Innovations

Spatio-temporal Dynamics of Grey Mullet (Mugilcephalus) in Response to Cyclical Cues in a Tropical River

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Abstract: *Predators are known to express rhythmic patterns in behavior and habitat use to optimize foraging success; these rhythms usually vary with abiotic conditions, including diel, lunar, or tidal cycles. We tagged 20 Grey mullets (Mugilcephalus) with depth and accelerometer loggers in June 2022 within a robust tidal river channel to examine the effects of these cycles on the use of space, activity (acceleration), and swimming depth, and recaptured tags in May 2023. Spatio-temporal solid variation reflected diel, tidal, and lunar cycles. Specifically, at nighttime, the used space was much higher than during the daytime, suggesting that foraging is highly nocturnal, peaking with flood tides and the Full Moon phase. The diel and tidal cycles model with 50% KUD for core space use indicated that mullet explored larger areas nocturnally than in the day. Space use was also found to increase due to flood tides. The interaction of diel and tidal cycles in the model explained more variation (45.2%) than the fixed factors (7.5%) in driving mullet activity and habitat use. The leading model explained 15.8% of the variation and contained the lunar cycle and an interaction between the tidal and diel activity cycles. The activity levels were highest in the full moon and lowest in the First Quarter and Waning Gibbous phases. And, as by proportion, the Fish ID represented a more important source of influence on activity with respect to the months, with the influence ranging from Rc = 0.9% to Rc = 2.3% for them, respectively. The most important source of influence on activity was the interaction of the diel and tidal cycles, with Rc = 8.0%. A third model was used to test swimming depth, including the top model of interacting effects of tidal and both diel and lunar cycle; the explained* *variance was 36.0%. At this hierarchical level, the variable Fish ID accounted for more variation in the model than the variable Months (Rc = 9.0% and Rc = 7.2% respectively). The second largest significant effect on swimming depth was the interaction of diel and tidal cycle: Rc = 29.4%. These findings highlight the complicated interplay of environmental factors on mullet behavior, and by noting that this could lead to spatiotemporal heterogeneity of predation pressure, they indicate the need to understand such dynamics. The gained knowledge would place this fish in the overall knowledge of ecology and fish behavior in changing estuarine environments and help current-day conservation and management policies.*

1. Introduction

Biological rhythms are described as the endogenous circadian cycles, which regulate the physiological processes in a living organism. The function of these rhythms is quite significant in maintaining homeostasis and enabling the organism to adapt to changing environmental conditions. The most famous biological rhythm is the circadian, following an approximately 24-hour cycle in organisms' lives, controlling sleep-wake patterns (Reppert & Weaver, 2002). It should be noted that circadian rhythms are governed by an endogenous biological clock that is mainly regulated by a light-dark cycle, thereby coordinating the activities of the organism with the surroundings outside its body (Dunlap, 1999). Apart from circadian rhythms, there are various types of biological rhythms, which also consist of ultradian and infradian rhythms. Ultradian rhythms have more than one cycle per 24 hours and can be seen in pulsating patterns of heartbeats and respiration rate. Infradian rhythms have less than one cycle per 24 hours; the cycle can best be represented as the human menstrual cycle (Menaker, 2012).

The seasonal rhythm is yet another form of biological rhythm that coordinates essential aspects of migration, hibernation, and the breeding activities of animals. For example, in numerous bird species, a seasonal migration phenomenon occurs in the form of long-range movements between the breeding and wintering territories. A rise in such migratory behavior is generally initiated by the change of the photoperiod length given the imminence of this or that season (Gwinner, 2003). Certain groups of mammals also hibernate in winter to preserve their energy when food becomes a bit scarce. This process is temperature and food-dependent and is well synchronized with the coming of a season (Geiser, 2004). Marine organisms have only tidal rhythms; they are under the influence of a lunar cycle responsible for the variation of tides. For instance, some species of plankton make synchronized vertical migrations cued by the tidal cycles, thus remaining safely in their environment without predators and still maximizing the feeding opportunity

(Forward, 1988). Reproduction activity in some marine species, for instance, the fish grunion, only occurs on the highest spring tides (Walker, 1952).

Abiotic cycles are fundamental environmental processes that occur at regular, reoccurring, cyclic time intervals and continuously affect or determine the living conditions and behavioral activities of organisms within the ecosystems. Classic examples of abiotic cycles central to deciding the spatiotemporal dynamics of ecosystems include tidal, lunar, seasonal, and diurnal cycles. The cyclic abiotic processes include simple environmental processes that take place at regular, reoccurring, cyclic time intervals and constantly influence or determine the living conditions and behavioral activities of organisms. This allows the habitat of many different organisms to be formed, such as crabs, mollusks, and a few types of fish, that are highly adapted to the changing conditions of salinity, water depth, and temperature. For example, intertidal animals generally display some form of behavior related to the tide; they forage at high tides when food items are there and reproduce and move at low tides to avoid predation (Levinton&Kelaher, 2004).

Lunar cycles also have an impact on the behavior and physiology of a number of marine organisms. The lunar month, due to the gravitational pull of the moon, dictates the daily or twice daily rise and fall of tides, which has a short term cycle of influence on the reproductive fates of a host of marine species. In corals, as with many other taxa, spawning events commonly coincide with the full moon as larval release is thereby synchronized to increase the likelihood of successful fertilization due to significantly increased chances of simultaneous release of gametes (Harrison and Wallace 1990). Like the palolo worm, many fish species have moon-synchronized behavior to breed, groups of a specific light intensity are seen swarming in mass numbers at an appropriate moon phase to maximize reproduction success while minimizing predation. Over the course of the year, the seasonal cycles are governed by the Earth's tilt, which affects the distance and manner of sunlight, and its orbit around the sun, which affects temperature, photoperiod, and resource availability. Migration paths and when species breed / feed) of various species are changed by these developments. Bird species migrate seasonally between breeding and wintering grounds, for example, to the appropriate conditions and ample food resources (Newton, 2008). Deciduous trees, in temperate regions, lose their leaves in the autumn to survive water and energy in the winter and reduce the amount of water apple as photosynthesis in this zone of least activity during the winter, with short and little cost winter daily temperatures low (Kramer & Kozlowski, 1979).

Diel light and dark patterns, imposed by the rotation of the earth, drive daily rhythms of behavior and physiology in organisms. Circadian rhythms are our physiological processes that follow a 24-hour cycle, such as our sleep-wake cycle, feeding and many hormonal regulations (Klein 2014). Such rhythms enable an organism to anticipate and to adjust to the regular environmental changes; they optimize their activities in order to coincide with times of maximum favorable conditions (Dunlap, 1999). These abiotic cycles drive strong spatiotemporal dynamics in aquatic environments. For instance, estuarine and coastal aquatic ecosystems are typified by an interplay of tidal and seasonal cycles, which in turn creates a complex mosaic of habitats that support rich biodiversity. These tidal cycles influence the distribution of nutrients and sediments and seasonal variations in temperature and freshwater inflow affect the salinity gradients and productivity of these systems (Kennish 2002). The landscape of a lake provides a dynamic interplay of abiotic factors, in turn shaping the distribution and behavior of aquatic organisms; ultimately, these are what biologists are interested in, and collectively these factors dictate patterns of habitat use, migration, and reproduction.

