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Revealing Chronotypes Across Aquatic Species Using Acoustic Telemetry

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Received: 5 February 2025 | **Revised:** 1 July 2025 | **Accepted:** 17 August 2025

Funding: This work was supported by MCIN/AEI/10.13039/501100011033/FEDER, EU, CLOCK Project (Grant No. PID2019-104940GA-I00), Research Foundation Flanders (FWO), María de Maeztu Centre of Excellence (CEX2021-001198), the Leibniz-Community within the Pact for Innovation and Research (BTypes project) and the German Ministry of Education and Research (grant no.033W024A), Ministerio de Ciencia, Innovación y Universidades, Spanish Governments. MCIN/AEI/10.13039/501100011033 and by the European Union NextGeneration EU/PRTR (RYC2021-032594-I), METARAOR Project (Grant No. PID2022-139349OB-I00), MCIN/AEI/10.13039/501100011033/FEDER, EU, Vicenç Mut postdoctoral grant (PD/041/2021), FPI pred-octoral fellowship from the Direcció General d'Innovació i Recerca of the Balearic Islands Government (Ref. FPI/2167/2018), The Research Council of Norway, CODCHANGE, CodChange, Axencia Galega de Innovación (GAIN) (IN607D 2023/007), COST Action – The European Animal Tracking Network, CA18102. The Czech National Agency for Agricultural Research (project no. QK23020002 'Pikeperch fry production, and their adaptabiliy and optimization of their stocking into open waters'). The Ministry of Agriculture af the Czech Repubic (project no. QK21010131 "Optimization of the management in carp ponds with 1-year production cycle in terms of co-feeding methods and mass balance").

Keywords: behavioural types | biotelemetry | circadian-related behaviours | hidden semi-Markov models | repeatability

ABSTRACT

Acoustic telemetry offers valuable opportunities to investigate individual variability in circadian-related and other behaviours and how environmental cues shape these patterns in wild fish populations. However, this potential has not yet been fully exploited.

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We conducted a meta-analysis on 44 datasets from 34 distinct marine and freshwater species and different types of data (acoustic detections, depth, acceleration and positioning). Our aim was to explore the potential of acoustic telemetry in identifying chronotypes as consistent among-individual differences in circadian-related behaviours. First, we applied hidden semi-Markov models to classify individual time series into active and rest states. Subsequently, we computed two classical circadian-related behavioural traits: awakening time (as the activity onset) and rest onset (as the activity offset). Subsequently, we identified distinct phenotypes by decomposing behavioural variation into within- and among-individual components based on repeatability scores. We found evidence of distinct chronotypes in 17 species, with average repeatability scores of 0.52 for awakening time and 0.43 for rest onset, revealing that chronotypes are common in aquatic species. Our findings highlight that both the data type, particularly acceleration sensors, and the number of detections are effective tools for exploring chronotypes. Our study proposes a novel approach to characterising daily activity patterns in aquatic species, predominantly in fishes, and provides guidelines for investigating chronotypes across diverse taxa. We emphasise the promise of biotelemetry and advanced statistical models for improving our understanding of the behaviour of aquatic species and highlight the value of synthesising across large data sets collected in networks of biotelemetryprojects.

1 | Introduction

Chronotypes are defined as among-individual differences in circadian-related behaviours, which remain relatively stable over time due to the regulation of the internal circadian clock and are modulated by environmental and anthropogenic factors (Ehret 1974; Helm et al. 2017; Roenneberg et al. 2007). The circadian-related behaviours commonly considered to identify chronotypes are the timing of activity onset and offset (Roenneberg et al. 2003). In humans, chronotypes have been extensively studied due to their link to sleep, well-being and health (Navara and Nelson 2007) and are often categorised along a morning–evening continuum. Morning types, as the name suggests, tend to favour morning activities, typically starting their activity and rest earlier, with their cognitive and physical performance peaking earlier in the day. By contrast, evening types prefer evening activities, generally starting their activity and rest later, with their optimal cognitive and physical performance occurring later in the day (Bauducco et al. 2020; Webb and Bonnet 1978).

In animals, chronotypes are often characterised by consistent among-individual differences in activity-rest patterns, fulfilling the criteria of conventional behavioural types (Réale et al. 2007; Sih et al. 2004). Accordingly, chronotypes can be estimated using the repeatability (R) score, a widely used index for identifying behavioural types (Dingemanse and Dochtermann 2013). The R score represents the proportion of the total variance in a behavioural metric of interest that is explained by differences among individuals (Nakagawa and Schielzeth 2010). Various authors have used R scores to describe chronotypes in terrestrial animals (Chmura et al. 2020; Dominoni et al. 2013, 2014; Graham et al. 2017; Maury et al. 2020; Rittenhouse et al. 2019; Schlicht et al. 2014; Schlicht and Kempenaers 2020; Steinmeyer et al. 2010; Stuber et al. 2015). This body of evidence suggests that, as in humans, other terrestrial animals also display consistent among-individual differences in circadian-related behaviours. However, chronotypes have often been overlooked in aquatic animals (Bloch et al. 2013; Helm and Visser 2010). Numerous studies indicate that fish exhibit chronotypes (Slavík and Horký 2012; Závorka et al. 2016), supported by an extensive body of literature on circadian rhythms in fishes in laboratory settings (Blanco-Vives and Sánchez-Vázquez 2009; López-Olmeda et al. 2006; Lucas-Sánchez et al. 2013; Reebs 2002). Generally, there have been very few attempts to estimate the R scores of circadian-related behaviours in the wild (but see Alós et al. 2017 and Martorell-Barceló et al. 2024 for a set of studies in *Xyrichtys novacula* (Labridae)).

