Interactive Drivers of Activity in a Free-Ranging Estuarine Predator

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Abstract

Animal activity patterns evolve as an optimal balance between energy use, energy acquisition, and predation risk, so understanding how animals partition activity relative to extrinsic environmental fluctuations is central to understanding their ecology, biology and physiology. Here we use accelerometry to examine the degree to which activity patterns of an estuarine teleost predator are driven by a series of rhythmic and arrhythmic environmental fluctuations. We implanted free-ranging bream *Acanthopagrus australis* with acoustic transmitters that measured bi-axial acceleration and pressure (depth), and simultaneously monitored a series of environmental variables (photosynthetically active radiation, tidal height, temperature, turbidity, and lunar phase) for a period of approximately four months. Linear modeling showed an interaction between fish activity, light level and tidal height; with activity rates also negatively correlated with fish depth. These patterns highlight the relatively-complex trade-offs that are required to persist in highly variable environments. This study demonstrates how novel acoustic sensor tags can reveal interactive links between environmental cycles and animal behavior.

Introduction

From a history of biochronological study, we can derive several overarching relationships which are relatively consistent among animals: 1) photoperiodic cycles are the most powerful entraining agent of circadian rhythms; 2) intra- and inter-specific interactions contribute to this behavioral rhythmicity [1]; and, 3) rhythms in behavior are often associated with exogenous processes over other scales [2]. Consequently, the ability to measure and characterize activity patterns is central to our understanding of the physiological, ecological and social aspects of natural systems. Inter-specific variation in rhythmicity and interactions with other organisms are tightly linked; playing a fundamental role in shaping the evolution of natural systems [3].

Rhythmic behaviors often represent traits which have evolved in response to many biotic factors including predation risk [4,5], food availability and quality [5], and abiotic influences such as light and tide (over short time periods), and temperature and turbidity (over longer time periods). For example, adaptive foraging strategies and habitat use mediated by diel rhythms can facilitate sympatry by partitioning access to resources [6]. Further, minimizing predation risk whilst optimizing energetic gain is often achieved by organisms through behaviours linked to exogenous rhythms [7,8]. A common strategy for some fishes involves increased activity related to foraging at night, which facilitates both avoidance of visual predators and increased access to nocturnally active prey [9]. In understanding the links between external influences and behaviour, it is important to concurrently consider multiple entraining sources, and interacting factors that affect an organism's choice or strategy (e.g. prey quality, predation risk and habitat).

Many studies in aquatic systems have investigated behavioral rhythmicity at the diel scale. Examples include diel vertical migration in pelagic fish and krill [10–12], photoperiod entrained activity patterns in freshwater fish [13], and diel patterns in habitat usage in coral reef fish [14]. Aquatic systems, however, present a series of agents that may entrain behavioral rhythms, some of which are not experienced in the terrestrial sphere. One such example is tidal exchange; a sub-diel rhythm occurring in marine and estuarine environments approximately twice over a single diel period in some parts of the world [15,16], the strength of which is also influenced by lunar cycles. Consequently, factors co-occurring at different frequencies in aquatic systems can lead to concomitant effects on the behavioral patterns which are entrained to them [17]. This is particularly evident in estuarine environments, where tidal cycles can greatly affect both ambient hydrographic conditions [18] and connectivity with particular habitats [19]. Thus, the interactive effects of multiple exogenous factors may have important implications for understanding partitioning of time and space at the species level, and inter-specific interactions at the ecosystem level.

Studying the activity patterns of mobile aquatic animals in their natural habitat is logistically difficult. This is principally due to the difficulties associated with observing individuals underwater, at night [20,21], in turbid environments and at depths which cannot be readily accessed for observation [22]. Telemetry approaches have helped to address these difficulties, and modern technology

facilitates the simultaneous collection of space use, movement and abiotic information (e.g. temperature and depth) at fine temporal scales [23,24]. Recent advances have seen the inclusion of accelerometer sensors alongside acoustic transmitters within implantable tags. These can measure, log and transmit acceleration data to acoustic receivers without a need for retrieval, and have emerged as a powerful tool for studying activity rates of free-ranging aquatic organisms [7,25,26].

