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Mestrado em Biologia Marinha

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Abstract

Understanding the spatial ecology and behaviour of coastal fishes is critical for the design of marine protected areas (MPAs). Acoustic telemetry, combined with advanced modelling approaches, provides high-resolution insights into residency, activity, and habitat use, key information for a proper design of spatial protection measures.

In this study, we acoustically tracked fifteen Labrus bergylta individuals over more than two years within the Atlantic Islands of Galicia National Park, generating over 4.5 million detections. After filtering and excluding fate dates, valid trajectories were reconstructed using Continuous-Time Correlated Random Walk models, yielding more than 3.1 million estimated positions. Residency analyses revealed that 67% (10) of individuals exhibited very high site fidelity (IWR $\geq$ 0.95), while others showed intermediate fidelity with occasional excursions beyond the array. Only one fish displayed virtually no residency.

Estimated activity spaces ranged from 6,870 to 23,120 m^2, with daytime ranges significantly larger than at night and peaking in late spring–summer, reflecting reproductive activity. Swimming speed was positively related to bottom temperature and showed seasonal variation as well as crepuscular peaks. Hidden Markov Models distinguished two behavioural states (resting vs. active), with an average activity budget of 56.5% resting and 43.5% active. State transitions were influenced by diel cycle and habitat type, though with strong inter-individual variability. Revisitation patterns revealed long-term fidelity to a small number of discrete core areas, located on rocky substrates and often shared across day and night.

Overall, L. bergylta exhibited a dual movement strategy of strong site fidelity interspersed with occasional exploratory excursions. These findings confirm the importance of structurally complex hard-bottom habitats as persistent refuges and support the effectiveness of fixed spatial protections. By linking fine-scale behaviour with habitat use over extended timescales, this study advances the ecological understanding of temperate reef fishes and provides robust evidence to inform the management and evaluation of coastal MPAs.

Keywords: Acoustic telemetry, High-resolution tracking, spatial ecology, random-walk, Hidden-Markov-Models, Recursion

Resumo

Compreender a ecologia espacial e o comportamento dos peixes recifais é fundamental para a conservação da biodiversidade marinha e para o desenho de áreas marinhas protegidas (AMPs) eficazes. Espécies residentes em ecossistemas costeiros frequentemente apresentam padrões complexos de movimento e uso do habitat, moldados tanto por fatores intrínsecos como idade, sexo e estado reprodutivo, quanto por fatores extrínsecos, como variações sazonais, ciclo dia-noite e disponibilidade de refúgios. A telemetria acústica surgiu nas últimas décadas como uma ferramenta revolucionária para investigar esses processos. Com a instalação de matrizes de receptores subaquáticos e o uso de transmissores em indivíduos de interesse, é possível monitorar de forma contínua e em alta resolução o comportamento espacial de organismos marinhos, oferecendo uma base empírica robusta para estratégias de conservação.

Neste estudo, aplicámos a telemetria acústica para investigar a ecologia espacial de Labrus bergylta, vulgarmente conhecido como bodião ou peixe-cuco, uma espécie recifal de águas temperadas que desempenha papéis ecológicos relevantes nos ecossistemas costeiros do Atlântico

Nordeste. Quinze indivíduos foram marcados e monitorados ao longo de um período superior a dois anos no Parque Nacional Marítimo-Terrestre das Ilhas Atlânticas da Galiza, uma área marinha protegida de elevada importância ecológica e socioeconómica. Durante este tempo, foram registadas mais de 4.5 milhões de detecções acústicas, constituindo um dos conjuntos de dados mais extensos e detalhados já obtidos para esta espécie.

Após um processo rigoroso de filtragem, no qual foram eliminadas detecções isoladas, erros de posicionamento e sinais associados a mortalidades ou falhas de transmissores, reconstruímos as trajetórias de movimento utilizando modelos de Caminhada Aleatória Correlacionada em Tempo Contínuo (CTCRW). Estes modelos são particularmente adequados para dados de alta resolução, pois permitem inferir trajetórias contínuas mesmo em intervalos com ausência de deteções diretas. O resultado foi um total superior a 3.1 milhões de posições estimadas, descrevendo de forma fidedigna os padrões de deslocamento dos indivíduos monitorizados.

As análises de residência revelaram padrões marcantes. Dois terços dos indivíduos (67%, n = 10) exibiram índices de residência ponderada (IWR) iguais ou superiores a 0.95, evidenciando fidelidade espacial extremamente elevada ao longo de todo o período de monitorização. Outros quatro indivíduos mostraram fidelidade intermediária, com valores de IWR entre 0.70 e 0.79, o que indica permanência prolongada na área de estudo, mas intercalada com excursões ocasionais para além dos limites da matriz de receptores. Apenas um peixe demonstrou praticamente ausência de residência, sendo registado apenas no limite da área e num único evento de deteção. Estes resultados confirmam que L. *bergylta* apresenta, na sua maioria, um comportamento fortemente sedentário, permanecendo em áreas relativamente restritas durante longos períodos.

Os espaços de atividade, estimados através da modelagem CTCRW, variaram entre 6,870 e 23,120 m², com média de 13,780 ± 5,150 m². Observou-se um padrão claro de variação diurna e sazonal: os espaços utilizados durante o dia foram significativamente maiores do que à noite, atingindo picos na primavera e no início do verão, coincidindo com a época reprodutiva da espécie. Durante a noite, por outro lado, os indivíduos mantiveram áreas de atividade muito mais restritas e relativamente constantes ao longo do ano, sugerindo comportamento de repouso noturno em refúgios específicos.

A velocidade de nado também foi analisada e mostrou uma relação positiva com a temperatura de fundo. Os peixes apresentaram maior atividade locomotora em águas mais quentes, ainda que o efeito absoluto da temperatura fosse relativamente pequeno. Foram identificados padrões claros de variação diária e sazonal: a atividade reduziu-se no final do verão e aumentou novamente durante períodos de transição, com picos marcados ao amanhecer e ao entardecer. Estes resultados corroboram a ideia de que L. *bergylta* possui ritmos nictemerais consistentes, com preferência por maior atividade durante o dia e redução noturna.

A utilização de Modelos de Markov Ocultos (HMMs) permitiu identificar dois estados comportamentais distintos: repouso e atividade. O estado de repouso foi caracterizado por deslocamentos mínimos (comprimento de passo mediano de apenas 0.11 m), enquanto o estado ativo exibiu comprimentos de passo substancialmente maiores (3.94 m em média). A análise revelou que, em média, os indivíduos passaram 56.5% do tempo em repouso e 43.5% em atividade, embora com forte variação entre peixes (17–94% em repouso; 6–83% em atividade). Ao incluir variáveis ambientais como covariáveis nos modelos, verificou-se que tanto o ciclo dia-noite como o tipo de habitat influenciaram significativamente as transições entre estados em alguns indivíduos, mas não em todos. Isto reforça a ideia de que existem diferenças comportamentais individuais marcantes, possivelmente relacionadas a idade, sexo ou condição fisiológica.

As análises de revisitação e agrupamento espacial revelaram que a maioria dos indivíduos regressava repetidamente a um número reduzido de áreas nucleares discretas, utilizadas como refúgios e centros de atividade. Foram identificados de uma a três áreas principais durante o dia e entre uma e seis durante a noite, com médias de 2.07 e 2.86 áreas respetivamente. Em muitos casos, estas áreas sobrepunham-se espacialmente entre os períodos diurno e noturno, evidenciando a utilização de refúgios persistentes e de alta importância ecológica. Todas as áreas identificadas estavam associadas a substratos rochosos ou de elevada complexidade estrutural, sublinhando o papel crucial deste tipo de habitat para a sobrevivência e o comportamento sedentário de L. *bergylta*.

De forma geral, os resultados apontam para uma estratégia de movimento dual: a maioria dos indivíduos combina forte fidelidade espacial a áreas restritas com eventuais movimentos exploratórios para além dos limites habituais. Esta combinação sugere que, embora sejam altamente residentes, os peixes mantêm alguma plasticidade comportamental, possivelmente relacionada com procura de alimento, reprodução ou defesa territorial.

Do ponto de vista da gestão e conservação, estes resultados são altamente relevantes. A elevada fidelidade ao local e a dependência de habitats rochosos complexos confirmam a importância da proteção espacial fixa como medida eficaz para garantir a persistência de populações de L. *bergylta*. Além disso, o estudo reforça que a conservação de áreas marinhas protegidas deve considerar não apenas a extensão geográfica, mas também a qualidade e diversidade de habitats incluídos. A integração de informação sobre comportamento em escala fina com dados de uso do habitat em escalas temporais prolongadas fornece uma base sólida para avaliar e otimizar o desenho de AMPs.

Em conclusão, este estudo contribui significativamente para o avanço do conhecimento sobre a ecologia espacial de peixes recifais de águas temperadas. Ao documentar padrões de residência, variação sazonal de atividade, influência do ciclo dia-noite e dependência de habitats complexos, fornece evidências empíricas robustas para fundamentar políticas de conservação e gestão sustentável. Os resultados demonstram que a combinação de telemetria acústica de alta resolução com modelos analíticos avançados constitui uma abordagem poderosa para compreender a dinâmica espacial de espécies marinhas, com implicações diretas para a conservação da biodiversidade e o uso sustentável dos recursos costeiros.

Palavras-chave: Telemetria acústica, Monitoramento de alta resolução, Ecologia espacial, Caminhada aleatória, Modelos de Markov ocultos, Recursão

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1. Introduction

The movement and behavior of fish are central to understanding their biology and ecology, and they play a critical role in shaping conservation and management strategies (Block et al., 2011; Abecasis et al., 2014; Cooke et al., 2022; Lowerre-Barbieri et al., 2025). Spatial behavior influences access to resources, reproductive success, and predator avoidance, thereby affecting individual fitness and population dynamics (Nathan et al., 2008; Hussey et al., 2015). As coastal ecosystems are increasingly impacted by anthropogenic pressures such as habitat degradation, overfishing, and climate change, quantifying how fish interact with their environment and respond to spatiotemporal variability has become essential for adaptive, evidence-based management (Cooke et al., 2016).

Recent studies have shown that individual variation in spatial ecology strongly shapes population-level responses. For instance, ballan wrasse (*Labrus bergylta*) display fine-scale site fidelity with diel and seasonal behavioural differences (Villegas-Ríos et al., 2013; Mucientes et al., 2019), while white seabream (*Diplodus sargus*) expands their home ranges during reproduction (Abecasis et al., 2015). Such variability directly influences vulnerability to fishing and the effectiveness of marine protected areas (Villegas-Ríos et al., 2021). Differences in home range size, activity patterns, and site fidelity can affect connectivity, population resilience, and consequently the efficacy of spatial conservation measures such as marine protected areas (MPAs) (Villegas-Ríos et al., 2017; Goetze et al., 2021). For instance, if most individuals within a population have home ranges larger than the area of the reserve itself, then these fish will frequently move outside the protected boundaries, exposing them to fishing pressure and thus limiting the effectiveness of the reserve (Kramer & Chapman, 1999; Villegas-Ríos et al., 2021). Recognising the behavioural diversity within populations is thus critical, as “one-size-fits-all” conservation strategies risk overlooking essential intra-population variability.