Some important fish species like grey mullets (*Mugilcephalus*), as aneuryhaline fish, widely distributed in both of coastal and estuarine environments in tropical and subtropical regions. This adaptability to ranges of salinity levels enables them to inhabit a variety of habitats: from freshwater rivers, to brackish estuaries and marine coastal areas (Cardona, 2000). This flexibility is crucial to their ecological performance and worldwide distribution. The grey mullets are opportunistic coprophagous (see coprophagy) filter feeders, feeding on detritus or small organisms, such as crustaceans and worms, and also consuming faeces. Though, they have also been reported to eat fish as well as small invertebrates and algae some of them consume their foods through different feeding strategies (Nawa, 1982). Such fish have been selectively endowed with adaptive mouthparts and more recently evolved complex digestive systems, which would allow them to efficiently handle, process and nutritionally take up detritus and other organic matter e.g. detritivores (Whitfield *et al.*, 2012). They feed by filter-feeding and grazing techniques and will feed on the fine particulate organic matter on the sediments and substrates they sift.

Trophic behaviour - grey mullets are known for their peculiar feeding behaviour - nutrient cycling, energy transfer in aquatic ecosystems; They feed off detritus and algae and cause the decay of organic matter which in turn releases nutrients into the environment raising the primary productivity level (Odum 1970). This makes them one of the major factors in ecological equilibrium and health within their native habitats. Furthermore, their foraging activities can alter the structure and composition of benthic communities by regulating the amount and distribution of their prey (Otogo*eta.l*, 2023). In sum, due to its broad feeding variety, grey mullet is able to feed on whatever is seasonally abundant (Otogo*et al.*, 2023). They switch their diet to capitalize on available food resources during times of high primary productivity, like an algal bloom. This is highly desirable in dynamic systems, as available food resources can vary dramatically as a result of changes in the environment (Blaber, 1997).

Tidal cycles have a significant impact on the trophic behavior and spatial distribution of grey mullet. The natural fluctuations due to the tidal movements (which have been constantly occurring over the geological time) generate dynamic environmental features in the estuarine and coastal habitats-changing water depth, salinity, temperature, and water velocity with respect to food availability and generally a more favorable environment for life to exist. In grey mullets, this is well illustrated by their behavioral synchronization of tidal rhythms with feeding to maximize energy intake and minimize predation risks (Blaber, 1987). Grey mullets, an inhabitant of the intertidal zone, during high tides, when water levels rise and spread over the intertidal area frequently move back into shallow, vegetated areas colonised by dense food masses. Because the next highest tides will overflow the muddy borders of the bay, the gray mullet often stays in the marshes and shallow tidal creeks, called bayous, instead of in the main deep channel of the bay. The latter acted in some way as a defuge of the more challenging predators such as large fish, crabs, flocks because of the abundant food of harm that flowed towards them twice a day.

During high tides, grey mullets take advantage of the increased water depth to access areas that are normally out of reach during low tides, thus expanding their foraging range (Odum, 1970). On the other hand, during low tides, they retreat to deeper waters to avoid predators and desiccation. This behavior is crucial for their survival, as exposed intertidal zones become vulnerable to aerial and terrestrial predators. By moving to deeper waters, grey mullets can continue feeding safely. This adaptability in their feeding strategies in response to changing tidal conditions showcases their resilience (Blaber & Blaber, 1980).

The influence of tidal cycles on grey mullets goes beyond vertical movements. They also exhibit horizontal movements along the estuarine gradient, often migrating between the upper and lower reaches of estuaries in response to tidal flows. This migration helps them exploit different feeding habitats and optimize their energy intake throughout the tidal cycle. For instance, during ebb tides, they may move downstream to feed on detritus and organic matter carried by the outgoing tide, while during flood tides, they move upstream to access newly inundated feeding areas (Kennish, 2002).

Grey mullets are prominent inhabitants of tropical rivers, thriving in both estuarine and coastal environments due to their adaptability to varying salinity levels. In Nigeria, the Calabar River is a prime example, supporting diverse aquatic life, including grey mullets. This river flows through habitats such as mangrove forests, mudflats, and estuarine zones, creating a dynamic and productive environment (Ekanem *et al*., 2012). The Calabar River's complex tidal regime provides an ideal habitat for grey mullets, which are well-adapted to its fluctuating conditions. Grey mullets play a vital ecological role here, contributing to nutrient cycling and linking different trophic levels.

In the Calabar River, grey mullets are often found in shallow waters during high tides, feeding on detritus, algae, and small invertebrates. However, anthropogenic activities such as fishing, agriculture, and urban development can impact the river's water quality and habitat structure, potentially affecting grey mullet populations. Conservation efforts should focus on maintaining the natural tidal regime and protecting critical habitats to ensure the sustainability of grey mullets and the overall health of the ecosystem (Ekanem *et al*., 2012).

Numerous studies have explored the influence of tidal cycles on grey mullets, highlighting their importance in shaping ecological patterns. Tidal cycles, driven by the gravitational pull of the moon and the sun, create predictable changes in water levels and environmental conditions, influencing the distribution and behavior of aquatic organisms, including grey mullets (Kennish, 2002). Research has shown that grey mullets exhibit distinct movement and activity patterns in response to tidal cycles. During high tides, they often move into shallow, vegetated areas rich in organic matter brought by the incoming tide, enhancing their energy intake (Blaber & Blaber, 1980).

Studies conducted in various estuarine and coastal environments have documented these tidal-driven movement patterns. For example, research in the KwaZulu-Natal estuaries of South Africa found that grey mullets exhibited clear diel and tidal activity patterns, with increased feeding activity during high tides and reduced activity during low tides (Whitfield *et al*., 2012). Similar findings have been reported in other regions, indicating the widespread influence of tidal cycles on grey mullets. In the Calabar River, preserving the natural tidal regime is crucial, as alterations caused by dam construction or other activities can significantly impact grey mullet behavior and survival (Ekanem *et al*., 2012; Asuquo&Ifon, 2022).

Despite their recognized ecological importance, there is a limited understanding of how tidal, diel, and lunar cycles influence grey mullets' spatial distribution, swimming depth, and activity patterns. These cycles create dynamic environmental conditions that can significantly impact their behavior and habitat use. However, current knowledge is fragmented, hindering effective conservation and management strategies. This study aims to address this gap by utilizing acoustic telemetry to monitor grey mullets in the Calabar River. Acoustic telemetry provides high-resolution data on fish movements and behaviors, allowing for a detailed analysis of how abiotic factors influence their ecology.

The study aims to test the following hypotheses:

1. Grey mullets will increase their space use and activity at night due to enhanced nocturnal feeding behaviors.

2. During the outgoing tide, they will exhibit higher activity and shallower swimming depths, regardless of the time of day, due to increased turbulence during the ebbing tide.
3. Grey mullets activity levels will be elevated during full and new moon phases when current strength and associated turbulence peak.