The determination of chronotypes relies on fine-scale monitoring of activity-rest cycles under natural conditions in a sufficiently large number of individuals to effectively disentangle individual and population-level sources of behavioural variation (Roenneberg et al. 2007). In humans, chronotypes are typically measured using a combination of sleep measurements collected through activity telemetry devices and questionnaires that show the individual's sleep preferences (Di Milia et al. 2013). In terrestrial animals, various techniques have been used to measure activity-rest patterns, including infrared beams, video analysis, pressure plates, jiggle cages, locomotor activity cages, telemetric devices and accelerometer monitors (Mann et al. 2005). In aquatic environments, traditional techniques for monitoring the behaviour of free-living animals have not been readily available, limiting our understanding of the particularities of chronotypes in aquatic organisms (Helm et al. 2017). Over the past two decades, advances in acoustic telemetry have significantly improved our ability to monitor free-living aquatic populations (Hussey et al. 2015), providing novel opportunities to study chronotypes in large numbers of individuals (Nathan et al. 2022).

Acoustic telemetry is the most widely used tracking system for aquatic environments and has become a powerful tool to improve our knowledge of the behaviour, ecology and conservation of fish (Lennox et al. 2023; Matley et al. 2022). This technology is based on implanting an acoustic transmitter in the fish, which emits codified signals with unique identifiers (Lennox et al. 2023). These signals are typically detected by an array of receivers strategically deployed within the study area (Heupel et al. 2006). Acoustic telemetry has been used to identify diel activity–rest patterns in various species in both freshwater and marine environments. Some examples are *Perca fluviatilis* (Percidae; Nakayama et al. 2018), *Silurus glanis* (Siluridae; Brevé et al. 2014), *Cyprinus carpio* (Cyprinidae; Monk et al. 2023), *Serranus cabrilla* (Serranidae; Alós et al. 2011), *Serranus scriba* (Serranidae; March et al. 2010),

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Labrus bergylta (Labridae; Villegas-Ríos et al. 2013), *Diplodus sargus* (Sparidae; Aspillaga et al. 2016), *Dentex dentex* (Sparidae; Aspillaga et al. 2017), *Cheilinus undulatus* (Labridae; Chateau and Wantiez 2007), *Pterois volitans* and *Pterois miles* (Scorpaenidae; McCallister et al. 2018), *Naso unicornis* and *Naso lituratus* (Acanthuridae; Marshell et al. 2011), *Chlorurus sordidus*, *Scarus ferrugineus* and *Scarus fucropurpureus* (Scaridae; Pickholtz et al. 2022). None of these studies, however, specifically addressed the *role* of circadian-related behaviours to determine the existence of chronotypes in these species. Notably, only Alós et al. (2017) and Martorell-Barceló et al. (2023, 2024) utilised a combination of hidden Markov models (HMMs; Patterson et al. 2009) and acoustic detection time-series data to effectively decompose the population- and individual-variance components for circadian-related behaviours, providing robust evidence for the existence of chronotypes in *X. novacula*. To date, the full potential of acoustic telemetry in exploring chronotypes in a set of species remains underexplored.

Acoustic transmitters can also be complemented with sensors that record environmental parameters such as temperature and depth, or even measures of body acceleration as a direct indicator of activity levels (Cooke et al. 2004; Donaldson et al. 2014; Hussey et al. 2015). Acceleration sensors are particularly useful at detecting activity-rest patterns. For instance, *Carcharinus perezi* (Carcharhinidae) exhibits greater activity levels at night, associated with foraging (Shipley et al. 2018). Depth sensors are also efficient to detect activity-rest patterns. Shifts in individual vertical distribution, resulting in daily behavioural patterns, are widespread among aquatic organisms (Neilson and Perry 1990; Watanabe et al. 1999). Andrews et al. (2009) used acoustic tags with depth sensors in *Hexanchus griseus* (Hexanchidae) to show that individuals inhabited deeper and colder waters during daytime and actively hunted in shallower and warmer waters. Individuals may also exhibit daily behavioural patterns in their space use from pelagic to littoral sites (Monk et al. 2023; Nakayama et al. 2018). Acoustic telemetry is particularly valuable in discerning these 'horizontal daily' migrations, as it not only offers detections and sensor data but also provides positional information and detailed daily activity-rest patterns. For example, Watson et al. (2019) showed that some *Oncorhynchus mykiss* (Salmonidae) used different areas of a lake for foraging during the day and resting at night.

Although previous evidence suggests that using acoustic telemetry along with associated sensors is a valuable approach to assess chronotypes, this method presents three significant challenges. First, depending on the setup of the acoustic network, if the receiver density is too low, detecting the activity onset and offset might be difficult and imprecise, making differences among individuals undetectable. Second, depending on the transmitters' emission period, the temporal resolution may not be sufficient to disentangle the activity start and end times. Third, the number of individuals that can be tracked simultaneously is often limited due to signal collision in some coding systems. This occurs when multiple transmitters emit signals simultaneously on the same frequency, causing interferences that prevent their detection (Binder et al. 2016). Recent advancements in high-resolution telemetry systems mitigate some of these issues (Baktoft et al. 2015; Lennox et al. 2023; Nathan et al. 2022). In particular, some of the new tracking systems address signal collision through improved emission protocols, such as the Binary Phase-Shift Keying (BPSK) coding system. This approach allows transmitters to emit short signals with a low probability of collision (< 1 ms; Aspillaga, Arlinghaus, Martorell-Barceló, Follana-Berná, et al. 2021; Lennox et al. 2023). Similarly, Code Division Multiple Access (CDMA) has been employed in some acoustic telemetry systems to address code-collision challenges. For example, the Lotek MAP system, as previously assessed (see Baktoft et al. 2015), uses CDMA to enable effective simultaneous tracking of multiple tagged individuals. Regarding the measurement of chronotypes, high-resolution telemetry systems not only allow us to evaluate the chronotypes by drastically increasing the number and frequency of detections but also allow for an increase in the number of monitored individuals, thereby enabling population-level studies necessary to accurately attribute individual differences to behavioural variation (Martorell-Barceló et al. 2023, 2024).