In recent years, research on the movement ecology of aquatic organisms has advanced considerably (Hussey et al., 2015; Jacoby & Piper, 2023; Matley et al., 2022), yet important gaps remain concerning the drivers and ecological implications of fish movement behaviour. Although many studies have described movement patterns and quantified conventional metrics such as activity levels or home range size (Espinoza et al., 2011; Friess et al., 2021; Green et al., 2015; Williamson et al., 2021), some of them have addressed the latent behavioural states underlying these patterns. The integration of advanced statistical frameworks, such as continuous-time correlated random walk (CTCRW) models (Johnson et al., 2008) and Hidden Markov Models (HMMs), has opened new opportunities to reconstruct individual trajectories and infer hidden behavioural states in the wild. In particular, HMMs have become a powerful tool due to their straightforward implementation and their ability to incorporate environmental covariates, thereby facilitating the identification of ecological processes driving movement (Langrock et al., 2012; McClintock & Michelot, 2018). Nevertheless, while HMMs have been widely applied in terrestrial animals, their use in acoustic telemetry studies is particularly common for teleostsl (Bacheler et al., 2019; Pereñíguez et al., 2023)

This is particularly important because it allows researchers to investigate fine-scale behaviours and movement patterns at the individual level, providing insights into habitat use, foraging or reproductive strategies, and responses to environmental variability that would otherwise remain hidden. CTCRW models are commonly used to regularize tracking data collected at irregular time intervals by representing animal movement as a continuous process with temporally correlated steps, explicitly accounting for measurement errors and generating smooth, biologically plausible trajectories (Johnson et al., 2008; Aspillaga et al., 2021). This approach is particularly valuable in high-resolution acoustic telemetry systems, where detection gaps and positional outliers can obscure fine-scale movement patterns and hamper the estimation of accurate movement metrics (Vidal, 2024; Aspillaga et al., 2021). HMMs, are probabilistic models that infer unobserved behavioural states from observed movement metrics, assuming that the movement process switches between discrete states with distinct parameterisations, typically in step length and turning angle, allowing for quantitative characterisation of behaviours such as foraging or resting (Langrock et al. 2012). HMMs are increasingly recognised as a robust framework in movement ecology, enabling objective classification of behavioural states from fish trajectories while incorporating environmental covariates (Leos-Barajas et al., 2017; Bacheler et al., 2019).

In Galicia, Labrus bergylta Ascanius, 1767 is a common resource for the Galician small-scale fishing fleet, among the three most landed species over the last decade (www.pescadegalicia.com; last accessed: 09 Aug 2025). *Labrus bergylta* occurs along the north-east Atlantic from Norway to Morocco and the Mediterranean Sea, inhabiting rocky reefs and kelp beds from the shoreline to depths of around 60 m (Bañón et al., 2010; Porteiro et al., 1996; Talbot et al., 2012; Treasurer, 1994). L. *bergylta* is a key species in the coastal ecosystem off NW Spain. Moreover, L. *bergylta* has gained increased socio-economic value as a cleaner fish in Norwegian salmon aquaculture, used to control sea lice infestations (Blanco Gonzalez & de Boer, 2017; Treasurer, 1994), underscoring the species' growing importance beyond traditional fisheries.

Few studies have focused on the spatial ecology of this species. For instance, in Galicia, Villegas-Ríos et al. (2013) used acoustic telemetry to examine the spatial behaviour of the ballan wrasse, *Labrus bergylta*, demonstrating strong site fidelity and habitat dependence inside waters of National Park Illas Atlánticas of Galicia (NW Spain). Fish exhibited small home ranges (0.091 ± 0.031 km^2) and pronounced diel variation in movement during the day and night. These findings suggest that this species with restricted movements and sedentary behaviour may be particularly responsive to small-scale marine protected areas (MPAs). However, to date, no study in this region has analysed individual high-resolution trajectories of *Labrus bergylta*.

Building upon earlier work that reported high residency and small home ranges (Villegas-Ríos et al., 2013), this study aims to characterize the long-term spatial and behavioural ecology of L. *bergylta* using high-resolution acoustic telemetry based on multiyear monitoring of fifteen individuals within the National Park Illas Atlánticas de Galicia. Specifically, we aim to:

i) evaluate the influence of internal and external drivers on activity levels and spaces,

ii) infer latent behavioural states through Hidden Markov Models applied to positioning data, and

iii) identify recursive positions at the individual level.

By addressing these objectives, this work contributes to a growing body of research on how behavioural diversity shapes the responses of coastal fish to environmental and anthropogenic pressures, thereby informing more nuanced and effective conservation and fisheries management strategies.

2. Material and methods

2.1 Study area

The research was conducted in the Cíes Archipelago, located at the outer margin of the Vigo Estuary in northwestern Spain (Figure 1). This archipelago forms part of the National Park Atlantic Islands of Galicia (PNMTIAG), which spans approximately 31 km², where artisanal commercial fisheries are allowed, while recreational fishing is forbidden (Xunta de Galicia, Conselleira de Medio Ambiente, Territorio y Vivienda, 27/12/2018). Beyond its ecological significance, the Cíes Archipelago holds substantial socio-economic importance, being an important fishing ground for the local small-scale fishing fleet according to Cambié et al. (2012). The study area is characterised by shallow coastal waters ranging from 0 to 40 m in depth, dominated by rocky outcrops interspersed with sandy substrates. The region experiences a mesotidal regime, with tidal ranges reaching up to 4 m, and is influenced by Atlantic swells, seasonal upwelling, and variable oceanographic conditions that sustain a high diversity of benthic and pelagic communities (Vilas et al., 2005).

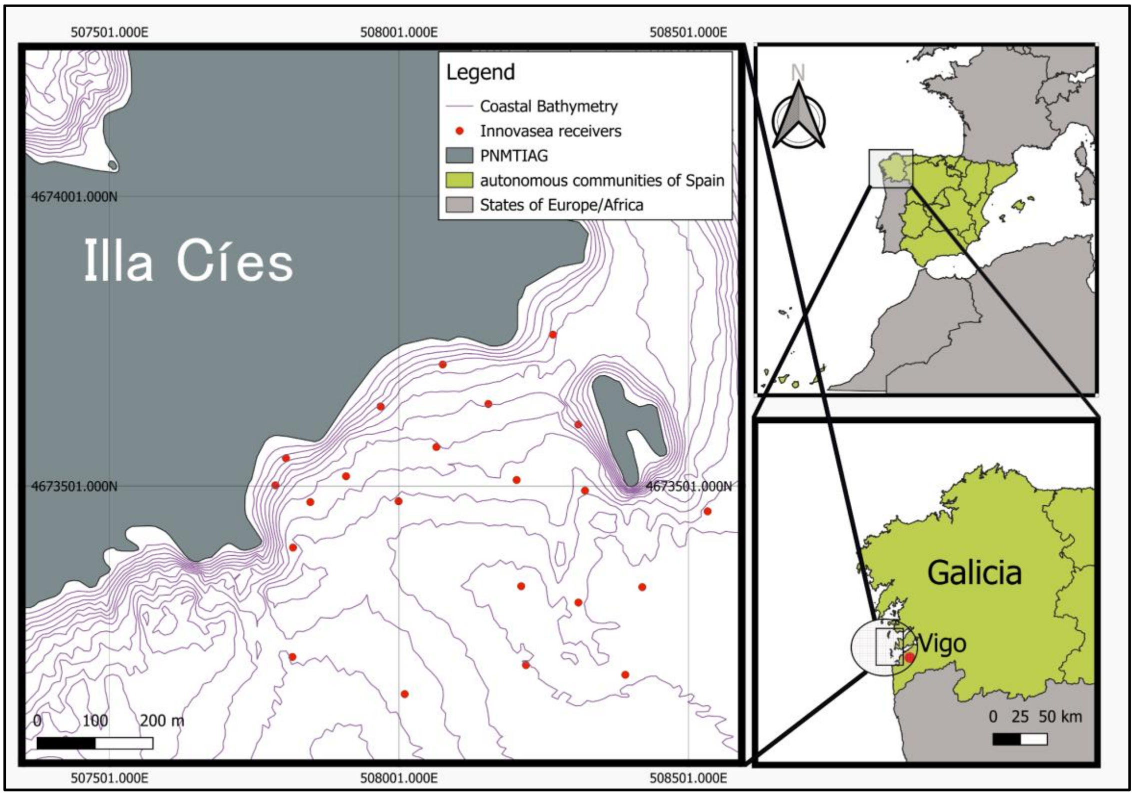

Figure 1: Overview of the study area covering Europe, the northern coast of Africa, and the autonomous community of Galicia (top-right and bottom-right panels). The left panel provides a detailed view of the Cíes Archipelago, including coastal bathymetry (1-m contour lines), the acoustic receiver array (Innovasea receiver), and the marine boundaries of the PNMTIAG park (highlighted in the small rectangle at the bottom right).

2.2 Acoustic telemetry array and fish tagging

A fixed acoustic telemetry array composed of 20 monitoring stations was deployed across the study area, incorporating a total of 20 omni-directional receivers (Innovasea VR2W) and 20 synchronisation tags. Receivers were placed at depths ranging from 3.3 to 13.1 m, with inter-station distances of approximately 150 m, corresponding to 50% of the detection probability observed during the range test (Leeb et al., 2021).

Because of the ensuring effective coverage and spatial overlap across the array (Figure 1) and allowing for high-resolution positioning based on time-of-arrival differences among multiple receivers. Two Innovasea reference transmitters (V13 and V16) were placed in fixed positions within the receiver array to evaluate potential environmental influences on detection patterns and positional error estimates (Kessel et al., 2014; Espinoza et al., 2011). To characterise the sea floor type of the study area, the habitat classification was based on previous surveys conducted within the PNMTIAG using Remote Operated Vehicles, scuba diving, and sample collection. Although habitats were initially classified using the EUNIS scheme, they were simplified into two categories: soft and hard bottoms. A total of seven data loggers (Star-Oddi DST centi-T©) were deployed at selected telemetry stations to record sea-bottom temperature every 30 min. These devices were deployed at various depths and locations throughout the study area, providing fine-scale temporal and spatial coverage of temperature variation near the seafloor. This variable was later used to investigate potential environmental influences on animal behaviour.

Between 6 and 21 May 2019, a total of 15 *L. bergylta* individuals were captured and tagged within the Cíes Archipelago (Table 1). Specimens were collected by scuba divers and brought to the surface for processing. Upon capture, each fish was anaesthetised with 100 mg/L tricaine methanesulfonate (MS-222) for 2–3 min, measured for standard length, and surgically implanted with an Innovasea V13P-1x acoustic transmitter. Tags had an estimated battery life of approximately 2.3 years, enabling long-term monitoring of individual movements (Table 1). Transmitters were inserted into the peritoneal cavity following established surgical procedures designed to minimise tag loss.
The tagging procedure complied with Spanish national animal welfare regulations (Real Decreto 53/2013, 1 February 2013, published in B.O.E. nº 34, 8 February 2013) and was authorised under experimental animal project permit ES360570202001/19/FUN01/BIOL AN.08/AAF01.

2.3 Data processing

2.2.1 Data filtering

All acoustic detections were initially filtered to remove potential false positives, defined as isolated detections not followed or preceded by other detections at the same receiver within a 24-hour window (Meyer et al., 2007). This filtering step minimised the inclusion of spurious signals caused by environmental noise or signal reflection.
The fate and corresponding 'fate date' of each tagged fish were determined by analysing temporal patterns in position data throughout the study period as described by Villegas-Ríos et al. (2020). Only detection periods deemed biologically reliable, where tag fate could be confidently assessed, were included in downstream analyses (Freitas et al., 2008).

2.2.2 Estimate positions

High-resolution position estimates were obtained through the VEMCO Positioning System (VPS; Innovasea), which computes fish locations using time-of-arrival differences across multiple synchronised receivers (Smith, 2013). Each estimated position was associated with a horizontal positioning error (HPE) value, a unitless measure of uncertainty. To calibrate HPE against real positional accuracy, reference tag data were used to obtain HPEm values (positional error in meters). HPE values were binned and compared with corresponding mean HPEm values following the method of Smith et al. (2013). The HPE limit was chosen based on the cumulative mean HPEm over the bins, retaining >90% of estimated positions with an average horizontal positioning ~3 m.

2.2.3 Trajectory modelling

To reconstruct animal trajectories and ensure sufficient temporal resolution for subsequent behavioural analyses, we applied a Continuous-Time Correlated Random Walk (CTCRW) model using the crawl package (2.3.0 Version) in R (Johnson et al., 2022) to the estimated positions (see 3.3.2). In the CTCRW model, animal velocity is represented as a bivariate Ornstein–Uhlenbeck process, which captures the tendency of movement to persist in a given direction while gradually changing under the influence of random fluctuations. This produces more realistic trajectories than a simple random walk. At the same time, the observation model accounts for positional uncertainty (derived from HPE), ensuring that the estimated track distinguishes between true animal movement and location error. The resulting interpolated tracks were used to compute fine-scale movement metrics (activity space and swimming speed) and served as input for further behavioural modelling using HMMs.