This study used accelerometry with the broad objective of understanding activity rhythms in a species inhabiting a highly variable estuarine environment. Specifically, we used bream *Acanthopagrus australis* as a model to test for the interactive effects of diel, tidal and lunar rhythms on activity patterns, alongside several arrhythmic fluctuations. *Acanthopagrus australis* is a sparid endemic to the east coast of Australia, and spend the majority of their lifecycle in estuaries and inshore coastal waters [27]. The species feeds primarily on molluscs, polychaetes and crustaceans [28], and are thought to exploit bare substrates, seagrass beds and mangroves as foraging habitats [29].

Materials and Methods

Study site and acoustic array

The study was conducted in the Georges River, in the southern Sydney metropolitan area (34.008°S, 151.119°E). The river is 96 km long and drains a catchment of 960 km^2, with the upper limit to the estuary being the Liverpool Weir 45 km upstream. The Georges River estuary is primarily urbanised [30,31], and has experienced substantial shoreline modification and heavy urban pollution inputs. The Georges River contains limited saltmarsh habitat, but the mid-estuary contains considerable mangroves and small mangrove lined tributaries adjacent to the Georges River National Park. Fish were captured and tagged in this study in the vicinity of this area, at approximately 33.977° S 151.036° E (Fig. 1). An array of 34 Vemco VR2W acoustic receivers (Vemco, Halifax, Nova Scotia) was deployed throughout the entire estuary, and data from this array is presented elsewhere [7]. Here, we confined our dataset to acceleration (hereafter acceleration is used to refer to the data collected by the tags, and activity is used to refer to the behaviour that the data is describing) and depth measurements collected at the three receivers near Picnic Point in the Georges River, such that activity and depth data could be correlated to the explanatory variables collected at that location (see below, Fig. 1). The range of VR2W receivers is approximately 300 m [21,32,33], so these three receivers were spaced approximately 500 m apart, thus collecting data for approximately 1.5 km of river.

Accelerometry transmitters and tagging

As accelerometry transmitters represent a relatively new technology, a brief introduction into the technical aspects of the tags is provided here. The accelerometer in Vemco tags can be programmed to collect either bi-axial or tri-axial acceleration data, with a user-specified sampling window and range of transmittable measurements. The acceleration sensor has a measurable range of ± 29.4 m s^{-2} on each axis, and these values are used to calculate a composite root mean square acceleration estimate from the selected axes. The resultant vector is transmitted acoustically to the VR2W receiver, in the range 0–3.4 m s^{-2} (tri-axial accelerometer) or 0–4.9 m s^{-2} (bi-axial accelerometer). Any vectors greater than these ranges are transmitted as the maximum value (for example, a RMS estimate from a tri-axial accelerometer of 5.2 m s^{-2} will be transmitted as 3.4 m s^{-2}). Tri-axial accelerometer measurements represent a general activity index of the fish; including surge (forward-backward) motion, dorsoven-tral movement, and lateral movement components, measured at 5 or 10 Hz on each axis. Bi-axial accelerometers measure two axes (dorsoventral movement and lateral movement), usually at a higher frequencies (10 Hz). Tri-axial accelerometers are analogous to overall dynamic body acceleration (ODBA [34,35]), whereas bi-axial are analogous to partial dynamic body acceleration (PDBA [36]). As surge represents lower sustained acceleration as opposed to the dorsoventral and lateral undulations of a swimming fish, tri-axial vectors will usually be smaller than biaxial vectors. This coupled with greater frequency of measurement mean bi-axial vectors represent a more precise reflection of tail beat patterns or swimming speed.