In this study, we compiled and analysed datasets from various acoustic telemetry studies that had purposes other than the study of chronotypes. Our objective was to explore the potential of acoustic telemetry for detecting circadian-related behavioural variations and to evaluate the possibility of computing *R* scores that describe chronotypes in different species. Our specific objectives were 1) to identify species-specific characteristics that allow for effective chronotype analysis using acoustic telemetry data; 2) to evaluate various types of data (detections, depth, activity, or positions) that can be used to capture circadian-related behavioural variation, thereby improving chronotype estimation and 3) to compare *R* scores for chronotypes across several aquatic species. The results of this study enhance our understanding of circadian-related behavioural traits in wild aquatic populations and provide guidelines for designing future research to address chronotypes using acoustic telemetry.

2 | Methods

2.1 | Data Collection

We sourced telemetry datasets from various researchers across Europe and the Atlantic, including datasets retrieved through the European Tracking Network (ETN, https://www.europeantrackingnetwork.org/en; Abecasis et al. 2018) and other telemetry networks (e.g., the Lake Telemetry Network; Jarić et al. 2023). These networks aim to reinforce the collaboration among researchers and offer a more holistic understanding of animal movement patterns across varying spatial scales and species. We collected a total of 44 datasets covering 34 distinct aquatic species, including marine and freshwater species, spanning a range of habitat types (see Table S1). For datasets obtained directly from the ETN, we used the *etn* package (Huybrechts et al. 2025) developed for R software (R Core Team 2022). All datasets were based on acoustic telemetry data. When available, data from built-in sensors (depth and activity) or positioning from high-resolution telemetry systems were also included. These datasets also contained information about the body size of the tracked individuals.

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For statistical reasons, a minimum number of tracked animals is required to determine whether a species exhibits chronotypes. Consequently, datasets with fewer than seven individuals were excluded from further analyses. Although there is no strict rule on the minimum number of individuals required, our previous experience suggests that seven individuals is a reasonable threshold to obtain robust results. In one case, two datasets belonging to the same genus (*S. ferrugineus* and *S. fuscopurpureus*) were combined to form a unique dataset (*Scarus*) to achieve the minimal sample size (see Table S1), assuming that both species present similar behaviour (Pickholtz et al. 2022). The remaining datasets were visually inspected to identify the individuals with clearly defined activity-rest patterns (as shown in Figure 1B–F; Table 1). For this purpose, we examined the general activity patterns of each individual on a 3-h basis: number of detections (Figure 1A,B), activity (Figure 1C,D) and depth (Figure 1E,F). We excluded six datasets when a clear day–night pattern could not be identified (e.g., Figure 1A; see Table S1). The absence of a clear pattern in these datasets was primarily caused by a lack of data as a consequence of the experimental design, which was not conducive to collecting data for effectively estimating activity-rest patterns. This exclusion does not suggest the absence of chronotypes in these species but rather indicates that the data collection methodology used was not suitable for our specific objectives.

Each selected dataset was processed using specific time steps, chosen independently for each case based on the species' behaviour and the nature of the data: number of detections, mean step lengths between consecutive positions, depth, or activity. To select the most suitable time step for each dataset, we created temporal sequences with 5, 10 and 15-min intervals. For each specific case, we then chose the shortest time step that most accurately captured individual variation and represented the day/night cycle. We acknowledge that diel variation in receiver detection efficiency may affect detection-based metrics; however, our analysis focuses on inter-individual differences in timing, which are less likely to be confounded by this effect. This approach allowed us to adapt to the biological and methodological characteristics of each dataset (e.g., species mobility, tag type or density of receiver network), ensuring that the time resolution was appropriate. The selected time step for each dataset is detailed in Table 1.

2.2 | Fitting Hidden Semi-Markov Models

For the computation of the circadian-related behavioural traits, following Alós et al. (2017), we randomly selected data from 15 consecutive days for each individual and decomposed the individual time series into a temporal sequence of behavioural states (active vs. resting) using a hidden semi-Markov model (HSMM) approach (Guédon 2003). The HSMM was fine-tuned to the characteristics of each dataset by adjusting the initial distribution and accounting for the diurnal or nocturnal activity patterns of the species. The duration of a state in a conventional HMM follows a geometric distribution, which leads to an exponential decrease in the likelihood of remaining in the same state over time. An HSMM accommodates a wider array of state duration distributions, thereby specifically modelling the time spent in each state, which is particularly interesting for decomposing diel behaviours (Guédon 2003). Furthermore, state transitions in an HSMM take place after a variable number of time steps, as dictated by the state duration distribution. HSMMs offer a better fit for certain types of data due to their additional flexibility in modelling state durations, despite requiring more computational resources for training and analysis compared to conventional HMMs. Through this approach, we could customise the model to incorporate specific parameters for species and individuals. We applied the HSMM with the function *hsmmfit* from the package *mhsmm* (O'Connell and Højsgaard 2011) for the R software (R Core Team 2022). The final output for each individual time series was a temporal sequence of two behavioural states (active vs. rest), which was used to compute the awakening time and rest onset.

2.3 | Computation of the Circadian-Related Behavioural Traits

Based on the results of the HSMM, we assumed that a higher number of detections, higher activity, deeper depths and longer distances between positions indicated periods of activity. This assumption was needed for the computation of circadian-related behavioural traits, although their implications are addressed in subsequent sections. We categorised our datasets as diurnal if all individuals exhibited maximum activity during the day, as nocturnal if their peak activity was during the night, and as dual if containing both diurnal and nocturnal individuals. We recognise that this assumption might not perfectly capture reality, but such two-state categorisation is necessary for the computation of the circadian-related behavioural traits and is independent of the *R* scores estimation for chronotypes. We used the local sunrise and sunset data, considering their daily variations, for each acoustic tracking experiment to calculate two circadian-related behavioural traits: awakening time as the activity onset (min) and rest onset as the activity offset (min). For diurnal individuals, we defined the awakening time relative to sunrise and rest onset relative to sunset. Conversely, for nocturnal individuals, we defined the awakening time relative to sunset and rest onset relative to sunrise. Days in which the awakening time occurred after half of the daytime or rest onset past the midpoint of the nighttime were excluded from the subsequent analyses. For the diurnal individuals, we removed days with less than half the daytime of activity (activity < (sunrise—sunset) / 2). Similarly, for the nocturnal individuals, we removed days with less than half the nighttime of activity (activity < (sunset—sunrise $(n+1)$) / 2). At this stage, we excluded additional datasets in subsequent analyses due to the low number of individuals meeting the specified conditions. Finally, we considered 17 datasets from 16 freshwater and marine species in the final analyses.