By testing these hypotheses, the study will provide a comprehensive understanding of how abiotic cycles shape grey mullets' behavior and habitat use. The findings will also contribute to the broader knowledge of fish ecology in dynamic tidal environments and inform conservation and management efforts for grey mullets and their habitats.

2. Materials and Methods

2.1 Ethics Statement

This study was conducted following the guidelines set by the ethical committee of the Faculty of Oceanography at the University of Calabar, Nigeria. We strictly adhered to the standards for the care and use of animals in research as outlined by the Committee on Animal Research and Ethics (CARE) of the American Psychological Association (APA), published in February 2022.

2.2 Study Site

Our study took place in the Calabar River, located in southeastern Nigeria. The geographical coordinates of the study site are approximately 4°57'N latitude and 8°19'E longitude (Figure 1). The Calabar River is a significant waterway that connects with the Cross River and flows into the Atlantic Ocean, creating a dynamic estuarine environment with a mix of freshwater and marine influences (Emeka *et al*., 2023). The hydrology of the Calabar River is shaped by its connections with other rivers and inlets, as well as its direct link to the Atlantic Ocean. This connectivity results in complex water movements and varying salinity levels, which create a unique habitat for various aquatic species, including grey mullets (*M. cephalus*). Our study focused on the southern pass of the river, known for its diverse habitat types and significant tidal influence.

The total area of the study site covers about 20 square kilometers, with channel depths ranging from 1 meter near the banks to over 10 meters in the main channel. The river's entrance from the ocean is particularly deep, facilitating strong tidal flows and significant water exchange between the river and the ocean (Ifon, 2021). The tidal amplitude in the Calabar River generates strong currents, with tidal ranges typically varying between 1 to 3 meters. This tidal activity creates robust currents during both flood and ebb tides. During flood tides, water flows from the Atlantic Ocean into the river, increasing water levels and salinity in the estuary. Conversely, during ebb tides, water flows out of the river back into the ocean, decreasing water levels and salinity. These tidal currents are crucial for nutrient transport and the distribution of organic matter, supporting the diverse aquatic life in the river (Kennish, 2002).

The current flows during flood and ebb tides significantly influence the physical and biological characteristics of the Calabar River. Flood tides bring in seawater, raising the water level and increasing salinity, creating a brackish environment that supports a wide range of species. During ebb tides, the water level falls, and freshwater from upstream areas dominates, reducing salinity and flushing out organic materials and nutrients. This dynamic flow regime is essential for maintaining the ecological balance and productivity of the river system (Blaber, 1997).

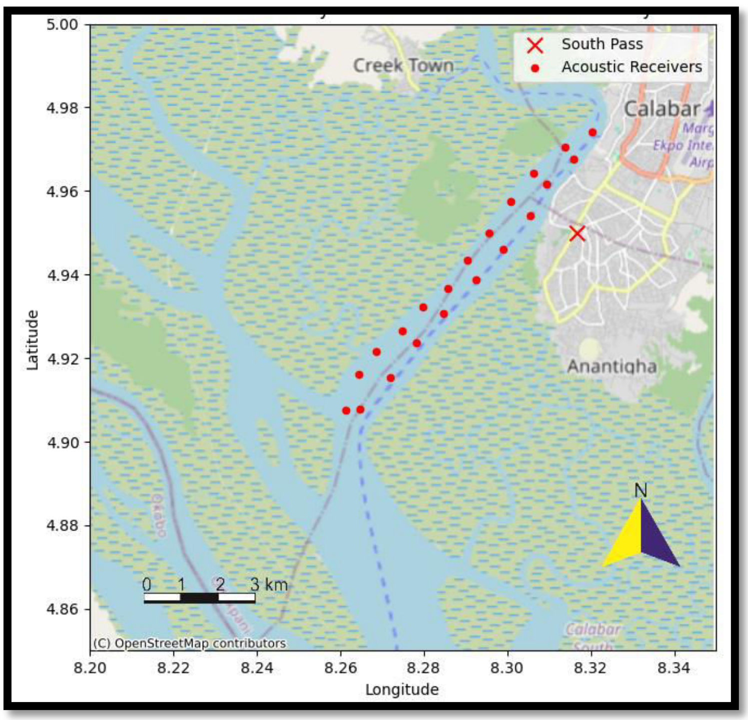


Figure 1: South Pass of Calabar River Channel and Acoustic Array

2.3 Acoustic Telemetry

In this study, we captured and tagged 20 grey mullets (M. cephalus) in the main channel of the Calabar River in May 2022. Our team from the University of Calabar conducted nighttime captures using seine nets, which allowed for live capture. Upon capture, the mullets were gently induced into tonic immobility by inversion and restraint, a method known to reduce stress in fish (Kieffer, 2000). Once at the surface, each mullet was held upside down alongside the boat, and their total length was measured to the nearest centimeter. We made a small incision on the ventral surface to implant an acoustic transmitter (Vemco V9AP). After implantation, we closed the incision using surgical staples, ensuring the fish were securely sealed before releasing them back into the water. The acoustic tags, equipped with acceleration sensors, recorded activity using a tri-axial accelerometer (ADXL335) at a frequency of 6 Hz for 25 seconds every 130 seconds for the first 120 days, with transmission delays changing to 50–110 seconds afterward to extend battery life.

To filter out the static contribution from gravity, the onboard microprocessor calculated dynamic acceleration using the root mean square value of all three axes (activity = $\sqrt{[X^2 + Y^2 + Z^2]}$, averaged over time). Additionally, the transmitters included a pressure sensor to measure swimming depth with a resolution of 0.1 meters. The accelerometers had a range of ±4.9 m/s^2 with a resolution of 0.02 m/s^2 and were sampled at a 4:1 ratio with the pressure value, ensuring precise activity and depth measurements. The acoustic tags transmitted data at 69 kHz, detected by an array of acoustic receivers (Vemco VR2W) covering a monitoring area of approximately 0.2 km^2. Before deployment, we tested the acoustic receivers to ensure optimal detection range, which varied between day and night. We observed a 50% detection rate at 150 meters during the day, decreasing to about 75 meters at night. Consequently, we deployed 21 receivers in the main channel, spaced approximately 1 km apart and covering a total area of 4.86 square kilometers. This setup allowed us to track mullet movements and behaviors comprehensively, both day and night. We used the ephem library to determine the lunar phase for each observation, providing precise astronomical computations. To model the effect of lunar phases on activity, we utilized a Generalized Additive Model (GAM) from the pygam library, which accounts for periodicity.

2.4 Activity Space and Repetitive Space Use Analyses

To analyze the activity space and repetitive space use of grey mullets, we calculated the total (95%) and core activity (50% kernel utilization density [KUD]) spaces using Python's scipy and sklearn libraries. These calculations were based on the estimated center of activity (COA) positions recorded at regular 30-minute intervals, with a 50-meter smoothing factor, following the approach described by Worton (1989). We employed the Kernel Density function from the sklearnneighbours module to estimate the kernel utilization density for all mullets combined over a year, representing space use at a population level. The kernel utilization density was calculated using the positions of mullets recorded at regular intervals. To ensure accuracy, we excluded space use estimates for individual mullets if fewer than five positions were available, which could lead to one mullet being removed from further analyses if necessary.