Prior to model fitting, trajectories were split into segments separated by gaps of detections longer than 12 hours, which likely represented periods when individuals were outside the detection range. Only segments with more than 10 detections were retained for modelling. The CTCRW model interpolated positions at 120-second intervals. A fixed positioning error of 3 m was applied, based on estimates from the horizontal positioning error. To ensure spatial consistency and reduce extrapolation uncertainty, interpolated positions were subsequently filtered using a 25-m radius around the last observed VPS position.

2.4 Estimation of movement metrics

Different data were used to estimate three movement metrics to characterise individual spatial behaviour: i) filtered detections to estimate the residency index and ii) interpolated positions by the CTRW model to estimate the activity space and average swimming speed.

2.4.1 Residency index

Filtered detections were used to estimate residency patterns. Detections from all receivers in the acoustic array were grouped to analyse spatial fidelity to the study area. Although the Residency Index (IR), defined as the number of days a fish was detected (Dd) divided by the monitoring period (Dt), is commonly used (Meyer et al., 2007), in this study we also applied the Weighted Residency Index (IWR), following the method proposed by Kraft et al. (2023), to better capture individual spatial fidelity over time. Both IR and IWR range from 0 (no residency) to 1 (continuous presence), but the IWR adds temporal weight by incorporating the spread of detections, distinguishing between individuals consistently present over time and those detected in brief periods.

The IWR was calculated using the following formula:

$$IWR = \frac{Dd}{Dt} \times \frac{Di}{Dt}$$

Where:

- Dd = number of days the individual was detected
- Dt = total number of days between the first detection and the end of the monitoring period (e.g., battery life, individual survival)
- Di = number of days between the first and last detection

2.4.2 Activity space

To quantify the spatial extent of individual movements within the study site, we estimated weekly activity spaces using the 95% Kernel Utilisation Distribution (KUD), using the interpolated positions derived from the CTRW model, which is a widely applied probabilistic method that defines the area in which an animal is expected to occur 95% of the time (Worton, 1989). This approach captures both core use areas and broader spatial routines, providing insight into the habitat use and mobility patterns of *Labrus bergylta*.

KUDs were computed using the "adehabitatHR" package in R (0.4.22 Version) (Calenge, 2006). To ensure the robustness of the space-use estimates, only those weeks in which an individual was detected on at least five separate days were included. This criterion helped minimise biases from occasional detections and ensured that the derived KUDs reflected genuine spatial behaviour rather than sporadic presence. Individuals with fewer than two weekly estimates were excluded from the model in posterior analysis.

2.4.3 Swimming speed

As a proxy for activity level, average swimming speed was estimated using the interpolated positions derived from the CTRW model. Speed was calculated as the displacement between two consecutive positions divided by the time interval, yielding velocity values in meters per hour (m/h). The formula used was:

$$Speed = \frac{Distance}{\Delta t}\ x\ 3600$$

Where:

- *Distance* = displacement between two consecutive positions (in meters),
- Δt = fixed interpolation interval (120 seconds).

For each individual and each day, we computed the speed at all valid time steps throughout the 24-hour period and then averaged those values to obtain an average daily speed. This metric allowed for temporal comparisons of activity levels while minimizing the influence of outliers or short bursts of movement. Only days with at least 5 interpolated positions were retained to ensure reliable daily estimates.

2.5 Data Analysis

All analyses were performed in R 4.4.3 (Posit team 2025).

2.5.1 Modelling movement metrics

To investigate the main drivers on the individual movement behaviour, two key response variables were modelled:
(i) weekly activity space, estimated as the log-transformed 95% Kernel Utilisation Distribution (log KUD_{95}, log(m^2)), and (ii) swimming speed, calculated from successive positions and log-transformed to represent activity level (log Speed, log($m \cdot s^{-1}$)). Speed and activity space were log-transformed to satisfy model assumptions of normality and homoscedasticity.
Both variables were repeatedly measured at the individual level, suggesting a hierarchical data structure and temporal autocorrelation. To address this, we fitted generalised additive mixed models (GAMMs) incorporating both fixed and random effects and allowing for flexible non-linear relationships through smooth terms. To account for repeated measurements, a random intercept for Fish ID (a_i) was included in all models. Additionally, an autoregressive correlation

structure of order 1 (AR1) was applied to model residuals (ε_{it}) to account for temporal autocorrelation typical of fine-scale telemetry datasets (Dormann et al., 2007). Models were fitted using the *mgcv* package (1.9-1 Version) in R (Wood, 2017), with model selection performed via backward stepwise procedure based on Akaike's Information Criterion (AIC) to obtain the most parsimonious model (Wood et al., 2016); see Supplementary Material, Appendix 1, Table 1).
Linear predictors were modelled with coefficients (β_n), representing fixed effects, and α denoting the model intercept. Smooth temporal effects were represented by *f*, a non-parametric smoothing function using cyclic cubic splines, fitted with five knots to avoid overfitting while appropriately describing the non-linear effect of temporal variables such as day or week of the year (DOY, WOY) and hour of day (HOD) to capture seasonal and daily effects respectively. The residuals ε_{it} were assumed to be normally distributed random error, with mean 0 representing within-fish variation and, as observations were made sequentially over time (not independent). Moreover, the following explanatory variables were considered to model the movement metrics:

- TL_{it}: total length of fish *i* at time *t* (continuous).
- $Type_i$: morphotype (4 individuals displaying a spotted pattern and 11 individuals with a plain, unmarked coloration [Figure 2]) of fish *i.*
- $mean\text{-}temp_t$: bottom temperature of fish *i* at time *t* (continuous).
- $Daytime_t$: diel phase (categorical: day/night), based on local solar times computed using the suncalc package (0.5.0 version),(Thieurmel & Elmarhraoui, 2022).
- WOY_t: week of year (1–52) of fish *i* at time *t.*
- HOD_t: hour of day (0–23) of fish *i* at time *t.*
- DOY_t: day of year (0-365) of fish *i* at time *t.*

Therefore log-transformed weekly activity space (WAS_{it}) for individual *i* in week *t* was modelled using a Gaussian distribution as:

$$log(WAS_{it}) = \alpha + \beta_1 \cdot TL_{it} + \beta_2 \cdot Type_{it} + \beta_3 \cdot mean - temp_t + \beta_4 \cdot Daytime_t + f_1(WOY_t) + f_2(WOY_t \mid Daytime_t) + a_i + \varepsilon_{it}$$

and the log transformed daily swimming speed ($Speed_{it}$) for individual *i* at time *t* was modelled using a Gaussian distribution:

$$log(Speed_{it}) = \alpha + \beta_1 \cdot TL_{it} + \beta_2 \cdot Type_{it} + \beta_3 \cdot mean - temp_t + f_1(HOD_t) + f_2(DOY_t) + a_i + \varepsilon_{it}$$

2.5.2 Modelling latent behavioural states

To investigate latent behavioural states in the movement patterns of *Labrus bergylta*, we applied Hidden Markov Models to estimated positions derived from the CTCRW trajectories (see 3.3.3). This approach enabled the classification of fish movements into distinct, unobservable states inferred from movement metrics rather than directly visible in raw spatial tracks.
Step lengths (m) and turning angles (°) were calculated between consecutive positions and used as the observed variables in the HMMs. Step lengths were modelled using gamma distributions, and turning angles were modelled with wrapped Cauchy distributions, following established practices in movement ecology (Morales et al., 2004; Jonsen et al., 2005; McClintock et al., 2012). To ensure convergence and parameter stability we carried out a sensitivity analysis testing multiple sets of initial values and selecting the configuration that produced the most robust and biologically meaningful state classification. A two-state model structure was assumed based on the well-documented diel activity pattern of *L. bergylta*, which is typically resting at night and active during the day (Villegas-Ríos et al., 2013). All individuals were modelled jointly under a common parameter set.
The final configuration of initial parameters selected for each state were as follows:

- **Resting**: step length (gamma distribution) with mean = 0.106 m and SD = 0.105 m; turning angle with mean = 0 and concentration = 0.999.

- **Active**: step length (gamma distribution) with mean = 3.937 m and SD = 6.360 m; turning angle with mean = 0 and concentration = 0.813.

To assess whether environmental variables influence the likelihood of switching between behavioural states, we included diel period (day/night) and habitat type (soft or hard bottom) as covariates in the transition probabilities. We compared four model configurations: (1) without covariates, (2) including only diel period, (3) only habitat type, and (4) both covariates. Model selection was based on AIC. HMMs were implemented using the "momentuHMM" package in R (1.5.6 Version) (McClintock & Michelot, 2018).

2.5.3 Revisitation patterns

The interpolated positions from the CTRW were used to analyse spatiotemporal patterns in revisitations at a fine spatial scale (meters), to study the commonness of recursive movements. Analyses were conducted with the R package "recurse" (1.4.0 Version) (Bracis et al., 2018), specifically designed to extract revisitation metrics from animal movement data. Considering main behavioural traits of this species, high site fidelity and small space home ranges, this study focused on revisitation of a specific behavioural state, only locations classified as resting states by the HMM were considered (excluding active movement states from the recursive analysis). This decision follows evidence that many reef fish exhibit spatially structured movement patterns, often remaining in or returning to refuge-like habitats during periods of low activity, highlighted by diel habitat use tied to benthic structure (Hitt et al., 2011,Villegas-Ríos et al., 2013; Alós et al., 2011), and supported by methodological advances in acoustic telemetry that enable detection of site fidelity through fine-scale positional tracking (Heupel et al., 2006; Hedger et al., 2008). Such behaviour has important ecological implications, as it often reflects long-term habitat preference and potential dependence on specific microhabitats.

For each individual, the revisitation radius, a critical parameter defining the spatial extent for detecting returns, was established in 5 meters, producing an individual-specific radius that accurately represented site boundaries tailored to each fish's movement pattern. Once the revisits were estimated, to identify core areas of frequent use, the 20% of locations with the highest revisit counts were filtered. These points were then grouped into spatially distinct clusters using K-means clustering on their spatial coordinates (longitude, latitude), delineating key revisited sites. The Average silhouette method (Kaufman & Rousseeuw, 2009) was used to select the optimum number of clusters per fish. This temporal stratification revealed how site fidelity patterns shift between day and night.

This multi-step workflow, combining behavioural state classification, revisitation analysis, and spatial clustering, provides a high-resolution, behaviourally informed assessment of site fidelity during resting periods, offering insights into the movement ecology and habitat dependencies of *Labrus bergylta*.

3. Results

Between the first tagging event and the final data download, a total of 4,561,200 detections were recorded across the acoustic telemetry array. After filtering out isolated or erroneous detections, only valid records were retained for analysis. Individuals showing no movement, abrupt detection loss, or continuous presence at a single receiver were classified as mortalities or tag failures and excluded (Figure 2). The final dataset included only individuals with valid detection histories, yielding an average of 665,717 ± 4,281 detections per fish.

In 6 of the 15 individuals, a possible capture event was inferred, as their last detections occurred within the telemetry array and no subsequent movement patterns indicative of migration were observed. Accordingly, the fate date was assigned to the day of the final detection and classified as "catch" (Table 1). In contrast, individual TAC-LRT-13 was last detected at the extreme western edge of the telemetry array, suggesting a potential migration outside the study area.

3.1 Residency

Ten of the fifteen tagged individuals (67%) exhibited high site fidelity, with both internal and total residency indices (IRDi and IRDt) exceeding 0.95 and weighted residency indices (IWR) ≥ 0.95 (Table 1). These individuals consistently remained within the monitored area for the majority of the study period, showing a mean IWR of 0.96 ± 0.05 SD.