2.4 | Raw Repeatability

We calculated the raw *R* as an initial approach to investigate how consistent among-individual differences are in awakening time and rest onset. Raw *R* refers to the proportion of total variance in the trait that is attributed to differences among individuals, without accounting for potential confounding factors or covariates (Nakagawa and Schielzeth 2010). For a

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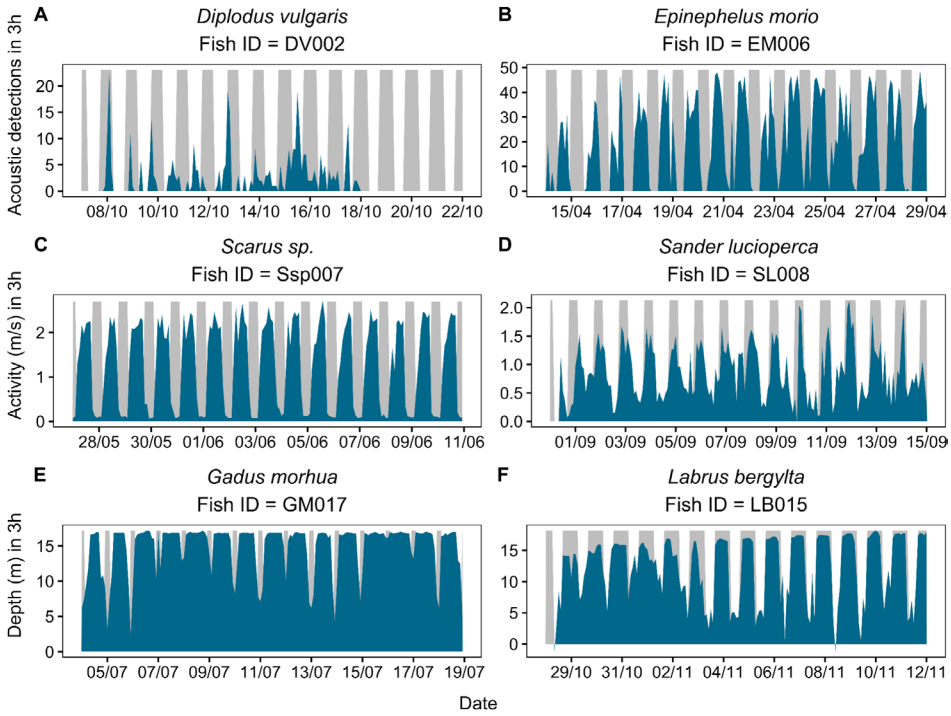

FIGURE 1 | Temporal sequence for the identification of activity-rest patterns. Examples of 3-h temporal sequences illustrating datasets with and without clear day/night patterns. The number of detections, activity and depth are shown in blue. Night-time periods are shaded in grey. The first row presents examples of acoustic detection (number of detections in 3 h): (A) Sequence without a clear day/night pattern from *Diplodus vulgaris*. (B) Sequence with a clear day/night pattern from the *Epinephelus morio*. The second row shows activity data (average m/s in 3 h): (C) Sequence with a clear day/night pattern from the *Scarus* dataset. (D) Sequence with a clear day/night pattern from *Sander lucioperca*. The third row displays depth data (average depth (m) in 3 h): (E) Sequence with a clear day/night pattern from *Gadus morhua* (GM_IMR dataset). (F) Sequence with a clear day/night pattern from *Labrus bergylta*.

specific trait, the raw *R* score was calculated as the between-individual variance V_{ind0} divided by the sum of V_{ind0} and the within-individual variance (or residual variance, V_{e0}). To properly decompose the raw phenotypic variance into between- and within-individual variances, we fitted a generalised linear mixed model (GLMM) to each dataset and circadian-related behavioural trait, using the MCMCglmm library (Hadfield 2010) built for the R software following Dingemanse and Dochtermann (2013). We fitted one GLMM to each dataset, including awakening time or rest onset as a response variable, the size of the individual as a fixed effect and the identifier (ID) of the individual as a random effect. We included the size as the unique common variable between datasets because we needed a fixed factor in order to run it. To assess the statistical significance of the *R* score, we combined the confidence intervals with the difference in the Deviance Information Criterion (DIC) between the complete GLMM and the constrained model (i.e., the model without the random effect, DIC_c). If this difference exceeded two and the confidence interval did not include zero, the *R* score was considered statistically significant (Alós et al. 2017; Harrison et al. 2015). The significance of body size (in cm) was indicated by the Markov Chain Monte Carlo *p*-value (pMCMC).

3 | Results

We computed *R* scores for the awakening time and rest onset in 17 datasets for 16 different marine and freshwater species (Table 1; Figure 2). Remarkably, 82% of datasets for awakening time and 94% for rest onset showed statistically significant *R* scores, ranging from 0.22 to 0.81 for awakening time and from 0.09 to 0.86 for rest onset. Statistically significant *R* scores were obtained for 14 datasets regarding awakening time and for 16 datasets regarding rest onset. The mean (± standard deviation) of these significant *R* scores was 0.52 ± 0.20 for awakening time and 0.43 ± 0.23 for rest onset, suggesting the presence of chronotypes across these datasets (Figure 2). The species with the highest *R* score, 0.81 [0.55–0.86], for awakening time was *Salmo trutta* (Salmonidae). The individual with the earliest awakening time (ST02) started its activity, on average, 343.75 min before sunrise, while the individual with the latest awakening time (ST03) started its activity, on average, 348 min after sunrise. The difference between these individuals in awakening time was 691.75 min (see Table S2). The species with the highest *R* score, 0.86 [0.71–0.95], for rest onset was *C. carpio*. The individual with the earliest rest onset (CC01) started its rest, on average, 207.67 min after sunset, while the individual with the latest rest onset (CC03) started its rest, on average, 544 min after sunset. This represents a difference of 336.33 min between them (see Table S2). Additionally, the species that exhibited the highest combined *R* score for both circadian-related behavioural traits was *Epinephelus morio* (Epinephelidae), 0.80 [0.72–0.87] for awakening time and 0.81 [0.76–0.87] for rest onset.