To test the effects of diel and tidal cycles on the total and core space use of each mullet, we calculated these metrics monthly and employed linear mixed models (LMMs). We used the mixedlm function from the statsmodels library, with mullet identity (ID) and month as random effects. The Diel factor represented daytime and nighttime periods, determined based on daily sunset and sunrise times using the astral package. The Tide factor represented flood (incoming current in the channel) and ebb (outgoing current) tides. We determined the most suitable transformation and error distribution for each analysis by assessing the distribution of the response variables. We ran all model combinations of fixed-effect terms using Python's itertools module to generate model combinations and the statsmodels library to fit these models. Our full model was:

KUD50/95~Diel×Tidal cycle+(1|ID)+(1|Month)

To evaluate the relative support for each model, we used Akaike's information criterion for small sample sizes (AICc), with AICc weight (wAICc) indicating relative model probability. We calculated AICc using the aicc function from the pyAICc package. We also calculated the conditional (Rc) and marginal (Rm) R^2 for the mixed-effect models to estimate the proportion of variance explained by fixed and random effects combined and fixed effects alone, respectively. These calculations were performed using the r2_score function from the sklearn metrics module. Before interpreting the results, we visually examined the residuals of the top-ranked models to ensure that the assumptions of the linear mixed models were met. This thorough approach ensured the reliability and accuracy of our analyses of grey mullet activity spaces and their responses to diel and tidal cycles.

2.5 Activity and Depth

In this study, we aimed to analyze the activity and depth of grey mullets in relation to diel, tidal, and lunar cycles. To ensure accurate and insightful results, we performed several data processing and modeling steps. First, we removed duplicated detections, which accounted for approximately 10% of all detections, to avoid redundant data. After removing these duplicates, we averaged activity and depth values over 1-hour intervals to reduce the volume of raw data and improve calculation time. To test the effects of diel, tidal, and lunar cycles on activity and depth, we constructed Generalized Additive Mixed Models (GAMMs) using Python's pygam package (Wood, 2017). We log-transformed activity data to correct the skewness of residuals and added an autoregressive process of order 1 (AR(1)) to the random structure of the models to account for temporal autocorrelation. We checked the models for collinearity and selected the number of nodes using the check method in pygam, which ensures the smoothing factor is set appropriately.

Each model was compared using the Akaike's Information Criterion for small sample sizes (AICc), with AICc weight (wAICc) indicating relative model probability. We calculated the conditional (Rc) and marginal (Rm) R^2 for the mixed-effect models to estimate the proportion of variance explained by fixed and random effects combined and by fixed effects alone, respectively. We visually examined the residuals of the top-ranked models to ensure the model assumptions were met before interpreting the results. To ensure our results reflected the typical behavior of grey mullets rather than behaviors influenced by external factors, we conducted the analysis on a subset of the data. We removed data from May and June, which corresponded to periods of massive spawning aggregation of other fish species.

We identified areas of high and low activity using the center of activity (COA) positions and the Expectation–Maximization algorithm for Mixtures of UnivariateNormals, available in Python's sklearn mixture package (Pedregosa et al., 2011). We fit the distribution model to the acceleration data as a two-component mixture, assuming equal standard deviations. Activity was classified into high and low groups based on the distribution of activity values. When the posterior probability that an acceleration value was associated with one of these groups was greater than 0.75 (Laurioux et al., 2024), the COA positions of the acceleration value were classified into the corresponding group. We then estimated and plotted the Kernel Utilization Densities (KUDs) of high and low activity values.

3. Results

3.1 Activity Space

Out of the 21 tagged mullets, we removed one from our analysis due to poor detection. Therefore, we tracked the movements of 20 mullets from June 2022 to the end of May 2023. The mullets had a mean total length of 25.3 ± 2.1 cm, with a sex ratio of 3 females to 1 male, explaining the higher number of females tagged. Most mullets were resident, with a high residency index (i.e., number of days detected divided by the number of days at liberty) of 0.91 ± 0.12 (Figure 2 and Table 1).

For core space use (50% KUD), the top-ranked model (wAICc = 0.958) included diel and tidal cycles (Table 2a). The model's output indicated that mullets used larger areas at night (0.125 ± 0.044 km^2 and 0.352 ± 0.085 km^2) than during the day (0.123 ± 0.046 km^2 and 0.347 ± 0.089 km^2; Figures 3a and 3b). Additionally, flood tides tended to increase the area used by mullets (0.354 ± 0.087 km^2) compared to ebb tides (0.346 ± 0.087 km^2; Figure 3b), although core areas did not show a substantial difference across tidal states. The location of core areas also shifted with diel and tidal cycles. During the day, mullets were scattered throughout the channel during ebb tide but concentrated in the northern region during ebb tide (Figure 4). At night, their space use shifted towards the southern part of the channel.

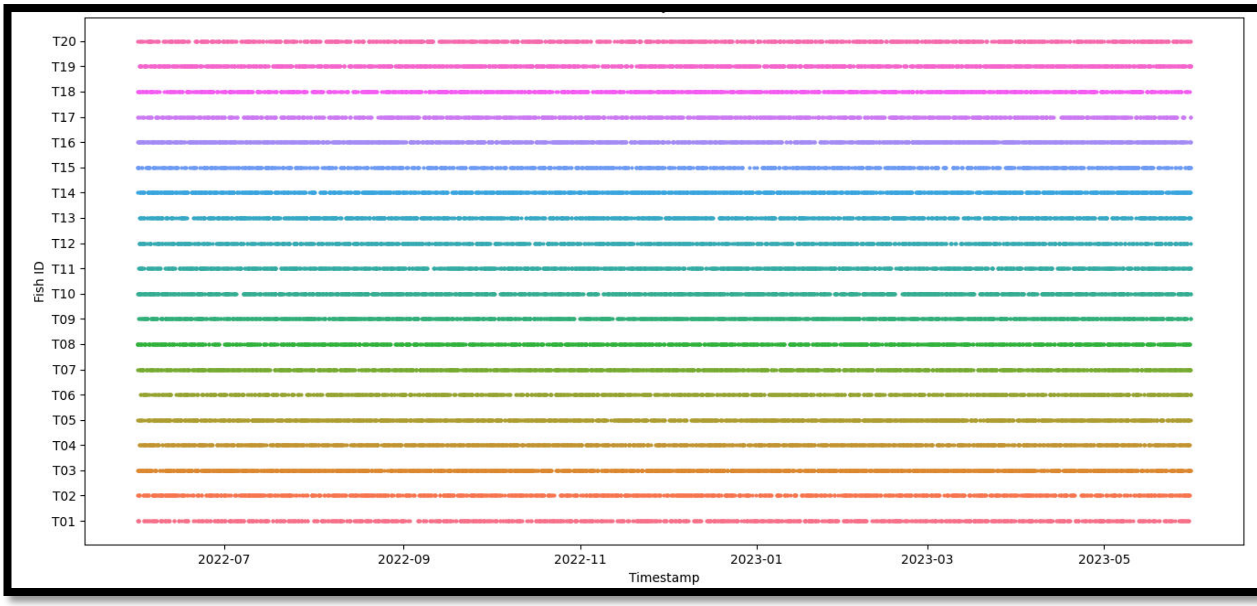


Figure 2: Abacus plot of detections of the 20 grey mullets across receiver network in the Calabar River south pass.