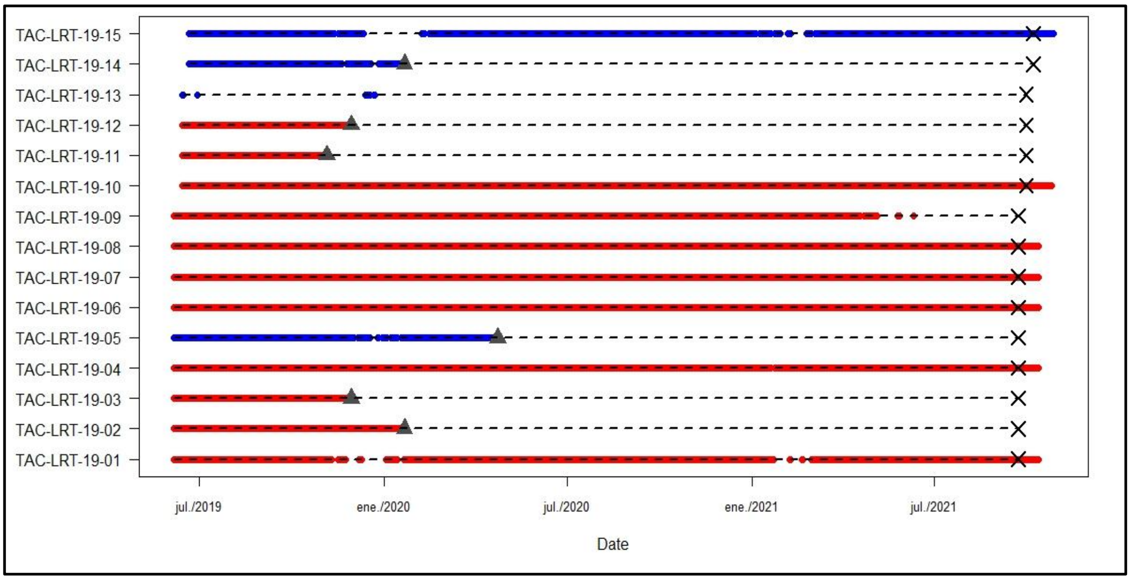

Figure 2: Abacus plot of Labrus bergylta individuals, colored by morphotype: plain (red) and spotted (blue). Triangles indicate the fate date, while grey crosses represent the last day of transmitter battery life.

Four individuals (TAC-LRT-01, TAC-LRT-09, TAC-LRT-14, and TAC-LRT-19-15) displayed intermediate site fidelity, with IWR values ranging from 0.70 to 0.79. Although these individuals remained within the monitored area for extended periods, they also undertook excursions beyond the array boundaries. As a result, their residency patterns were slightly less consistent than those of the high-fidelity group yet still indicate a strong overall attachment to the study site.

Notably, one individual (TAC-LRT-19-13) was detected just once at the edge of the array and had an IWR close to 0.00, indicating virtually no residency within the monitored area.

Table 1. Residency indices were calculated for each tagged individual at each detection station based on acoustic telemetry data. The number of days detected at a given station is denoted as D_d, the detection interval (from the first to the last detection) as D_i, and the total study duration as D_t. Two residency indices were derived: IR_{Di}, representing the proportion of time the individual spent at a station relative to its monitored period, and, IR_{Dt}indicating the proportion relative to the full duration of the study. Additionally, the Individual Weighted Residency Index (IWR) was calculated as a weighted version of IR_{Di}, incorporating station-specific weights. Total body length (cm) and fate date are included. The table spans pages 16–17.

ID	Total length (cm)	Dd	Fate Date	End of monitoring	Dt	Di	IR Di	IR Dt	IWR
TAC-LRT-19-01	36	758		2021-10-27	876	861	0.88	0.87	0.76
TAC-LRT-19-02	36	226	2020-01-21	2020-01-21	231	231	0.98	0.98	0.96
TAC-LRT-19-03	40	178	2019-11-29	2019-11-29	178	178	1.00	1.00	1.00
TAC-LRT-19-04	28	851		2021-10-27	876	861	0.99	0.97	0.96
TAC-LRT-19-05	34	293	2020-04-23	2020-04-23	324	324	0.90	0.90	0.82
TAC-LRT-19-06	42	857		2021-10-27	876	861	1.00	0.98	0.97
TAC-LRT-19-07	37	856		2021-10-27	876	861	0.99	0.98	0.97
TAC-LRT-19-08	42	857		2021-10-27	875	861	1.00	0.98	0.97
TAC-LRT-19-09	44	697		2021-10-27	875	737	0.95	0.80	0.75
TAC-LRT-19-10	32	862		2021-10-27	868	866	1.00	0.99	0.99
TAC-LRT-19-11	31	146	2019-11-05	2019-11-05	146	146	1.00	1.00	1.00

TAC-LRT-19-12	35	169	2019-11-29	2019-11-29	170	170	0.99	0.99	0.99
TAC-LRT-19-13	31	9		2021-10-27	868	193	0.05	0.01	0.00
TAC-LRT-19-14	32	192	2020-01-21	2020-01-21	216	216	0.89	0.89	0.79
TAC-LRT-19-15	28	721		2021-10-27	861	861	0.84	0.84	0.70

2

3.2 Trajectory modelling

Following the initial data processing and filtering steps, the trajectories estimated by the CTRWM comprising all tagged *Labrus bergylta* individuals included a total of 3,169,805 positions. Despite the implementation of an initial filtering based on spatial error metrics, pronounced outliers and abrupt deviations in movement trajectories were still observed (Figure 3, TAC-LRT-15). A subsequent filtering procedure was employed to remove these anomalies, resulting in trajectories that closely corresponded with those predicted by the CTCRW movement model (Figure 3). This concordance underscores the high spatial resolution and accuracy of the acoustic telemetry array. The CTCRW could not be applied to individuals with insufficient data (< 20 positions).

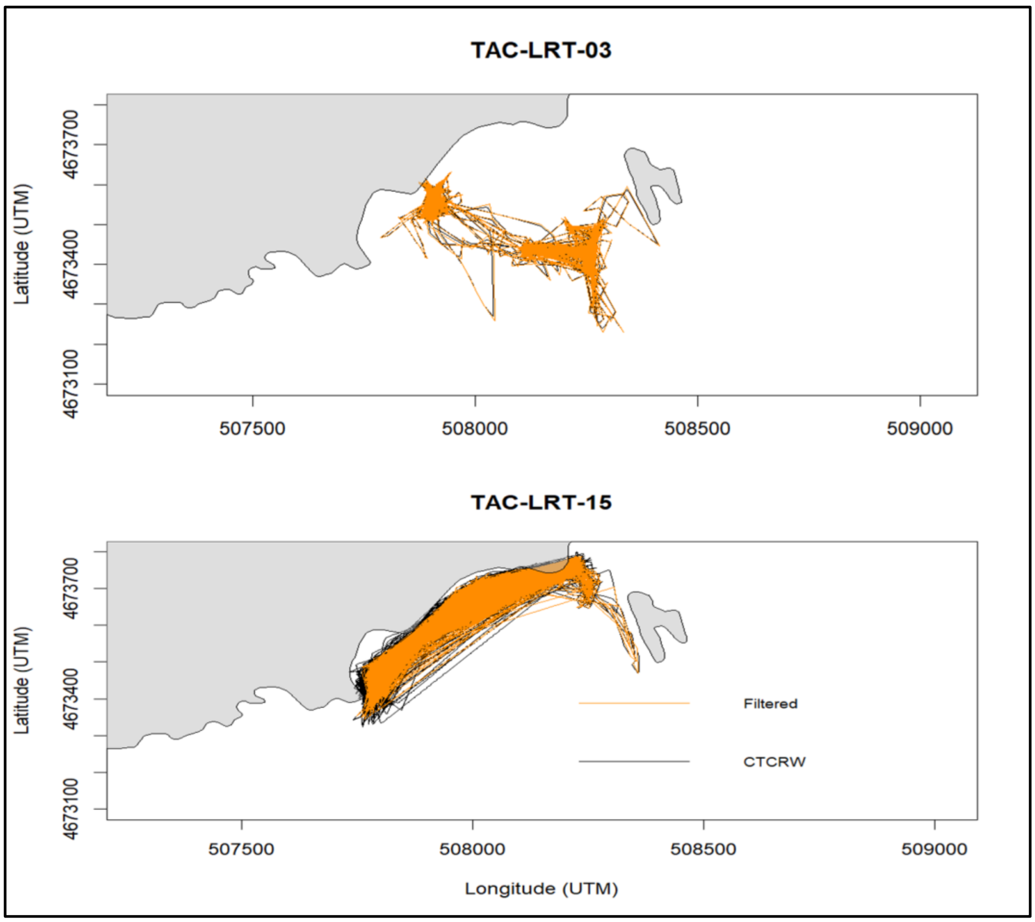

Figure 3. Movement trajectories of two selected Labrus bergylta individuals (TAC-LRT-19-03 and TAC-LRT-19-15). Orange lines represent movement paths based on positions retained after the initial filtering step, while black lines show the modelled trajectories generated using the Continuous-Time Correlated Random Walk (CTCRW) movement model. The grey areas indicate the coastline of the Parque Nacional Marítimo-Terrestre das Illas Atlánticas de Galicia.

3.3 Activity space

The estimated activity space of *L. bergylta* ranged from 6,870 m² to 23,120 m², with a mean ± standard deviation of 13,780 ± 5,150 m² (Supplementary Material Appendix 2, Figure 4). The optimal GAMM (Table 2; Supplementary Material Appendix 1, Table 1) revealed that weekly variation in activity space was significantly influenced by the interaction between diel period and week of the year, indicating a clear seasonal trend in movement patterns that differ between day and night (Figure 4). Activity space was consistently higher during daylight hours, peaking in late spring and early summer, and gradually decreasing toward winter. In contrast, nocturnal spatial behaviour showed no clear seasonal trend, suggesting stable small activity space during night hours throughout the year. This supports the conclusion that individuals are more active and spatially expansive during the day, regardless of the time of year. None of the rest of the explanatory variables showed significant effects on activity space.
The model accounted for individual-level variability through a random effect term, indicating individual differences in spatial use patterns.

Table 2. *Summary of the optimal GAMMs fitted to movement metrics of Labrus bergylta: (i) weekly activity space and (ii) swimming speed. Estimates are shown for parametric terms and smooth terms, with significance levels. Autocorrelation (ρ) and sample size (n) are reported for each model*

Parametric coefficients	**Estimate**	**Std. Error**	**z value**	**P-value**	**CI lower**	**CI upper**
(i) **Activity Space**						
Intercept	2.180	0.231	9.458	< 2e-1	1.727	2.633
Daytimenight	-0.654	0.1392	-4.699	0.000	-0.928	-0.381
Smooth terms	edf		x³			
WOY	0.010		0.002	0.449		
WOY:Daytimeday	2.663		5.067	0.001		
WOY:Daytimenight	0.0007939		0.000	0.440		
	Intercept	Residual				
Random (SD)	0.734	1.365			0.417	1.289
ρ = 0.0821 n = 467						
Parametric coefficients	**Estimate**	**Std. Error**	**z value**	**P-value**	**CI lower**	**CI upper**
(ii) Activity levels						
Intercept	-6.149	0.268	-22.960	<2e-16	-6.674	-5.624
Temp media	0.048	0.004	10.70	<2e-16	0.039	0.057
Smooth terms	edf		x³	P-value		
DOY	2.931		86.72	<2e-16		
HOD	3.000		5,356.57	<2e-16		
	Intercept	Residual				
Random (SD)	1.002	1.028			-0.387	2.391
ρ = 0.154 n = 69287						

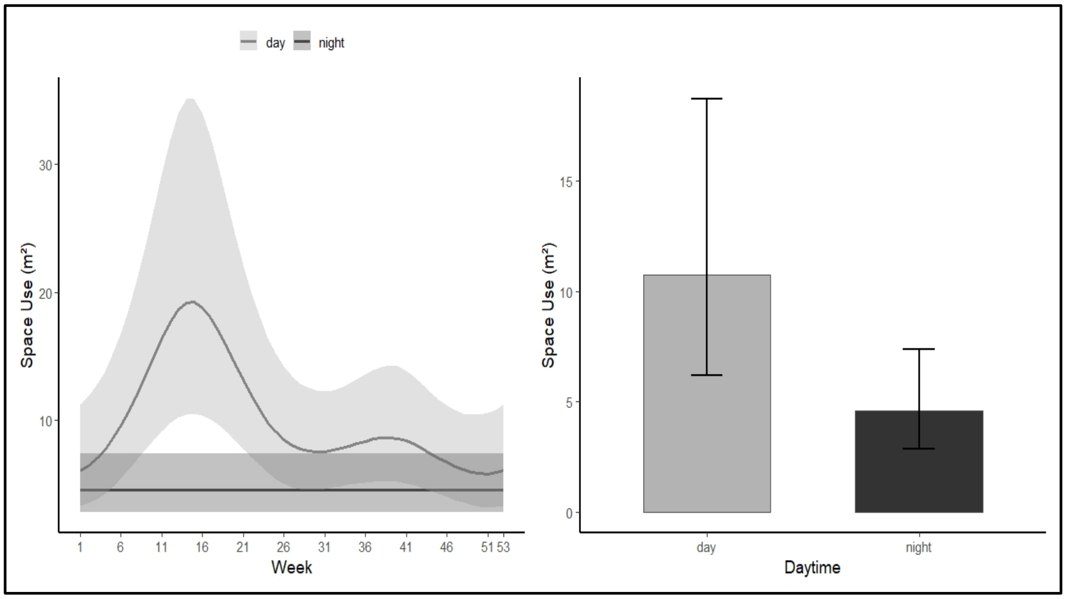

Figure 4. Predicted weekly activity space of L. bergylta as a function of week of the day (WOY) during daytime hours. based on the fitted GAMM. The solid line represents the model prediction. and the grey shaded area indicates. and the grey shaded area indicates the 95% confidence interval.

