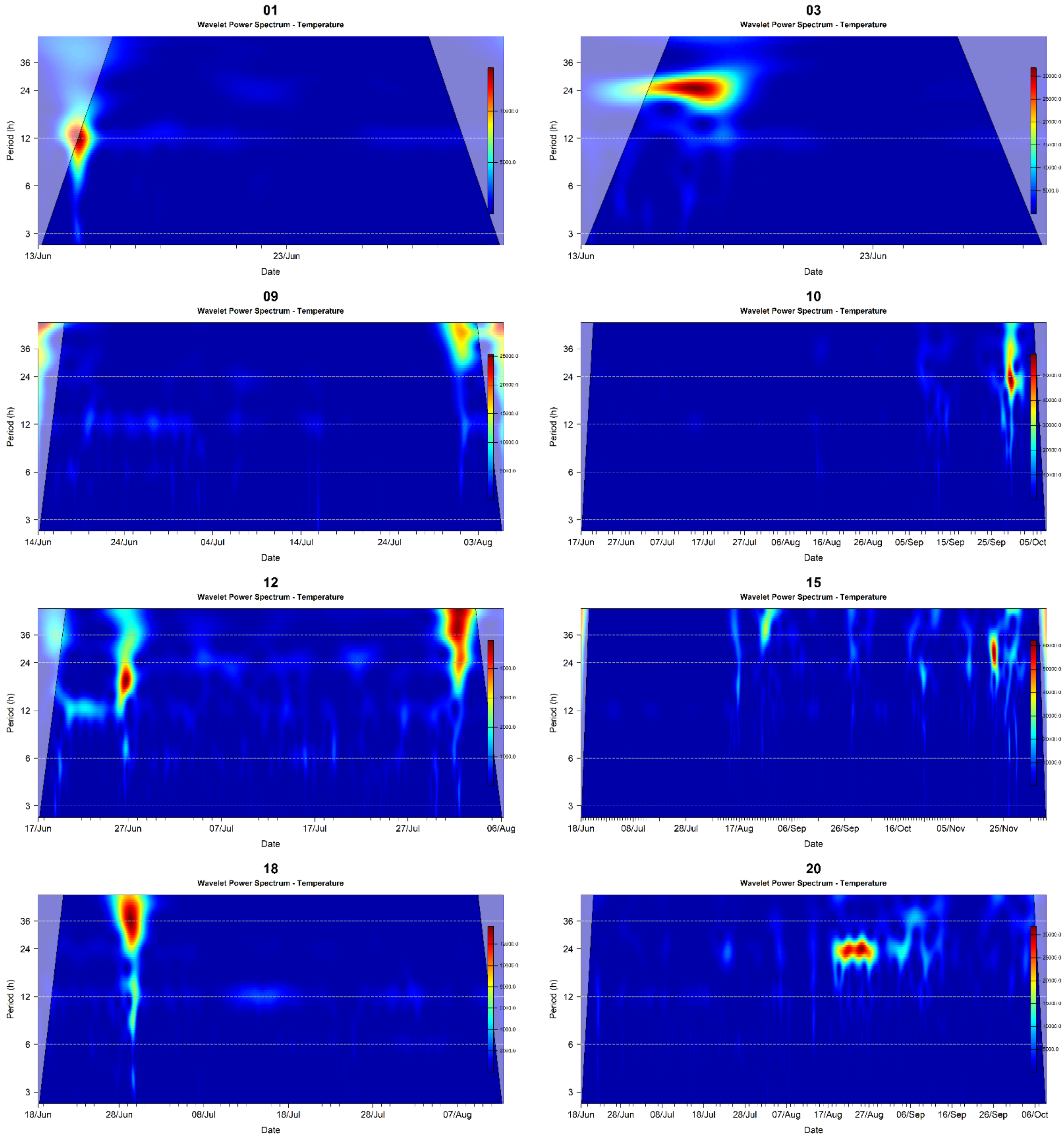
Supp figure 3.5 - Density of depth usage by month, color-coded by average temperature (1-m depth bins). X-axis shows the month abbreviations, y-axis shows depth in meters.



Supp figure 3.6 – Geolocation tracks from GPE3 files, only available for Tags from Meagre #1, #5, #10, #15 and #18.



supp figure 3.7 – Prediction models of geolocation tracks without added information (position inside of the estuary for fish #1, #3 #9, #10, #15 and #18) from CWTs results.



Supp figure 3.8 – Continuous wavelet transformations (CWTs) for Depth over the days. The x-axis represents the total days the tags were attached. The y-axis shows the frequency of cyclical patterns in hours. Patterns outside the cone of influence should not be interpreted. Wavelet power levels are represented by the colors, shown in the color ramp, from blue (low wavelet coefficient) to red (highest wavelet coefficient).