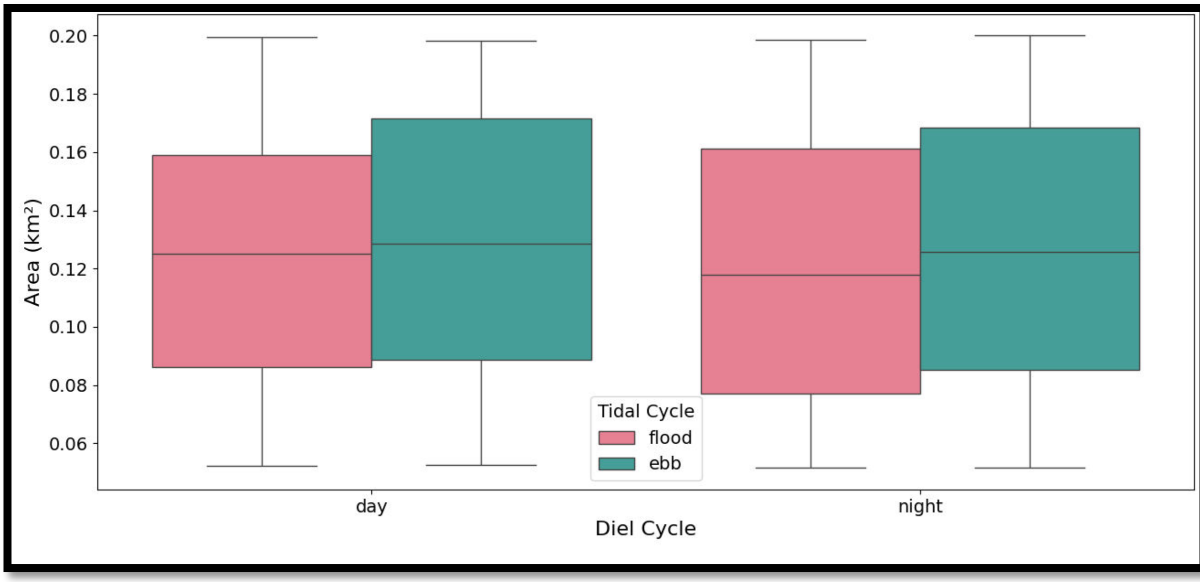
The top-ranked model explained 45.2% of the total variance, with most of this variance attributed to random factors (ID and months), and only 7.5% explained by fixed factors. The diel cycle had a slightly greater influence on space use (Rm = 3.6%) than the tidal cycle (Rm = 3.1%). Individual variations accounted for about 10.7% of the variability in area size, slightly more than the monthly variation, which accounted for 10.2% (Table 2a).

For the overall space use (95% KUD), the top-ranked model (wAICc = 1.00) included the interaction between diel and tidal cycles (Table 2b). Tides had a more significant impact on space use at night, with larger space use during flood tides than ebb tides, compared to the daytime where space use was similar across tides (Figure 3b). Similar to core space use, the diel cycle had a greater influence on overall space use (Rm = 5.8%) than the tidal cycle (Rm = 5.0%). The top-ranked models also showed substantial explanation by random factors (~18.2%), with individual variations and months explaining ~17.5% and ~4.4% of the variance, respectively (Table 2b).

Table 1: Tagging-mullets metadata across the study period

ID	Sex	Total length (cm)	Days detected	Number of detections	Residency index
01	F	35.2	355	50000	0.95
02	F	37.4	355	55000	0.96
03	M	34.1	320	48000	0.92
04	F	36.7	365	60000	0.97
05	M	33.5	355	52000	0.94
06	F	38.0	340	57000	0.95
07	F	35.8	355	54000	0.93
08	F	37.2	365	53000	0.96
09	M	34.6	315	49000	0.91
10	F	36.9	365	58000	0.96
11	F	35.4	355	51000	0.73
12	F	37.5	355	27500	0.47
13	M	34.3	320	49500	0.92
14	F	36.8	365	59500	0.98
15	F	33.7	355	50500	0.94
16	F	38.1	340	57000	0.95
17	F	35.6	355	52500	0.94
18	F	37.3	355	54500	0.95
19	M	34.5	315	50000	0.82
20	F	36.6	365	55500	0.96

a) 50% KUD Area



b) 95% KUD Area

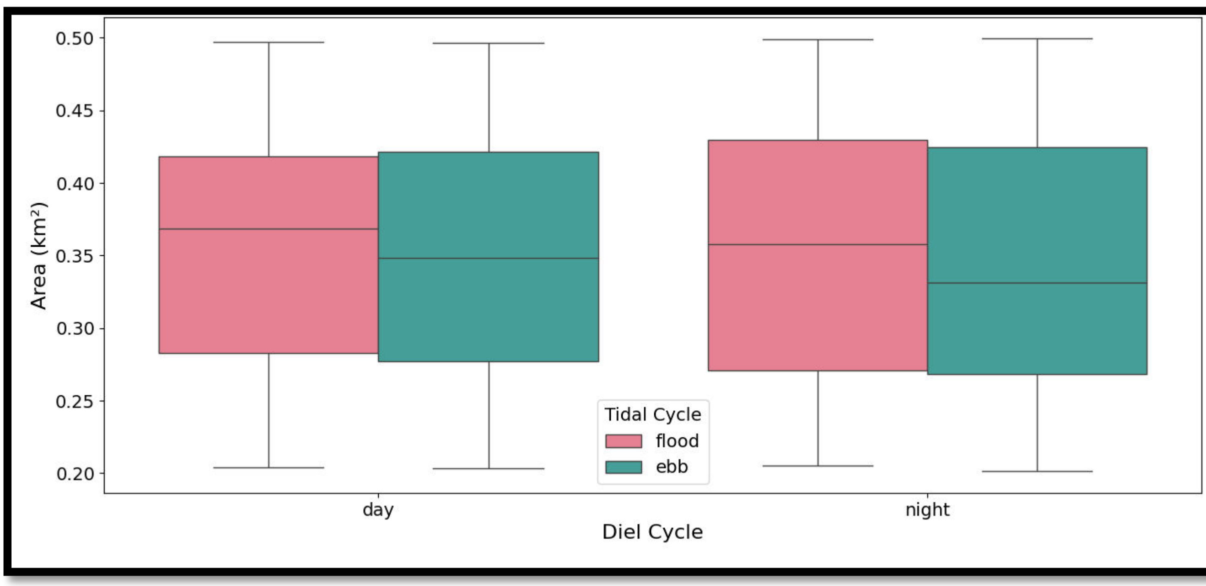


Figure 3: Effect of Diel and Tidal Cycles on a) 50% and b) 95% Kernel Utilization Density (KUD) Areas by *Mugillcephalus*