3.4 Swimming speed

Swimming speed was positively related to bottom temperature, with higher movement observed at warmer temperatures, although the effect size was relatively low (Table 2, Figure 5). The model further revealed both a seasonal pattern (DOY) and daily variation (HOD) in swimming speed, with activity showing a marked reduction toward the end of the summer season and elevated levels during crepuscular periods (dawn and dusk), coupled with an overall preference for daytime activity. No other predictors included in the model (Table 2) were significant.

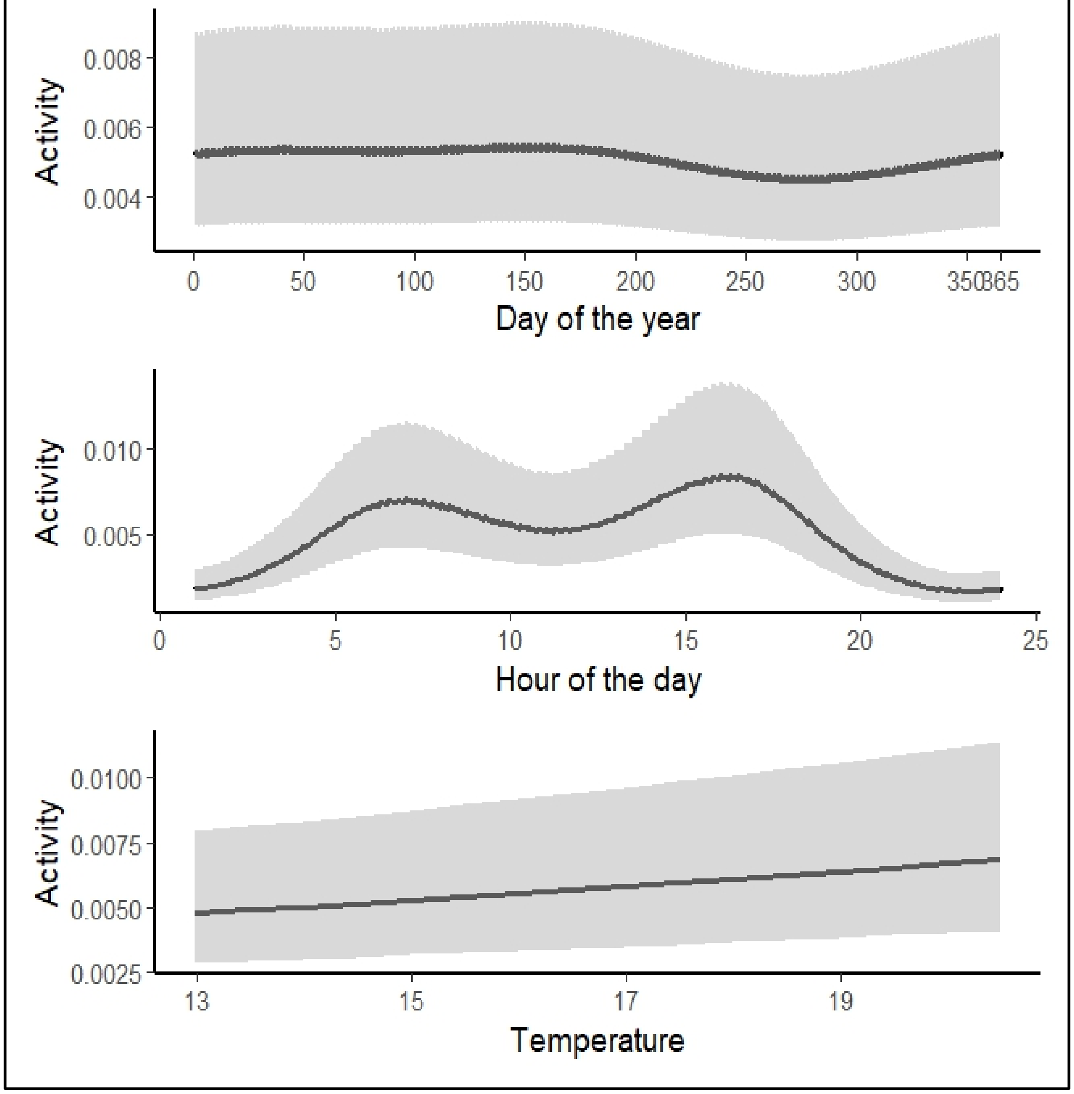

Figure 5. Predicted daily activity levels of L. bergylta as a function of day of the year (DOY). based on the fitted GAMM. The solid line represents the model prediction. and the grey shaded area shows the 95% confidence interval.

3.5 Behavioural states

The HMMs applied to *Labrus bergylta* movement data successfully identified two behavioural states: resting and active. These states were primarily differentiated by step length, with turning angle concentration providing limited additional discrimination (Figure 6). Median step length in the resting state was minimal (0.11 ± 0.11 m), while the active state exhibited a substantially greater median of 3.94 ± 6.36 m.

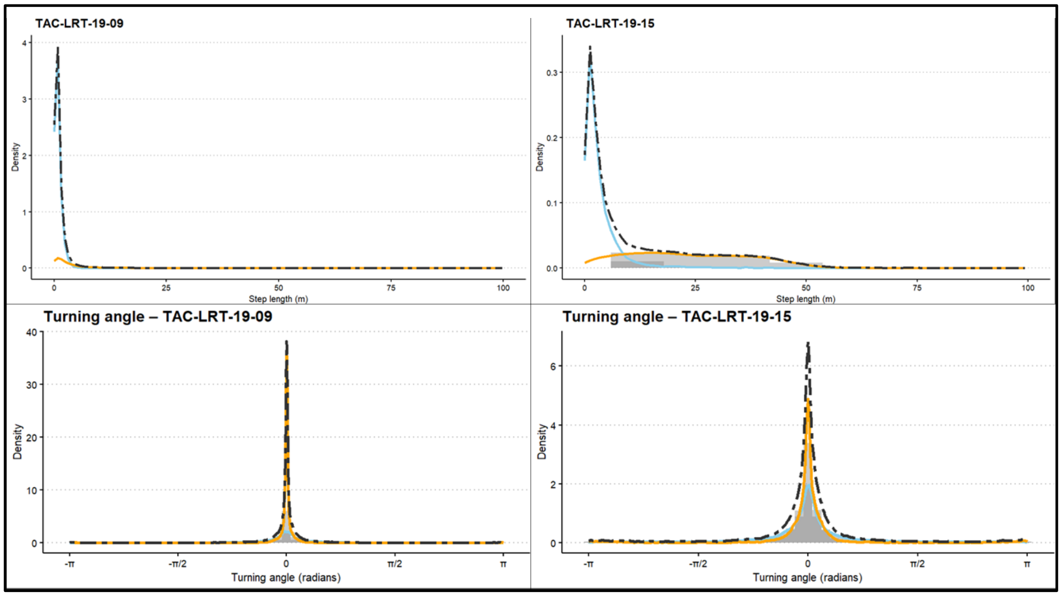

Figure 6. Histograms of step lengths (m) and turning angles for individuals TAC-LRT-09 and TAC-LRT-15. overlaid with state-dependent probability density functions estimated by the Hidden Markov Model (HMM). Coloured lines represent the fitted distributions for the active (orange) and resting (blue) behavioural states. while the dashed black line represents the combined distribution weighted by the proportion of observations in each state.

Across individuals, the average activity budget comprised 56.5% resting and 43.5% active behaviour, but with high variability (resting: 17.2–94%; active: 6–82.8%). Model selection based on AIC indicated that, for 5 of the 15 individuals, incorporating both diel cycle and habitat type as covariates improved model performance relative to covariate-free formulations. When considering diel cycle alone, only 4 of the 15 individuals showed improved fit, while including habitat type alone enhanced model performance for 3 of the 15 individuals. In contrast, models using only the initial parameters without covariates improved performance in 3 of the 15 individuals.

One notable case was an individual (TAC-LRT-13, 31 cm, spotted morphotype) that exhibited only a single behavioural state throughout the tracking period.

In summary, incorporating environmental covariates into HMMs enhanced the ecological interpretation of movement patterns, revealing that while diel cycle and habitat type can influence L. *bergylta* behaviour, these effects are not uniform and instead highlight marked individual differences (Figure 7).

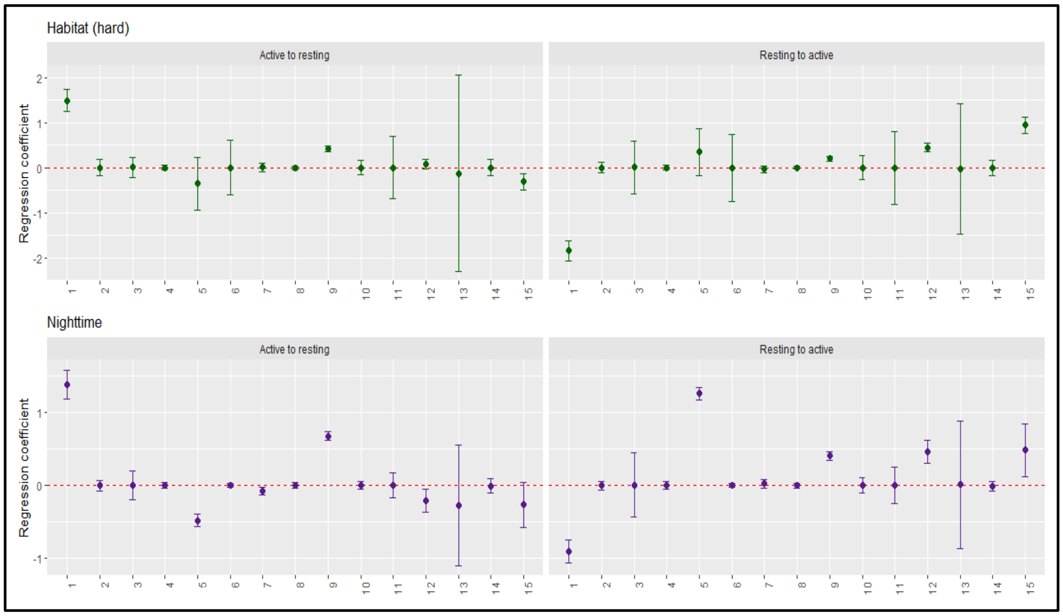

Figure 7: Estimated beta regression coefficients and 95% confidence intervals from the Hidden Markov Model for transitions between behavioural states (active → resting and resting → active) in relation to two key environmental covariates: habitat type (hard substrate) and diel cycle (nocturnal period). Positive coefficients indicate an increased probability of transition under the given condition. whereas negative coefficients indicate a decreased probability.

3.6 Revisitation patterns

Revisitation analysis based on HMM-classified resting positions revealed substantial inter-individual variability in fine-scale recursive movements, with the number of revisits during resting periods to specific locations differing markedly among tagged fish: some individuals repeatedly returned to a small number of core areas, while others distributed their revisits more broadly across the study area.