In the GLMM, we included body size as a fixed effect, as the unique common variable between datasets (Table 2). For most datasets, the effect of body size on awakening time was not

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TABLE 1 | Data used for the calculation of the *R* scores.

Species	Dataset	Data	Interval	N	Awakening time	Rest onset	DIC dif AT	DIC dif RO	Activity pattern	Size
Anguilla anguilla	AAn	Det	10	10	0.29 [0.25–0.56]	0.19 [0.12–0.38]	32	18	Nocturnal	73.1
Astacus astacus	AAs	Det	5	7	0.00 [0.00–0.42]	0.01 [0.00–0.47]	5	3	Nocturnal	52
Cyprinus carpio	CC	Pos	10	7	0.28 [0.11–0.59]	0.86 [0.71–0.95]	21	169	Diurnal	28.2
Dentex dentex	DD	Depth	5	15	0.27 [0.17–0.34]	0.21 [0.15–0.37]	43	59	Diurnal	56.8
Diplodus sargus	DS_UB	Depth	5	12	0.35 [0.25–0.53]	0.59 [0.36–0.68]	54	82	Dual	25.7
Epinephelus morio	EM	Det	10	15	0.80 [0.72–0.87]	0.81 [0.76–0.87]	256	310	Dual	54.4
Gadus morhua	GM_IMR	Depth	5	35	0.56 [0.47–0.65]	0.41 [0.27–0.46]	351	166	Diurnal	42.8
Labrus bergylta	LB	Depth	5	15	0.47 [0.39–0.72]	0.34 [0.26–0.41]	121	52	Dual	35.8
Perca fluviatilis	PF	Pos	5	7	0.00 [0.00–0.34]	0.58 [0.46–0.90]	8	91	Diurnal	36.3
Pollachius pollachius	PP	Depth	5	9	0.39 [0.26–0.52]	0.28 [0.19–0.40]	52	37	Dual	37.7
Serranus cabrilla	SCb	Det	15	8	0.00 [0.00–0.28]	0.46 [0.41–0.69]	4	46	Diurnal	15.1
Silurus glanis	SG_WUR	Depth	5	13	0.44 [0.25–0.56]	0.18 [0.11–0.32]	60	30	Dual	86.4
Sander lucioperca	SL	Act	5	11	0.40 [0.19–0.56]	0.66 [0.47–0.86]	52	127	Dual	43.8
Salmo trutta	ST	Depth	5	13	0.81 [0.55–0.86]	0.23 [0.09–0.56]	44	16	Dual	36
Scarus sp.	Scarus	Act	5	7	0.78 [0.61–0.87]	0.12 [0.06–0.31]	229	26	Diurnal	38.8
Xyrichtys novacula	XN_JSATS	Det	5	30	0.77 [0.73–0.86]	0.38 [0.24–0.44]	658	111	Diurnal	16.8
Xyrichtys novacula	XN_SUR	Det	5	14	0.61 [0.47–0.70]	0.65 [0.42–0.80]	115	109	Diurnal	18.4

Note: 'Species' refers to the scientific name of the species. 'Dataset' is the reference name of the dataset detailed in Table S1. 'Data' refers to the type of dataset (Det = detections, Pos = positions, Depth = depth and Act = activity). 'Interval' refers to the time step used to create the temporal sequences. 'N' is the number of individuals included. 'Awakening time' and 'Rest onset' indicate the respective *R* score, with 95% confidence intervals in brackets. 'Dic dif AT' and 'DIC dif RO' represent the difference between DIC and DIC_c for awakening time and rest onset, respectively. 'Activity pattern' classifies the species as diurnal, nocturnal, or dual. Lastly, 'Size' indicates the mean total length (cm) of the individuals for each dataset.

statistically significant, as indicated by wide 95% credible intervals (CI) that included zero and pMCMC values greater than 0.1 (Table 2). However, *D. sargus* (DS_UB dataset) showed a statistically significant negative effect of size on awakening time (Table 2), suggesting that larger individuals started their activity earlier than smaller individuals. Regarding rest onset, negative statistically significant effects were observed for *E. morio*, *Sander lucioperca* (Percidae), *Scarus* sp. and *X. novacula* (XN_JSATS dataset) (Table 2). This suggests that larger individuals of these species started their resting phase earlier than smaller individuals. By contrast, *L. bergylta* showed a positive statistically significant effect (Table 2), suggesting that larger individuals started their rest later than the smaller ones.