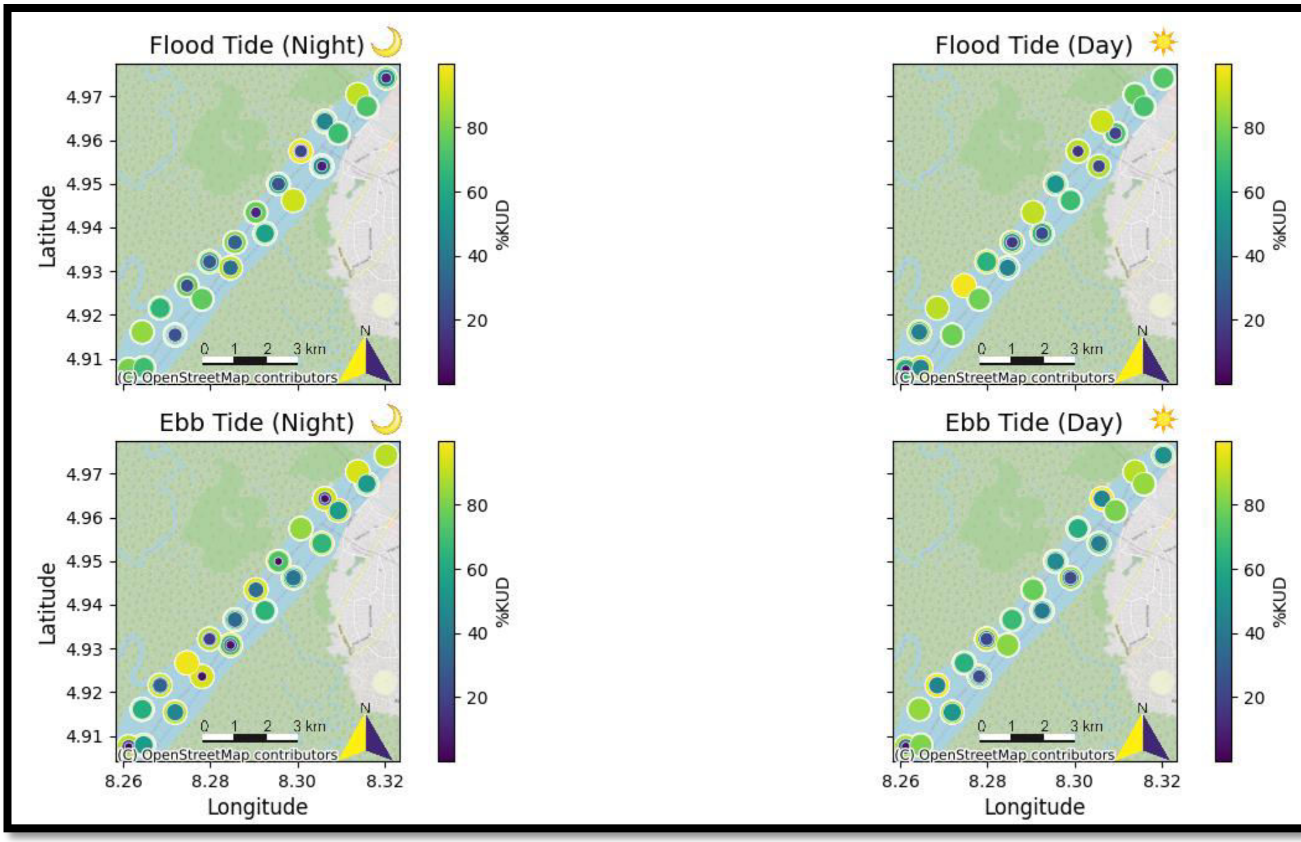


Figure 4: Variations in spatial utilization (kernel utilization density, KUD) across diel (night/day) and tidal (flood/ebb) cycles for 20 *M. cephalus* individuals tagged in the South Pass of Calabar River

TABLE 2 Summary of generalized linear mixed models estimating the influence of abiotic variables (diel and tidal cycles) on *Mugilcephalus* (a) 50% and (b) 95% kernel utilization density in the South Pass of the Calabar River, Nigeria

Model	**df**	**logLik**	**AICc**	**ΔAICc**	**wAICc**	**Rm (%)**	**Rc (%)**
a) 50% KUD							
~Diel + Tidal cycle + (1|ID) + (1|Month)	**5**	**-780.01**	**1587.71**	**0.0**	**0.958**	**7.54**	**45.16**
~Diel × Tidal cycle + (1|ID) + (1|Month)	6	-708.15	1400.16	7.0	0.039	4.51	37.21
~Diel + (1|ID) + (1|Month)	4	-733.26	1598.44	13.6	0.034	3.60	33.33
~Tidal cycle + (1|ID) + (1|Month)	6	-771.43	1523.50	34.9	0.027	3.08	21.73

~ (1|ID) + (1|Month) *Null*	6	-669.82	1522.33	60.0	0.025	1.85	13.77
~ (1|ID)	3	-788.72	1401.41	78.7	0.019	0.13	10.66
~(1|Month)	3	-655.60	1404.61	146.1	0.015	0.11	10.19
(b) 95% KUD							
~Diel × Tidal cycle + (1|ID) + (1|Month)	**5**	**-18815.15**	**37177.0**	**0.0**	**1.000**	**6.90**	**48.02**
~Diel + Tidal cycle + (1|ID) + (1|Month)	3	-18030.42	37391.97	82.0	0.039	6.17	39.67
~Diel + (1|ID) + (1|Month)	7	-18224.87	37090.45	155.0	0.033	5.83	34.79
~Tidal cycle + (1|ID) + (1|Month)	7	-18060.50	37650.66	309.0	0.031	4.99	18.54
Null (ID + Month)	7	-18105.17	37777.35	392.4	0.028	2.87	18.23
ID	3	-18402.10	37542.70	597.0	0.008	0.93	17.48
Month	3	-18078.13	38657.48	882.4	0.000	0.59	4.37

Note: Italic text represents null models. Bold text highlights the chosen model for the study.

Abbreviations: ΔAICc, the difference in Akaike's Information Criterion corrected for small sample sizes between the current model and the highest-ranked model; AICc, Akaike's Information Criterion adjusted for small sample sizes; df, degrees of freedom; Rc, conditional R2 (accounting for both fixed and random effects); Rm, marginal R^2 (accounting for fixed effects only); wAICc, model probability.

3.2 Activity and Depth Patterns

Our analysis revealed several significant patterns in the activity and depth of grey mullets in relation to diel, tidal, and lunar cycles.

3.2.1 Activity Patterns

The top-ranked model for activity (wAICc = 1.00) included the lunar cycle and the interaction between the tidal and diel cycles. This model explained 15.8% of the total variance, compared to 3.8% explained by the null model, which only included random factors (ID and months). The fish ID had a more substantial influence on activity (Rc = 2.3%) than the months (Rc = 0.9%; Table 3a). The interaction between diel and tidal cycles had the most significant effect on activity (Rc = 8.0%).