Using spatial clustering, discrete core areas were identified for 14 of the 15 individuals; cluster analysis was not possible for a single individual (TAC-LRT-13) due to an insufficient number of recorded resting positions over the tracking period. The number of spatial clusters per individual ranged from 1 to 3 during daytime and from 1 to 6 at night, with fish utilising on average 2.07 clusters during the day and 2.86 clusters at night. Spatial comparison of daytime and nighttime clusters indicated that, for most individuals, resting areas were either overlapping or located in proximity between diel phases (Supplementary Material, Appendix 2, Figure 3). This spatial consistency suggests a preference for specific refuges regardless of time of day (Supplementary Material, Appendix 2, Figure 3). An exception was observed in TAC-LRT-15, which exhibited a notably higher frequency of revisits to nocturnal clusters compared to diurnal ones (Figure 8), potentially reflecting a shift in activity space or nighttime refuge selection.

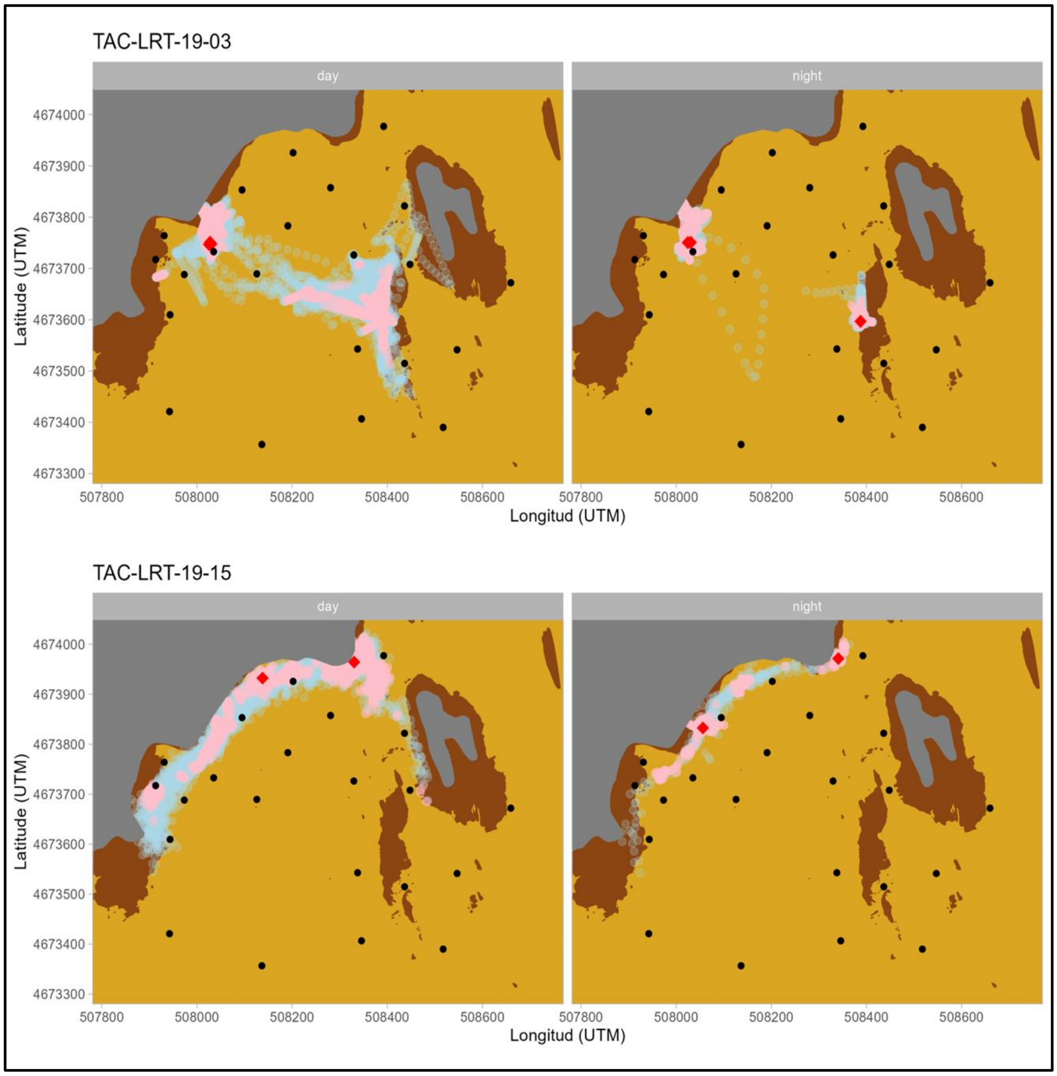

Figure 8. Results of the recursion analysis for individual TAC-LRT-19-03 and TAC-LRT-19-15 within the study area. Blue points indicate locations associated with active behavioural states. while red points correspond to resting states. as inferred from Hidden Markov Models. Red cones highlight revisitation hotspots. representing nodes of high recursion frequency and prolonged residence time. The background habitat layer illustrates substrate composition: darker brown areas indicate rocky bottoms. while lighter yellow regions correspond to soft sediments such as sand.

For most individuals, clusters identified during the day, and night overlapped spatially; however, in some cases, slight shifts in cluster positions were observed between day and night, even though the number of clusters remained consistent (Supplementary Material Appendix 2, Figure 3). Overall, cluster analysis revealed that all individuals predominantly used hard-bottom habitats for resting, with clusters consistently located near rocky or rock-like areas.

4. Discussion

Gaining insights into the spatial ecology and behavioural patterns of coastal fishes is crucial to inform conservation planning and to develop sustainable fisheries management strategies (Nathan et al., 2008; Hussey et al., 2015; Cooke et al., 2016). In this study, we combined long-term, high-resolution acoustic telemetry monitoring with advanced modelling approaches (e.g. CTRW and HMM) to generate novel insights into the movement and behaviour patterns of *Labrus bergylta* within the Atlantic Islands of Galicia National Park. Our results confirm and expand upon earlier findings of high residency, small activity spaces, and pronounced diel patterns in this species (Villegas-Ríos et al., 2013; Morel et al. 2013), while revealing substantial inter-individual behavioural variability with important ecological and management implications.

As demonstrated in recent acoustic telemetry studies (Leeney et al., 2024), evaluating residency (IWR) and movement behaviour is critical to assess whether the boundaries of a marine protected area adequately encompass the core habitats of target species and to ensure that spatial management strategies incorporate both resident and more mobile individuals. The residency patterns of L. *bergylta* in the study area revealed pronounced site fidelity, with most of the individuals exhibiting high residency (IWR ≥ 0.95). This result mirrors previous estimates previously reported for *Labrus bergylta* (Villegas-Ríos et al., 2013; Morel et al., 2013). High residency reflects strong site fidelity, which can enhance the effectiveness of spatial protection measures (Abecasis & Erzini, 2008). Similar high site fidelity has been documented for other demersal species, such as *Diplodus sargus* (Abecasis et al., 2015). However, the observed intra-specific variability, with at least one more transient individual, highlights the potential role of some fish in promoting habitat connectivity and spillover between protected and adjacent areas. These results align with previous studies on reef-associated fishes showing consistent site fidelity but inter-individual behavioural diversity, which may enhance population resilience while complicating generalized management prescriptions (Villegas-Ríos et al., 2013; Alós et al., 2017; Villegas-Ríos et al., 2017; Williamson et al., 2021).

The Continuous-Time Correlated Random Walk model successfully interpolated positions while accounting for temporal autocorrelation, generating biologically plausible trajectories and mitigating unrealistic jumps due to detection gaps (Johnson et al., 2008). A proper filtering procedure removed outliers and abrupt deviations, a common feature in high-resolution telemetry datasets (Bacheler et al., 2019; Williamson et al., 2021), resulting in trajectories highly consistent with observed positions. The use of this modelling approach to estimate fish trajectories from high resolution telemetry data represents significant improvement over previous research (Villegas-Ríos et al. 2013) that allow to evaluate in detail behavioural states at individual level. The mean step lengths for interpolated positions of the CTRW were short (< 20 m), reflecting restricted movement typical of territorial fishes, while occasional long displacements likely corresponded to exploratory excursions between core areas (Bacheler et al., 2019). Turning angles clustered near 0° and 180°, consistent with directional persistence during transits and reversals during area-restricted searches (Benhamou, 2004).

Weekly activity spaces within the study area were small (mean ≈ 0.014 km^2), consistent with previous estimates for L. *bergylta* (Villegas-Ríos et al., 2013) and other sedentary fishes (Alós et al., 2011). Daytime range expansion and increased step lengths suggest active foraging under daylight, followed by nocturnal contraction into shelters, similar to patterns reported for L. *bergylta* (Villegas-Ríos et al., 2013) and *Xyrichtys novacula* (Alós et al., 2012a). The model results revealed a significant interaction between diel and seasonal effects, with larger daytime ranges in late spring and early summer, consistent with peaks in foraging and reproductive activity (Villegas-Ríos et al., 2014). Seasonal range expansion during reproductive periods at daylight hours is consistent with labrid reproductive ecology, where mobility supports courtship and nest defence (Robertson, 1991; Alós et al., 2012a). The observed nocturnal spatial contraction, consistent across seasons, aligns with refuge-based behaviour described for L. *bergylta* (Dipper et al., 1977) and other benthic species (Porteiro et al., 1996; Leeb et al., 2021). Selective pressures towards low-activity phenotypes (Alós et al., 2012b) may influence the proportion of mobile versus resident individuals, with implications for protection strategies.

The swimming speed increased with bottom temperature and daylight hours, supporting temperature-driven metabolic theory in ectotherms (Kent & Ojanguren, 2015; Didrikas et al., 2009) and patterns of diurnal foraging (Bacheler et al., 2019). Post-spawning reductions in swimming speed may be linked to lethargy or shifts in prey availability, as observed in other temperate reef fishes (Lowry et al., 2012). However, these results do not agree with previous studies in the same area, i.e., Villegas-Ríos et al. (2013) reported maximum of daily distance travelled during the post-spawning season. Such differences could be a result of data resolution, since Villegas-Ríos et al. (2013) used centres of activity (30 min time bins) to estimate distance travelled.

Using Hidden Markov Models, increasingly applied in aquatic telemetry (Bacheler et al., 2019; Leos-Barajas et al., 2017), the movements of L. *bergylta* were categorized into 'active' and 'resting' states. Active states were characterized by long step lengths (>15 m), typical of directed foraging or transits between resource patches. Several studies working with demersal fishes have similarly identified these two states as key drivers of empirical movement data (Bacheler et al., 2019; Pereñíguez et al., 2023). Resting states showed minimal displacement (< 5 m), consistent with sheltering or inactivity. This marked separation mirrors patterns reported for *Balistes capriscus* (Bacheler et al., 2019) and *Raja undulata* (Vidal, 2024), where step length has consistently been identified as the most informative variable for behavioural classification. The predominance of active states during daylight is consistent with visual observations of L. *bergylta* foraging (Villegas-Ríos et al., 2013) and diel patterns in other reef fishes (B. *capriscus*: Bacheler et al., 2019; R. *undulata*: Leeb et al., 2021). Such intra-specific variability, also observed in other reef-associated fishes (Villegas-Ríos et al., 2013; Williamson et al., 2021), likely reflects differences in personality, habitat affinity, or energetic status. Diel variation was evident, with resting behaviour more frequent at night (69.2%) than during the day (60.3%), corroborating previous visual census and telemetry studies documenting nocturnal sheltering in L. *bergylta* (Dipper et al., 1977; Villegas-Ríos et al., 2013). Fish occupying hard-substrate habitats spent more time resting (mean: 76.4%), supporting the idea that these environments offer secure refuges or energetically advantageous resting conditions, as documented for reef and demersal species in structurally complex habitats (Bacheler et al., 2019). The influence of environmental drivers of behaviour differs among individuals, aligning with emerging evidence of heterogeneous behavioural responses within populations (Williamson et al., 2021). These divergent patterns highlight the role of behavioural plasticity (Villegas-Ríos et al., 2017), which may enhance population resilience but complicates generalised management prescriptions.