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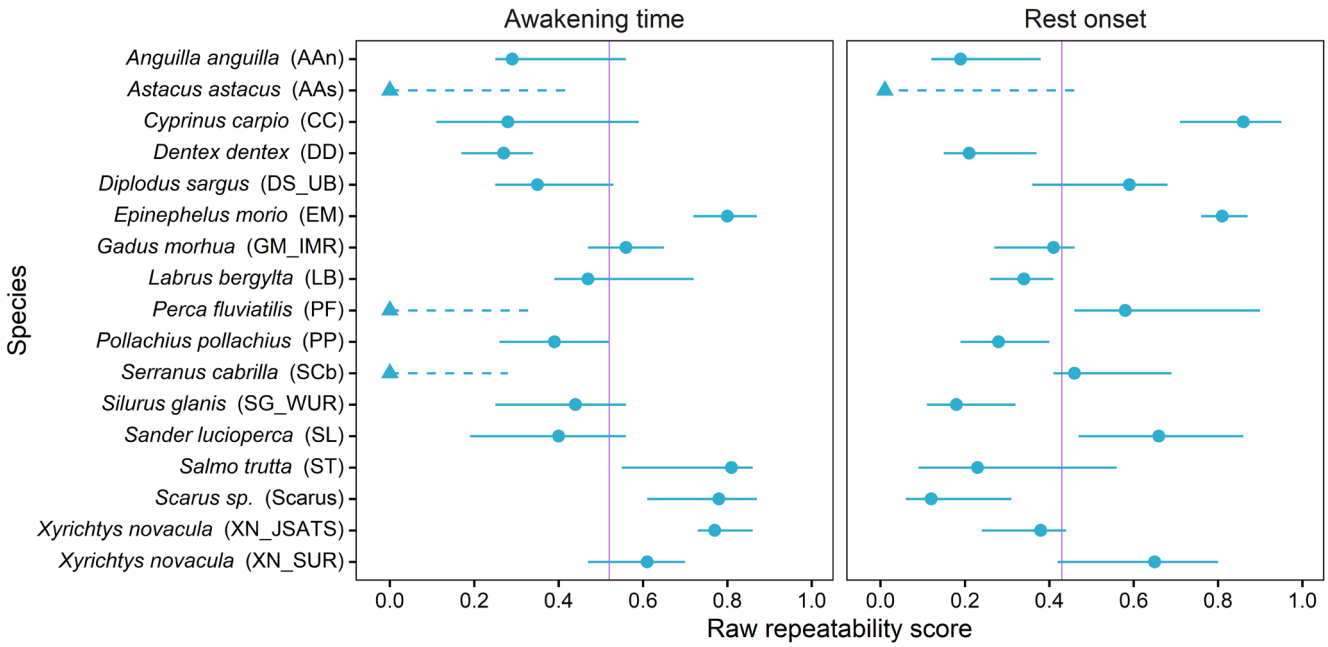

FIGURE 2 | Raw repeatability scores. The *R* scores are presented for each dataset separated by awakening time and rest onset, representing the mean (dot) and confidence intervals (CI, 2.50 and 97.50). Dots and lines indicate the statistical significance of the values: solid and dotted for statistically significant and dashed lines and triangles for non-statistically significant results. Violet vertical lines indicate the average *R* scores for significant values, 0.52 for awakening time and 0.43 for rest onset.

Overall, our analysis showed that chronotypes were present in most suitable datasets. We thus conclude that chronotypes may be a common behaviour in aquatic species in both marine and freshwater systems.

4 | Discussion

Our study provides the first comprehensive assessment of the contribution of individual variability in circadian-related behavioural traits (defining chronotypes) across a diverse range of wild marine and freshwater species, utilising acoustic telemetry data for their identification. We highlight several key findings concerning the raw *R* scores for awakening time and rest onset. We managed to calculate raw *R* scores for 17 datasets across 16 different species. Our findings suggest a potential existence of chronotypes across almost all species studied when their estimation was possible. Our findings suggest that, in addition to the already described chronotypes in *X. novacula* (Alós et al. 2017; Martorell-Barceló et al. 2024), species such as *Anguilla anguilla* (Anguillidae), *C. carpio*, *D. dentex*, *D. sargus*, *E. morio*, *Gadus morhua* (Gadidae), *L. bergylta*, *Pollachius pollachius* (Gadidae), *S. glanis*, *S. lucioperca*, *S. fuscopurpureus*, *S. ferrugineus* and *S. trutta* also exhibited consistent among-individual differences in both awakening time and rest onset, indicating the presence of chronotypes in these species. Furthermore, *P. fluviatilis* and *S. cabrilla* showed significant repeatability for rest onset, indicating potential chronotypes, although this should be confirmed through additional studies. These results also show the power of acoustic telemetry as a tool to study the presence and, in turn, ecological consequences of chronotypes. Overall, this study represents the first attempt to investigate chronotypes across different freshwater and marine species.

We determined the variation in circadian-related behavioural traits derived from HSMM fitted to a time series of acoustic telemetry data. From the data obtained via acoustic detections and depth sensors, we were unable to directly assign with certainty a high number of detections to a specific activity state (diurnal vs. nocturnal). However, making this assumption (a higher number of detections, deeper depths and longer distances between positions indicated periods of activity) is essential to enable the computation of the HSMMs, which are used to derive the awakening time and rest onset. It is important to acknowledge that this assumption may represent a potential limitation in our methodology, which future research could aim to address more directly, including whether species are diurnal or nocturnal based on their hunter or feeding behaviour instead of the number of detections. In specific cases, such as *X. novacula* due to its burying behaviour during nighttime, we are very certain that a higher number of detections reflected an increase in their activity (Alós et al. 2012). Furthermore, the small home range of this species ensures the continuous tracking of them (Aspillaga, Arlinghaus, Martorell-Barceló, Barcelo-Serra, and Alós 2021). However, in many other species, this diel pattern was less pronounced and remained more ambiguous. For example, in species like *Solea senegalensis* (Soleidae), it has been shown that a higher number of detections is associated with rest (Gandra et al. 2018). This may be due to the design of the receiver network, where fish are detected less frequently during periods of activity compared to when they are at rest and move less within the detection range of a receiver. A similar pattern is observed with depth sensor data. For instance, *G. morhua* is known to hunt actively in shallow habitats with limited receiver coverage (Olsen et al. 2012). In these species, lower detection counts or shallower depths tend to reflect periods of greater activity. Therefore, when interpreting detection and depth data within

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TABLE 2 | Results of the GLMM showing the effect of fish size.