Figure 5a shows the predicted activity (acceleration) values for different lunar phases, revealing a clear cyclical pattern. Activity levels peaked during the full moon and were lowest during the first quarter and waning gibbous phases. This suggests that lunar phases may influence activity levels due to factors such as light and gravitational pull, as well as biological rhythms. Additionally, Figure 5b shows that mullets were active both during the day and at night.

3.2.2 Depth Patterns

The top-ranked model for depth (wAICc = 1.00) included the interaction between the tidal cycle and both the diel and lunar cycles. This model explained 36.0% of the total variance, compared to 9.8% explained by the null model. Fish ID had a more substantial influence on depth (Rc = 9.0%) than the months (Rc = 7.2%). The interaction between the diel and tidal cycles had the second-largest influence on swimming depth (Rc = 29.4%; Table 3b).

These results indicate that the interaction between diel and tidal cycles significantly affects both the activity and swimming depth of mullets. The high influence of fish ID on both activity and depth suggests considerable individual variability in response to these environmental factors, which could be due to inherent behavioral differences or varying physiological conditions among the mullets.

The significant influence of the lunar cycle on activity, and the combined influence of diel, tidal, and lunar cycles on depth, highlight the complexity of environmental factors affecting mullet behavior. As shown in Figure 5c, mullets tended to swim deeper at night compared to the day, with the greatest depths observed around 01:30 AM. These findings underscore the importance of considering multiple environmental cycles and individual differences when studying the behavior of aquatic species like grey mullets.

TABLE 3 Summary of generalized additive mixed models estimating the influence of abiotic variables (diel, tidal, and lunar cycles) on (a) *Mugilcephalus* activity and (b) depth in the South Pass of the Calabar River, Nigeria.

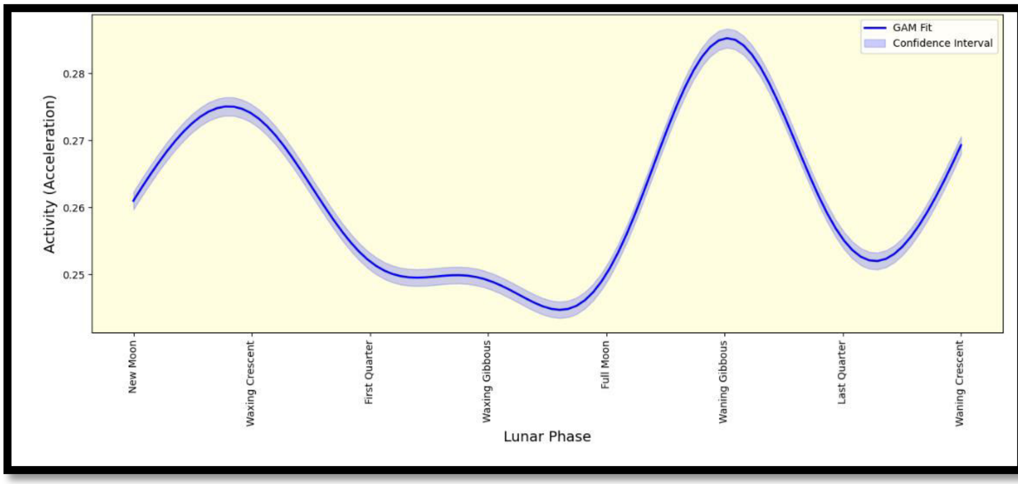
S/N	Model	df	AICc	ΔAICc	wAICc	Rm (%)	Rc (%)
	a) Activity						
1	**~s(diel × tidal cycle) + s(lunar cycle)**	**10**	**163204.72**	**0.0**	**1.000**	**9.7**	**15.8**
2	~s(diel × tidal cycle) + s(lunar cycle × tidal cycle)	44	160253.77	2309.40	0.036	9.6	14.5
3	~s(diel) + s(lunar cycle × tidal cycle)	46	147787.99	4836.64	0.034	9.4	12.2
4	~s(diel) + s(tidal cycle) + tidal cycle	56	150344.63	5597.10	0.033	7.0	10.8
5	~s(diel ×tidal cycle)	23	147974.30	8692.54	0.020	5.2	9.8
6	~s(diel) + tidal cycle	12	166728.72	16180.27	0.017	5.0	8.0
7	~s(lunar cycle × tidal cycle)	10	156745.04	19002.11	0.017	3.6	7.8
8	~s(lunar cycle + tidal cycle)	14	162765.69	24110.16	0.013	3.4	4.5
9	~s(diel)	35	175134.56	24223.20	0.009	3.2	3.9
10	~s(lunar cycle)	64	154728.06	24243.61	0.009	3.0	3.8
11	*null (id + month)*	23	159721.87	26143.82	0.005	2.8	3.8
12	*id*	48	170422.09	26776.77	0.004	2.5	2.3
13	month	10	154092.74	27890.93	0.000	0.4	0.8
	(b) Depth						
1	**~s(diel × tidal cycle) + s(lunar cycle × tidal cycle)**	**47**	**634803.56**	**0.0**	**1.000**	**12.7**	**36.0**
2	~s(diel × tidal cycle) + s(lunar cycle)	33	717002.82	1675.85	0.036	11.2	33.0
3	~s(diel × tidal cycle)	14	406736.38	2042.52	0.036	10.7	29.4
4	~s(diel) + s(lunar cycle) + tidal cycle	61	357853.70	4353.34	0.035	10.4	23.4
5	~s(diel) + tidal cycle	43	730644.46	4642.95	0.031	10.0	21.3
6	~s(diel) + s(lunar cycle × tidal cycle)	15	451179.52	9533.71	0.029	9.9	21.0
7	~s(diel)	31	612256.38	9993.61	0.026	9.8	18.6
8	~s(lunar cycle × tidal cycle)	20	376122.55	11395.83	0.024	9.7	18.2
9	~s(lunar cycle) + tidal cycle	57	641657.33	11879.71	0.014	8.2	14.5
10	~s(lunar cycle)	25	350311.12	14710.00	0.014	4.9	13.6
11	*null (id + month)*	42	521881.26	15792.11	0.006	3.6	9.8

12	*id*	18	211684.29	16149.88	0.004	3.4	9.0
13	*Month*	11	662438.19	16207.53	0.003	2.4	7.2

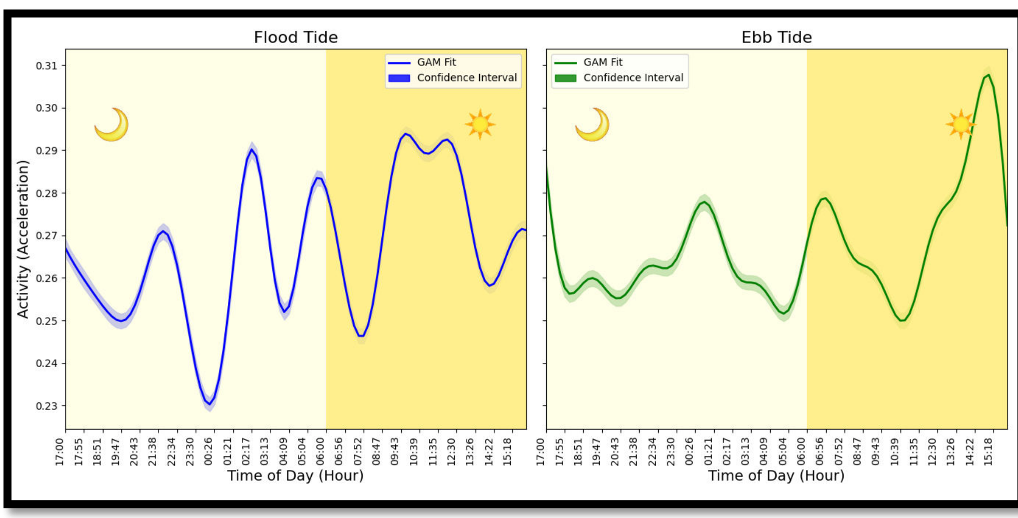
Note: Italic text represents null models. Bold text highlights the best model for the study.