The length of the sampling window for the acceleration sensor represents a compromise between battery life and ability to sample a variety of behaviors. The data collected over each sampling window likely reflects a variety of different behaviors, which are averaged out over the specified time. Consequently, with a longer sampling window, there is a greater chance of sampling a signal which corresponds to a discrete behavior, but that signal will be diluted by the remainder of the sampling window. Conversely, a shorter sampling window will provide a more precise estimate of the acceleration vector that represents a certain behavior, but because a smaller proportion of each cycle is sampled for acceleration the chance of actually detecting the behavior is lower.

Accelerometry transmitters used in this study were configured from the Vemco V9 range of sensor tags. We selected Vemco V9AP-2L accelerometry and pressure transmitters (69 kHz, 3.3 g in water, 66 mm length), with the accelerometer programmed to measure bi-axial (dorsoventral movement and lateral) acceleration at 10 Hz, over a sampling window of 33 s.

This study was carried out in strict accordance with the recommendations in *A Guide to Acceptable Procedures and Practices for Aquaculture and Fisheries Research*, 3rd Edition [37]. The protocol was approved by the Animal Care and Ethics Committee of both the University of NSW (Permit number 11/30A) and the NSW Department of Primary Industries (Permit number 09/01). All surgery was performed under anesthesia, and all efforts were made to minimize suffering. Capture and tagging of fish in the Georges River during this study was permitted under Section 37 of the NSW *Fisheries Management Act 1994*, through Scientific Research Permit number P03/0086 (issued by NSW Department of Primary Industries). Six *Acanthopagrus australis* (338–687 g) (hereafter called bream) were angled at Picnic Point in the Georges River in NSW, Australia in late May 2011 (Fig. 1). Transmitters were fitted internally using conventional surgical techniques [7,32]. The transmitter was placed within the body cavity such that the longest dimension was anteriorly-posteriorly oriented. Fish were held in an onboard tank until the effects of anesthetic were no longer evident, and then released back into the water at the site of capture. We anticipated minimal effects of tagging on fish behavior, and that these would be limited to the first days post-tagging (as has previously been found for bream [38]).

Environmental variables

Environmental parameters (temperature [°C], turbidity [neph-elometric turbidity units], and photosynthetically active radiation [PAR]) were recorded by a subsurface logger operated by the Botany Bay Water Quality Improvement Program at Picnic Point (Fig. 1). Lunar phase data (calculated daily on a scale of 0 = new, 1 = full) was obtained from Geoscience Australia (http://www.ga.gov.au/) and tidal heights (m) were collected from the Picnic Point tidal gauge (33.982°S, 151.000°E) operated by the Manly Hydraulics Laboratory (www.mhl.nsw.gov.au).
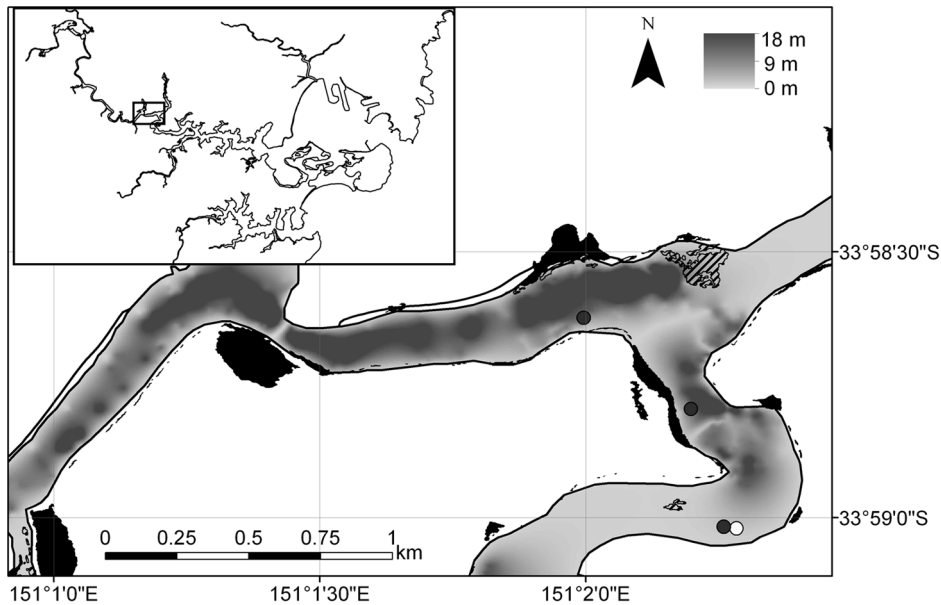
Figure 1. Map of the study area in the Georges River, southern Sydney, showing receiver locations (black circles), the Botany Bay Water Quality Improvement Program logger (white circle), *Zostera* sp. seagrass beds (hatched polygons), and mangroves (black polygons). A bathymetry surface is also shown as a gradient between 0 m and 18 m (shown in Figure legend in top right).
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Statistical analysis