		Awakening time				Rest onset			
Species	**Dataset**	**Post. Mean**	**l-CI**	**u-CI**	**pMCMC**	**Post. Mean**	**l-CI**	**u-CI**	**pMCMC**
Anguilla anguilla	AAn	−8.41	−25.89	3.35	0.4	−0.76	−9.70	6.46	1
Astacus astacus	AAs	2.66	−44.50	54.17	0.8	−3.75	−28.53	13.32	0.8
Cyprinus carpio	CC	−0.28	−0.84	0.53	0.2	0.03	−1.45	1.09	0.8
Dentex dentex	DD	0.69	−3.08	5.22	0.6	−0.37	−7.02	2.82	0.8
Diplodus sargus	DS_UB	**−10.31**	**−18.07**	**−3.95**	**<0.1**	−1.05	−23.36	16.29	0.6
Epinephelus morio	EM	1.03	−0.05	2.84	0.2	**−0.92**	**−1.69**	**−0.17**	**<0.1**
Gadus morhua	GM_IMR	−0.33	−4.04	3.21	1	0.05	−1.78	2.71	1
Labrus bergylta	LB	−3.50	−10.41	3.63	0.4	**6.25**	**0.00**	**17.71**	**<0.1**
Perca fluviatilis	PF	−1.16	−5.71	2.48	0.2	0.08	−8.20	7.31	0.6
Pollachius pollachius	PP	35.17	−6.30	98.83	0.4	−5.38	−47.63	58.09	0.6
Serranus cabrilla	SCb	−0.69	−3.24	1.22	0.6	−3.09	−10.94	3.82	0.6
Silurus glanis	SG_WUR	−0.12	−3.46	2.31	1	−0.98	−5.77	3.12	0.6
Sander lucioperca	SL	11.49	−66.68	56.17	0.8	**−71.93**	**−163.09**	**−9.36**	**<0.1**
Salmo trutta	ST	17.36	−17.77	53.74	0.4	−13.36	−31.09	8.96	0.2
Scarus sp.	Scarus	7.83	−6.88	18.86	0.4	**−3.41**	**−5.41**	**−2.02**	**<0.1**
Xyrichtys novacula	XN_JSATS	−7.69	−16.76	4.93	0.4	**−3.03**	**−4.40**	**−0.72**	**<0.1**
Xyrichtys novacula	XN_SUR	−0.63	−2.59	2.10	0.4	0.07	−0.08	0.28	0.4

Note: 'Species' refers to the scientific name of the species. 'Dataset' is the reference name of the dataset detailed in Table S1. 'Post.Mean' corresponds to the estimated posterior mean obtained in the GLMM. 'l-CI' is in reference to the lower 95% credible interval. 'u-CI' is in reference to the upper 95% credible interval. 'pMCMC' represents the Markov Chain Monte Carlo *p*-value. The first set of columns presents results for awakening time, and the second set for rest onset. Results are considered statistically significant if the 95% credible interval does not include zero and pMCMC is less than 0.1. Statistically significant results are highlighted in bold.

acoustic arrays to study chronotypes, it is important to carefully consider the species' biology in relation to the strengths and limitations of the receiver network.

On the other hand, acceleration sensors are designed to detect variations in fish activity (Brown et al. 2013). We investigated two datasets with this type of data, and our results showed that these species exhibited statistically significant *R* scores. *S. lucioperca* had an *R* score of 0.33 and 0.64, and *Scarus* sp. 0.74 and 0.15 for awakening time and rest onset, respectively, demonstrating that the activity sensors are very useful to detect chronotypes when individuals are continuously detected and tracked. For acoustic positioning, we computed step lengths (distances between successive positions) as an alternative activity metric. We assumed that greater distances between positions indicated high activity levels, whereas shorter distances reflected resting periods. This method was applied in two datasets, where *C. carpio* showed statistically significant *R* scores for both traits, and *P. fluviatilis* showed a statistically significant *R* score for rest onset (see Table 1). By contrast, in *Esox lucius* (Esocidae; EL_IGB dataset) and *Tinca tinca* (Tincidae; TT_IGB dataset) using the same type of data, *R* scores could not be computed due to a limited number of individuals with suitable data. Most likely reasons are long gaps in data when the individuals hide in structures and are not detectable on acoustic arrays. It is important to note that step length measurements are highly dependent on the time interval; thus, longer steps may result from less frequent detections and are also influenced by the receiver network configuration. Increasing the sample size (both in terms of individuals and time resolution, as well as enhancing the density of acoustic receivers) is crucial for determining the efficacy of this type of data in assessing chronotypes.

From the data initially received, some datasets were excluded for different reasons. Some datasets were unusable due to a low number of individuals tagged; some other datasets were excluded because day–night patterns could not be discerned with the available data, and in other cases, datasets were not considered because the HSMM did not fit (see Table S1). Although nearly half of the datasets were ultimately excluded, this does not imply that these species lack chronotypes. Instead, our results suggest that the experimental design, specifically the receiver network density, the number

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of individuals tagged and the time resolution of the tags, was inadequate for assessing chronotypes. Additionally, we should consider that in some species, the nature of the tracking data itself may not allow these day–night differences to be captured, regardless of the receiver network design, tag configuration, or other experimental parameters. Therefore, our findings underscore the need for future experiments explicitly designed to address the objective of revealing chronotypes, employing suitable experimental designs. Based on our results, we suggest that first, it is crucial to ensure that the receiver network sufficiently covers the entire home range of the tagged individuals to facilitate continuous tracking over the activity–rest cycle. Second, the temporal resolution of the data acquisition must be high enough to generate the data required to study chronotypes. And finally, enough individuals must be tagged to enable the *R* score calculation, providing robust estimates of among-individual behavioural variation. Based on our suitable datasets, we found evidence of chronotypes in almost all cases, suggesting that this behaviour may be widespread across many species.

The acoustic telemetry types of data (detections, positions, depth and activity) considered in this work to identify chronotypes displayed diverse degrees of effectiveness. However, we did not perform a species-level comparison using different types of data, as this was beyond the main objective of the present work; such an approach would be essential to properly assess the potential of each type of data, as their utility may be species-specific or even study-specific. Among the methods we evaluated, acoustic detections and acceleration sensors were the ones that most frequently yielded significant *R* estimates. Conversely, the distance between successive positions resulted in fewer significant chronotypes, implying that this technique may require additional enhancement if intended to be used to assess behaviour-related circadian traits (Table 1). This does not necessarily imply that this metric is inherently less effective, but rather that its performance may be limited under certain conditions or within a species-specific context.