Revisitation analysis of HMM-derived resting positions showed a fine-scale high site fidelity. These findings are consistent with the observations reported by Mucientes et al. (2019), who documented individuals of *Labrus bergylta* defending the same small territory, typically comprising a few rocks, across multiple reproductive seasons, ranging from 2 to 15 years. Nevertheless, there was a pronounced inter-individual variation in site fidelity. Cluster analysis identified discrete core areas for 14 of 15 individuals, with 1–3 clusters during the day and 1–6 at night (mean = 2.07 and 2.86, respectively).Some individuals exhibited strong fidelity to one or a few core areas, while others, revisited edge areas up to five times, displayed broader exploratory behaviour, frequently returning to peripheral zones of the study site. Multi-core area use has been linked to habitat heterogeneity, seasonal resource shifts, and risk avoidance (Bacheler et al., 2019; Leeb et al., 2021; Williamson et al., 2021). The inability to cluster one individual could represent a genuine biological phenomenon, such as persistent inactivity or extreme site fidelity or may result from limitations in detection frequency and spatial coverage, both of which can constrain behavioural inference in acoustic telemetry studies (Williamson et al., 2021).

The observed revisitation patterns support the interpretation of active foraging behavior during daylight hours and a shift toward more localized refuge use at night (Mucientes et al., 2019). Some of the individuals (p.e TAC-LRT-03, TAC-LRT-15) used overlapping or adjacent daytime and nighttime resting areas, indicating possible refuge selection across diel phases. This consistency supports previous descriptions of persistent refuge use in territorial fishes (Villegas-Ríos et al., 2013; Mucientes et al. 2019) and suggests that diel activity shifts typically involve short-range foraging rather than large-scale relocations. Only one fish exhibited greater revisits to nighttime clusters, potentially reflecting a shift in shelter preference or nocturnal habitat use.

Conclusions

By combining continuous-time movement modelling (CTCRW), environmental driver analysis (GAMMs), behavioural state inference (HMMs), and revisitation metrics, this multi-year, high-resolution acoustic telemetry study provides the most detailed long-term perspective to date on the spatial and behavioural ecology of *Labrus bergylta* within the Atlantic Islands of Galicia National Park. Our results demonstrate that individual behavioural variability and extrinsic factors (diel cycle, seasonal changes, habitat type) shape the activity patterns, activity space or behavioural states of *L. bergylta*. High residency and small activity spaces predominated in this species, corroborating earlier short and long-term observations (Villegas-Ríos et al., 2013; Mucientes et al., 2019). HMMs effectively distinguished active and resting states, revealing consistent diel rhythms, seasonal peaks in daytime activity space linked to reproduction, and habitat-driven differences in state transitions. The predominance of nocturnal resting and the frequent use of structurally complex hard substrates underscore the importance of these habitats as persistent refuges. Revisitation and cluster analyses confirmed long-term fidelity to a small number of discrete core areas for most individuals, often shared between day and night. However, variation in the number and spatial distribution of these core areas highlights behavioural plasticity. Overall, *L. bergylta* exhibits a dual movement strategy: strong site fidelity interspersed with occasional exploratory excursions. This combination supports the effectiveness of fixed spatial protections for most individuals. By linking fine-scale behaviour with habitat use over extended timescales, this study advances the ecological understanding of temperate reef fishes and provides a robust, evidence-based framework for designing and evaluating spatial management within coastal marine protected areas.

5. Acknowledgments

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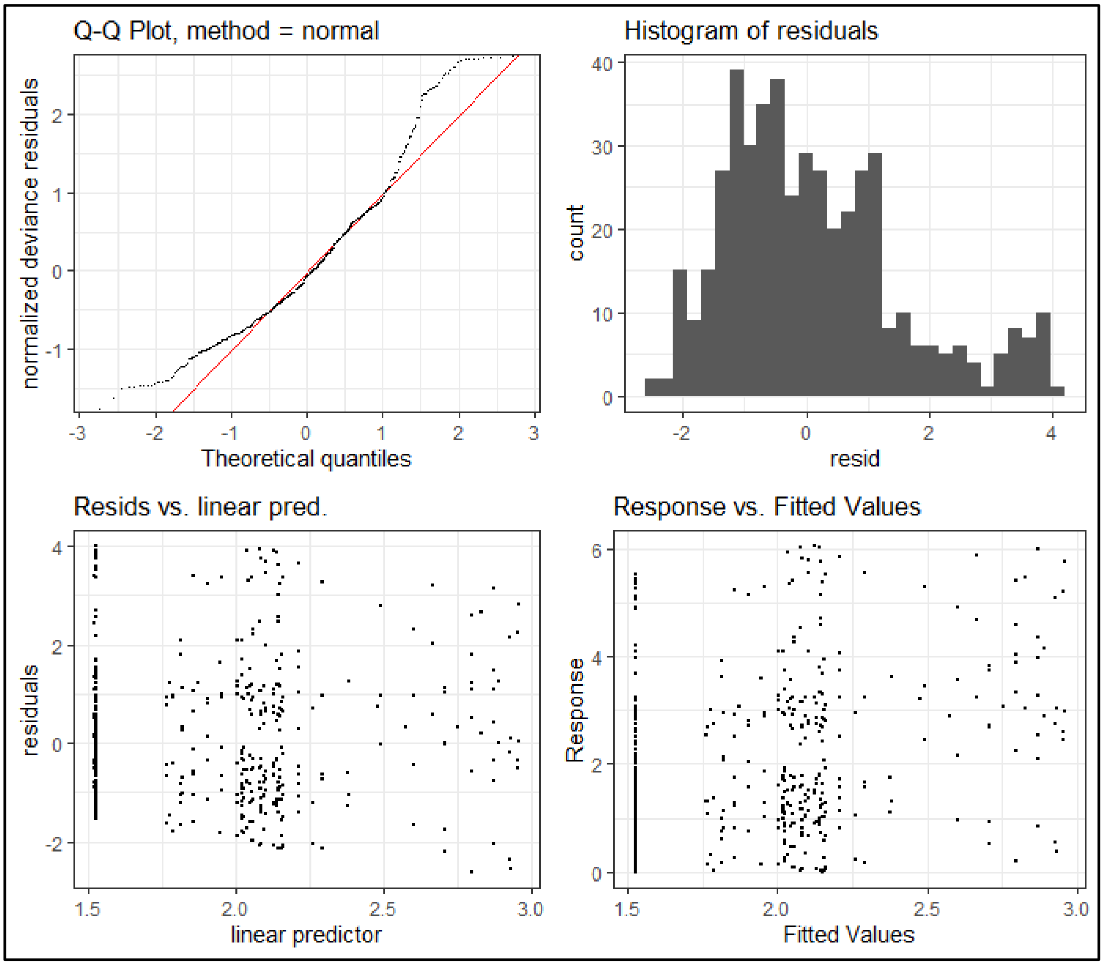
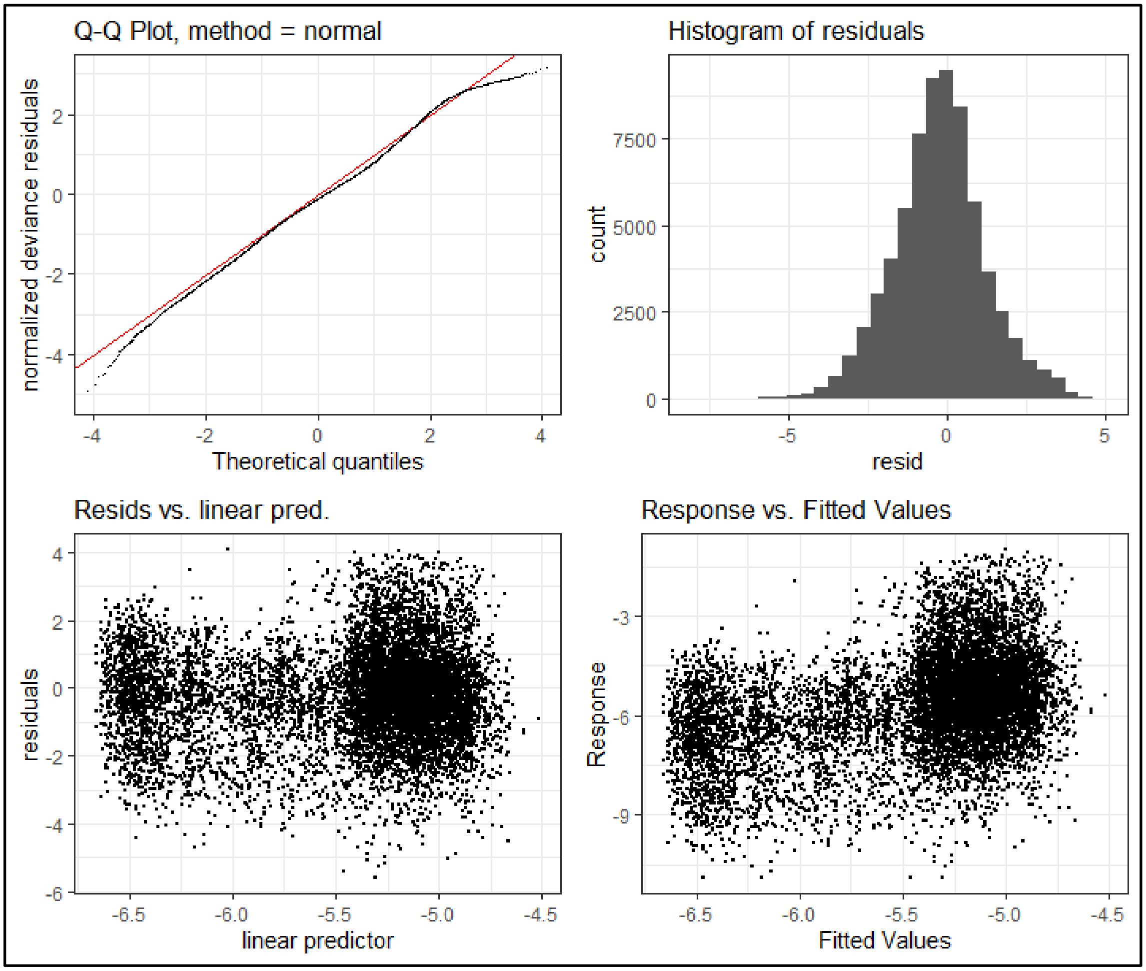
7. Supplementary Material

7.1 Appendix 1. Data Analyse



Supplementary Material. Appendix 1. Figure 1. Statistical summary of the Generalized Additive Mixed Models used to estimate Activity space.