Raw data produced in this study are stored in the Australian Animal Tracking and Monitoring Systems e-Marine Infrastructure Initiative Database (http://aatams.emii.org.au/aatams/). Depth (pressure) values were adjusted to Indian Spring Low Water (ISLW) height datum on tidal height at the time the sensor measurement was taken (approach described in [9]), and thus represent a relative measure of fish depth. Mean values for all variables (bream activity, bream depth, temperature, turbidity, PAR, tide height and lunar phase) were analysed as 15 min time bins for each individual across the monitoring period (25/5/2011 to 11/9/11), and a series of generalized linear models were constructed to identify the dominant drivers of bream activity. Since our main hypothesis involved the interactive effects of circadian and ultradian rhythms common in the estuarine environment on activity patterns, we included a *PAR·Tide* interaction term in the model. The full model was thus of the form:

$$Activity_t = \beta_0 + \beta_1 \cdot Temperature_t +$$
$$\beta_2 \cdot Turbidity_t + \beta_3 \cdot PAR_t + \beta_4 \cdot Tide_t \ldots$$
$$\ldots + \beta_5 \cdot Depth_t + \beta_6 \cdot Moon_t + \beta_7 \cdot PAR_t \cdot Tide_t + \varepsilon_t$$

where independent variables reflect those described earlier in the methods. To account for potential serial correlation in our data, we fitted models using generalized least squares and modeled the autocorrelation between successive data points following the approach described in [39]. Several models were run using the gls function in R v. 2.12.1 (using the Linear and Nonlinear Mixed-effects Models package [40]), to determine the type (auto-regressive [AR], moving average [MA], or both autoregressive and moving average [ARMA]) and order of the error structure which best described autocorrelation in our data, on the basis of Akaike Information Criteria (AIC [41]). This was then incorporated into models constructed to determine the best combination

Table 1. Tagging information for yellowfin bream (*Acanthopagrus australis*) tracked in the Georges River, showing the numbers of days on which data were recorded during the study period, the temporal window within which these data were recorded (e.g. for Fish 1, data were recorded on 89 days within a window of 100 d), and the number of activity and depth measurements from each tag recorded by the receivers shown in Figure 1.

Fish	Date tagged	Fork length (cm)	# days of data	Period (d)	Activity data	Depth data
1	16-05-11	28.0	89	100	11669	11785
2	17-05-11	24.0	49	54	7074	6981
3	19-05-11	30.0	92	110	17247	17202
4	02-06-11	30.4	7	58	196	203
5	02-06-11	27.9	11	76	408	423
6	02-06-11	26.0	11	66	476	472