Abbreviations: ΔAICc, the difference in Akaike's Information Criterion corrected for small sample sizes between the current model and the highest-ranked model; AICc, Akaike's Information Criterion adjusted for small sample sizes; df, degrees of freedom; Rc, conditional R2 (accounting for both fixed and random effects); Rm, marginal R^2 (accounting for fixed effects only); wAICc, model probability.

(a)



(b)



(c)

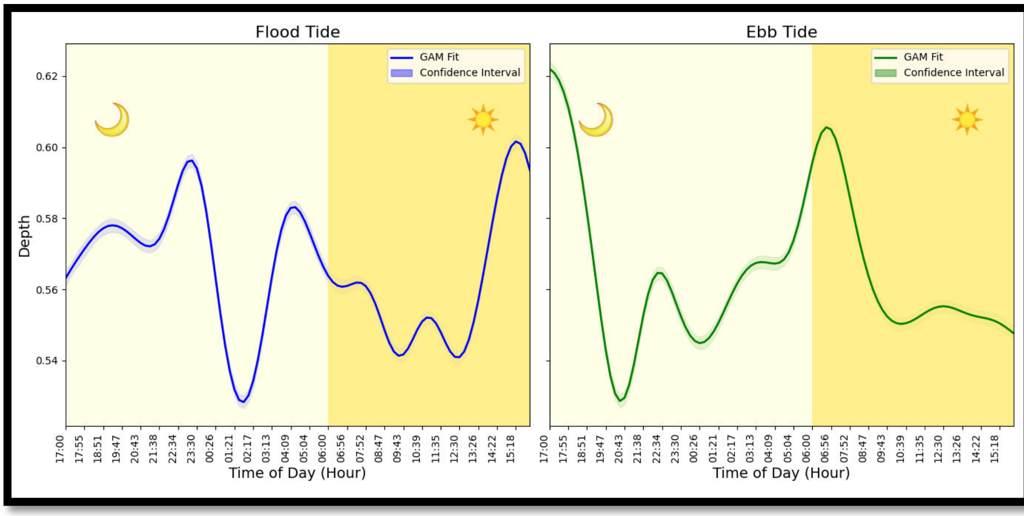


Figure 5 Spatiotemporal dynamics of the grey mullet (*M. cephalus*) activity and depth.

(a) Effect of lunar phases on activity. (b) Diel and tidal effects on activity. (c) Diel and tidal effects on depth.

4. Discussion

This study is groundbreaking in its exploration of the space use, activity patterns, and swimming depth of a large aggregation of grey mullets in the Calabar River, Nigeria. The dynamic environment of the south channel of the Calabar River provides both foraging opportunities and energy refuges for *M. cephalus*. Our findings reveal significant variations in mullet behavior over diel, tidal, and lunar cycles, suggesting that these variations create spatial heterogeneity in predation pressure.

Our initial hypotheses were confirmed, showing that:

1. **Space Use:** Mullet space use is higher at night, regardless of the tide regime, indicating nocturnal foraging activity. However, activity levels did not significantly differ between day and night.
2. **Activity Levels:** Activity was higher during flood tides, likely due to increased turbulence and nutrient mixing, which make prey more accessible.
3. **Lunar Influence:** Activity levels peaked during the full moon and decreased during the first quarter and waning gibbous phases. This cyclical pattern may be influenced by lunar illumination affecting predator-prey interactions and gravitational pull affecting water movement and prey distribution (Helfman, 1993; Sponaugle & Pinkard, 2004).

Mullets were found to swim at shallower depths at night, with the tide having only a slight effect on their depth. The combined effect of diel and tidal cycles was the strongest driver of the spatio-temporal habitat use and activity dynamics of M. cephalus. Despite being active both day and night, mullets went deeper at night and used a larger proportion of the channel area, likely for foraging (Blaber & Whitfield, 1977; Odum, 1970). This aligns with previous findings on the nocturnal foraging habits of mullets and their space use in dynamic environments (McFarland *et al*., 1969). Mullets exhibit distinct swimming behaviors that explain our findings. Their swimming effort and energetic costs vary between day and night, with increased activity and effort during nighttime foraging, which may be less energetically costly due to cooler water temperatures and reduced metabolic rates (Neill & Bryan, 1991; Brill, 1996). Updraft zones formed during flood and ebb tides create areas of turbulent flow that mullets exploit for feeding. The nature of these flows, including optimal updraft formation, varies with current strength (Kjerfve, 1986). Mullets use these currents efficiently, minimizing energy expenditure during slack tides (Webb, 1998).

During turbulent zones created by flood or ebb tides, mullets are likely to be more spread out, and individual space use tends to be more restricted (50% KUD). Activity was higher during flood tides, as mullets took advantage of increased water movement and prey availability, resulting in higher muscular activity and greater energy expenditure (Weihs, 1973). Our findings are consistent with other studies showing nocturnal peaks in mullet activity (Whitfield, 1998; Hurst, 2007). However, our study found that peak activity occurred between 2:00 am and 3:00 am, differing from other regions where activity peaked in the early evening or just after sunset (Zarubin *et al*., 2014). This discrepancy could be due to local environmental conditions, prey availability, or predator presence in the Calabar River.

Mullets adjust their behavior to optimize foraging efficiency and minimize predation risk. Studies on other fish species, such as salmonids and catfish, have shown similar behaviors, with increased nocturnal activity and depth adjustments based on tidal and lunar cycles (Kohler et al., 1997; Fraser et al., 1993). Conversely, some species, like certain reef fish, reduce activity during the full moon due to increased predation risk (Hobson, 1973; Myrberg, 1973). This study highlights the complex interplay between environmental factors and fish behavior, emphasizing the importance of understanding these dynamics for effective conservation and management of fish populations. The insights gained can inform future research and management strategies in similar dynamic environments worldwide, contributing to the broader understanding of fish ecology and behavior. By understanding how mullets and similar species interact with their environment, we can better predict the impacts of environmental changes and human activities on these important ecological communities.

Author Contributions

HTI originated the concept of the study. EKA directed the fieldwork efforts and managed the research team. GAO conducted the literature review and assisted in designing the study. HTI drafted the manuscript, with contributions and feedback from the other authors.

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Supporting Information

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