For future experiments aimed at assessing chronotypes, we recommend the use of acceleration sensors, as this methodology truly reflects the individual's activity levels (Pereñíguez et al. 2022), as long as the fish can be continuously monitored over a 24-h period; in other words, it remains within the detection range. However, our results also demonstrate that acoustic detections can be useful to identify chronotypes, but it is important to note that receiver detection efficiency can vary across the diel cycle due to environmental factors such as temperature, noise, or turbidity, which may affect the reliability of detection-based metrics (Payne et al. 2010). While the use of control tags is recommended to standardise detection efficiency, this limitation is likely less critical in the context of chronotype analysis. Such studies, focused on inter-individual differences in the activity onset and offset, are less likely to be confounded by systematic variations in receiver performance, as these would typically influence all individuals similarly within a given array. Moreover, prior work in *X. novacula* using detection-based chronotype estimates has shown biologically meaningful results that were not attributable to diel fluctuations in detection efficiency (Alós et al. 2012). Nonetheless, we recognise this as a methodological limitation and encourage the use of control tags or standardisation procedures in future studies relying on detection-based metrics to assess circadian-related behavioural traits.

The *R* scores estimated in this study reveal clear chronotypes across different species. For example, in the *G. morhua* dataset, awakening times ranged from 141.87 min before sunrise to 304.33 min after sunrise, resulting in a total difference of 446.2 min between the earliest and latest risers. Similarly, for *S. lucioperca*, rest onset times ranged from 585.71 min before sunset to 5.33 min after sunset, with a total difference of 591.04 min. These examples, along with the results presented in the Table S2, indicate a continuum in awakening times, with distinct early and later risers, as well as a continuum in rest onset times, with individuals consistently starting rest earlier and individuals consistently starting to rest later. These findings support the existence of both "morning" and "evening" individuals, consistent with classic human chronotype literature (Webb and Bonnet 1978). Conversely, studies on terrestrial animal chronotypes typically focus on the spectrum of daily activity duration, defining "short-activity types" as individuals with later awakening times and earlier rest onsets, and "long-activity types" as those with earlier awakening times and later rest onsets (Martorell-Barceló et al. 2024; Maury et al. 2020; Steinmeyer et al. 2010). In this study, we underscore the need for future research to investigate the correlations between awakening time and rest onset, accurately characterise chronotypes across candidate species, and examine the biological causes and ecological consequences of among-individual variation (Martorell-Barceló et al. 2018). To generate the knowledge needed to address these pressing questions, our study highlights the invaluable role of collaborative efforts, like those fostered by the ETN and the Lake Tracking Network, in enabling large-scale, multi-species research using biotelemetry datasets in multiple systems and across multiple species. Continued collaboration and data-sharing efforts will pave the way for broader and more comprehensive analyses in the field of aquatic animal behaviour (Jarić et al. 2023; Nguyen et al. 2017).

Acknowledgements

This article is based on the work from the COST Action—The European Animal Tracking Network (CA18102), supported by COST (European Cooperation in Science and Technology). Funding was provided by the CLOCK Project (Grant No. PID2019-104940GA-I00) and the METARAOR Project (Grant No. PID2022-139349OB-I00), funded by Ministerio de Ciencia, Innovación y Universidades, Spanish Government MCIN/AEI/10.13039/501100011033/FEDER, EU. This research was conducted within the framework of activities of the Spanish Government through the "María de Maeztu Centre of Excellence" accreditation awarded to IMEDEA (CSIC-UIB) (CEX2021-001198). This work is a contribution of the joint research unit IMEDEA-LIMIA. The study utilises data and infrastructure provided by VLIZ and INBO, with funding from the Research Foundation Flanders (FWO) as part of Belgium's contribution to LifeWatch. M.M.B. received support during the analysis through an FPI predoctoral fellowship from the Direcció General d'Innovació i Recerca of the Balearic Islands Government (Ref. FPI/2167/2018). During the writing and revision of the manuscript, M.M.B. was also supported by the CodChange project, funded by The Research Council of Norway. E.A. was supported by a Vicenç Mut postdoctoral grant (ref. PD/041/2021), funded by the Government of the Balearic Islands. D.V.R. was funded by a Ramón y Cajal Contract (RYC2021-032594-I) funded by the Ministerio de Ciencia, Innovación y

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Universidades, Spanish Governmnt MCIN/AEI/10.13039/501100011033 and by the European Union NextGeneration EU/PRTR; and by a grant by the Axencia Galega de Innovación (GAIN) through the program "Consolidación e estruturación de unidades de investigación competitivas e outras accións de fomento: Proxectos de persoal investigador con traxectoria excelente. IN607D 2023/007". R.A. received funding for the Behavioural Types project through the Pact of Innovation and Research by the Leibniz-Community and via an equipment grant for the razorfish work in Mallorca via the German Ministry of Education and Research (Grant No. #033W024A). R.A. is editor of Fish and Fisheries but was not involved in the peer-review and decision-making process associated with this manuscript. M.P. was funded by the Czech National Agency for Agricultural Research (project no. QK23020002 'Pikeperch fry production, their adaptability and optimization of their stocking into open waters'). M.Ř. was supported by the Ministry of Agriculture og the Czech Republic (project no. QK21010131 "Optimization of the managment in carp punds with 1-year production cycle in terms of co-feeding methods and mass balance") Open Access funding provided by the Havforskningsinstituttet.

Data Availability Statement

Datasets used in this study are openly available via the following Zenodo repository: https://doi.org/10.5281/zenodo.17131453.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Table S1:** faf70022-sup-0001-TableS1-S2.docx. **Table S2:** faf70022-sup-0001-TableS1-S2.docx.

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