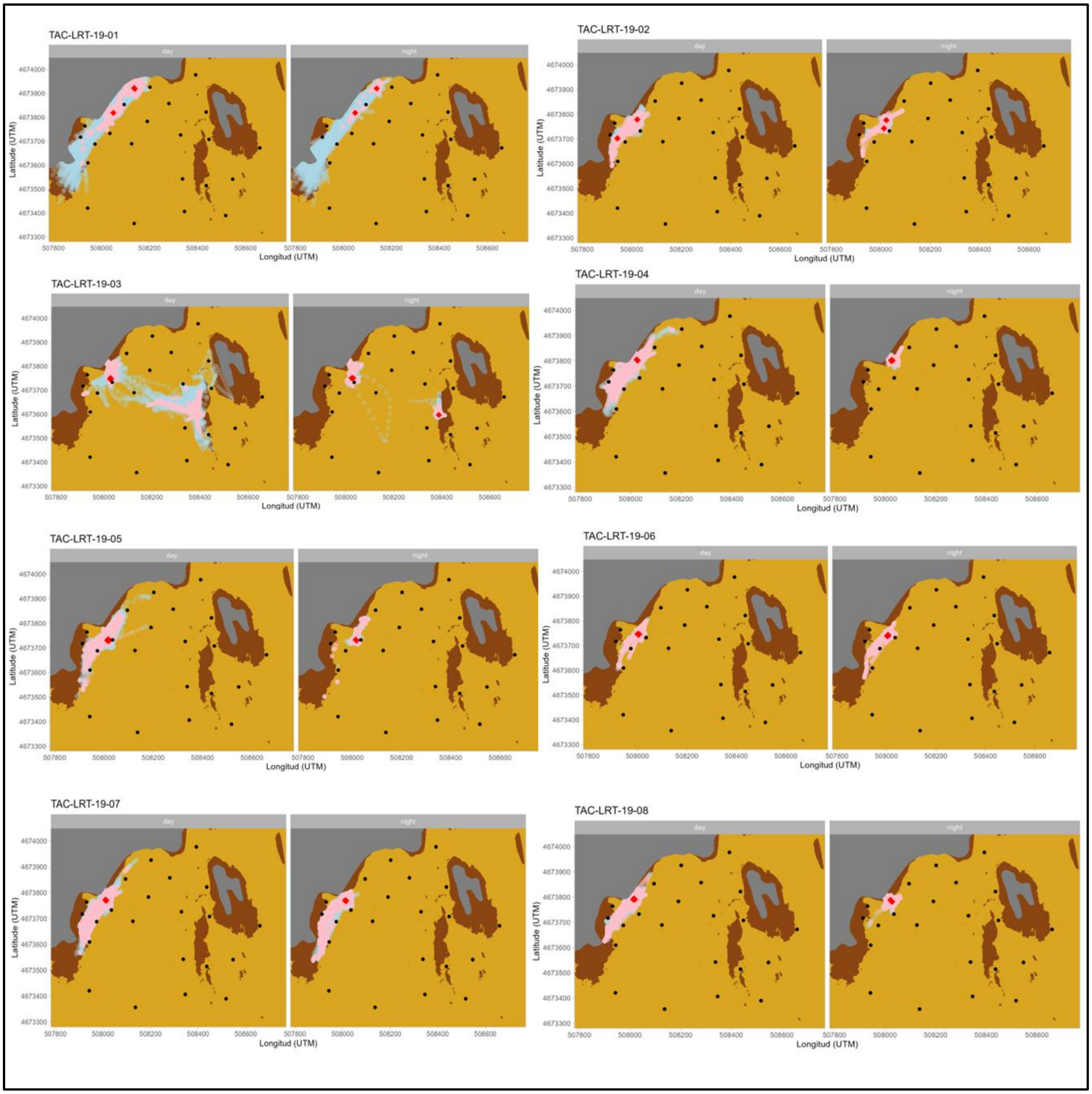
Supplementary Material. Appendix 1. Figure 2. Statistical summary of the Generalized Additive Mixed Model used to estimate activity levels.

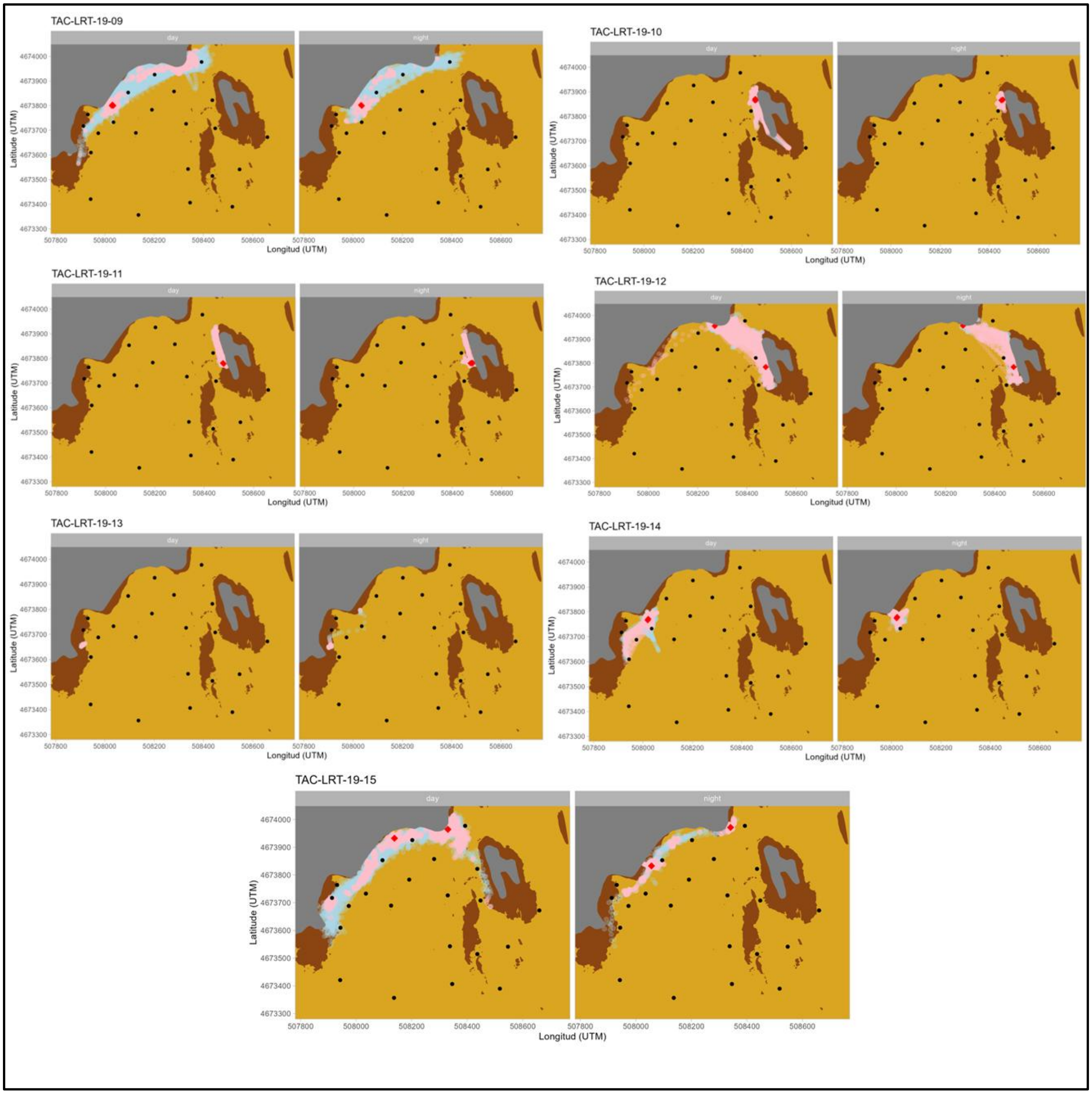
Supplementary Material. Appendix 1. Table 1. Statistical summary of the Generalized Additive Mixed Models (GAMMs) used for model selection based on the Akaike Information Criterion (AIC). Results are presented for: (i) Activity space, across six candidate models. and (ii) activity levels. across four candidate models. For each model. autocorrelation (ρ) and sample size (n) are reported. Models highlighted in bold represent the best-fitting models according to AIC. The table spans pages 37–38.

i) Activity space	
Model structure	***AIC***
P = α + Year + Daytime + TL + Type + Mean_temp + f(WOY) + f(WOY × Daytime) + a + ε	*1,665.995*
P = α + Year + Daytime + Type + Mean_temp + f(WOY) + f(WOY × Daytime) + a + ε	*1,664.178*
P = α + Daytime + Type + Mean_temp + f(WOY) + f(WOY × Daytime) + a + ε	*1,662.812*
P = α + Daytime + Mean_temp + f(WOY) + f(WOY × Daytime) + a + ε	***1,661.529***
P = α + Daytime + f(WOY) + f(WOY × Daytime) + a + ε	*1,661.921*
P = α + Daytime + f(WOY) + a + ε	*1,664.332*
ii) Activity levels	
Model structure	***AIC***
P = α + TL + Type + Mean_temp + f(DOY) + f(HOD) + a + ε	*196,855.5*

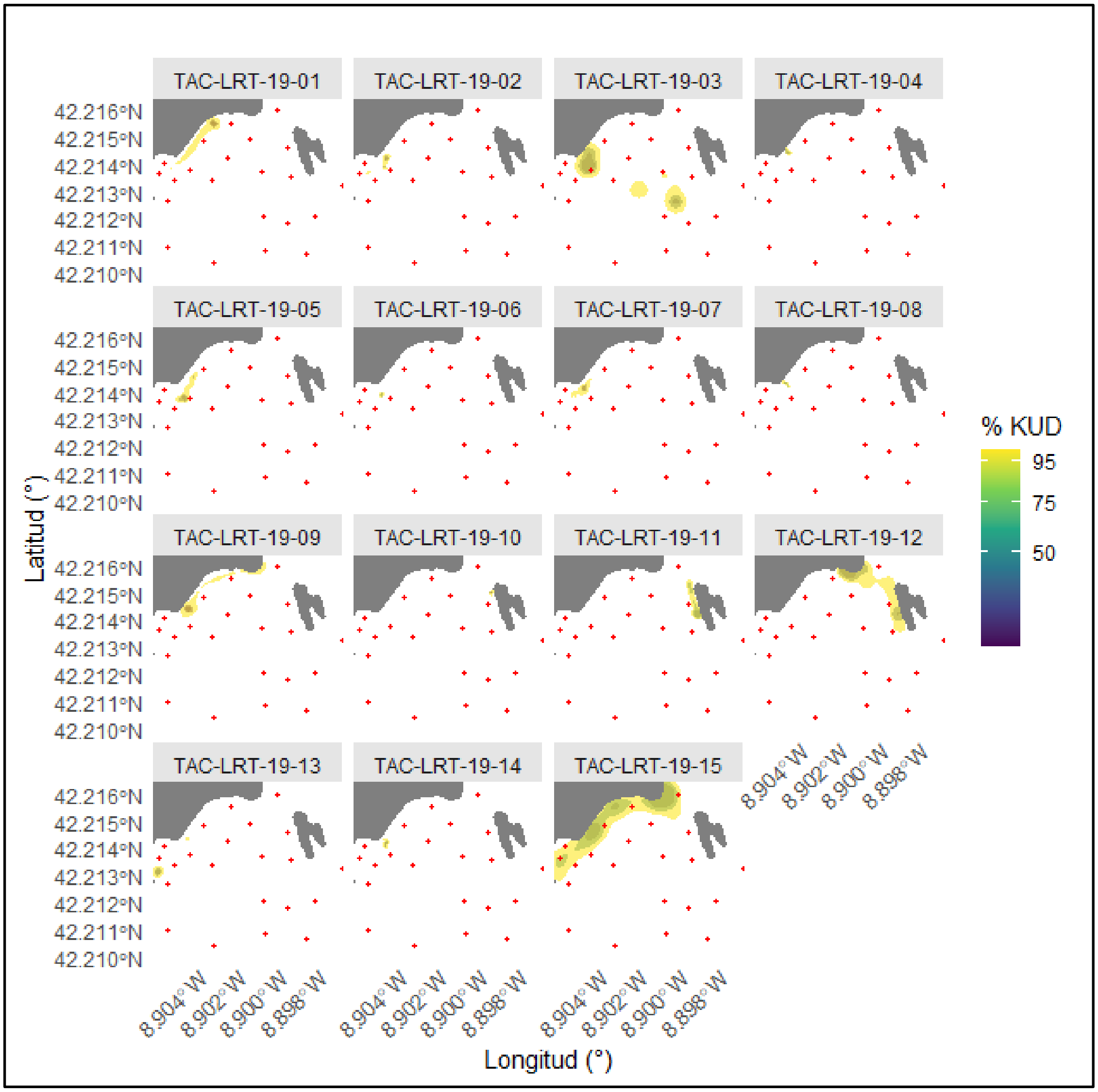
$P = \alpha + Type + Mean\_temp + f(DOY) + f(HOD) + a + \varepsilon$	*196,854.9*
$\boldsymbol{P = \alpha + Mean\_temp + f(DOY) + f(HOD) + a + \varepsilon}$	***196,854.7***
$P = \alpha + f(DOY) + f(HOD) + a + \varepsilon$	*196,966.1*

7.2 Appendix 2. Movement Analyse





Supplementary Material. Appendix 2. Figure 3. Results of the recursion analysis for all individuals within the study area. Blue points indicate locations associated with active behavioural states. while red points correspond to resting states. as inferred from Hidden Markov Models. Red cones highlight revisitation hotspots. representing areas of high recursion frequency and prolonged residence time. The background habitat layer illustrates substrate composition: darker brown areas correspond to rocky bottoms. while lighter yellow regions represent soft sediments such as sand. The figure spans pages 39–40.



Supplementary Material Appendix 2. Figure 4. 95% Kernel Utilization Distribution areas of all individuals within the study area. Red dots mark the locations of sampling stations.