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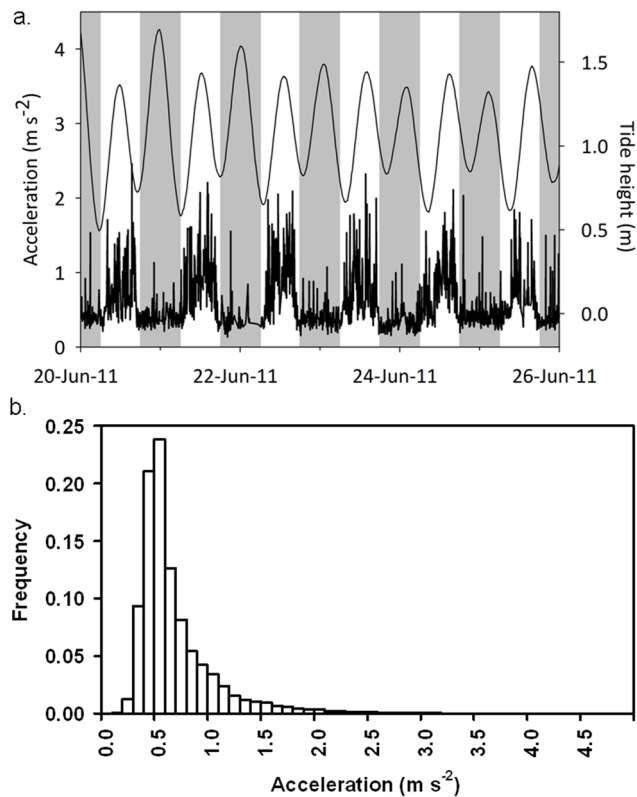
Figure 2. Actogram representative of fish activity (acceleration) across diel and tidal periods (a; data are for fish 3 in Table 1, between the dates 20th June 2011 and 26th June 2011), and frequency histogram of acceleration values measured in the study (b). Tidal height (a; secondary y-axis) is represented by the solid black line, and grey shading indicates night and white shading indicates day.
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of explanatory variables and their relative contributions to bream activity, using the gls function in conjunction with the stepAIC routine [42]. Activity data were log-transformed to achieve a Gaussian distribution, predictors were standardized following Aitken & West [43] and assessed on the basis of Akaike's Information Criterion (AIC), with terms eliminated from the model if their removal increased the AIC (ΔAIC) by less than 2.

Table 2. Optimisation of the autocorrelation function, showing the auto-regressive (AR, φ_n) and moving-average (MA, θ_n) correlation parameters for models of increasing order.

AR order (p)	MA order (q)	φ_1	φ_2	θ_1	AIC
0	0				1969.509
1	**0**	**0.17668**			**1772.993**
1	1	−0.07139		0.29979	1774.255
2	0	0.28949	−0.14868		1773.324

The AIC for each model was used to select the model which best described the error structure (shown in **bold**). As increasing complexity failed to produce models with a lower AIC, models with more than 2 auto-regressive and 1 moving average parameters were not run [39,44].
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All analyses were performed using R v. 2.12.1 (R-Core Development Team).

Results

A total of 37,070 acceleration values and 37,066 depth values were recorded from the six individuals (Table 1), which resulted in data for 15,014 and 15,091 15-min bins of acceleration and depth, respectively. Fish displayed substantial circadian rhythmicity, as well as some evidence for elevated activity rates associated with peaks in the tidal period (Fig. 2a). Acceleration values ranged between 0.2 and 4.0 m s^{-2}, with the majority of values ranging between 0.2 and 1.0 m s^{-2} (Fig. 2b).

Visual assessment of the autocorrelation function showed some correlation between the residual of each data point and multiple preceding data points, indicating autocorrelation was present in the data. Model results for the evaluation of autocorrelation are presented in Table 2; a first-order auto-regressive correlation structure provided the lowest AIC (1772.993), and was selected for further evaluation of the full model. Moving average and larger-order correlation structures were unnecessary as they failed to improve the AIC [39,44], and the first-order auto-regressive function accounted for most of the correlation between time lags.

The series of model runs to determine the combination of independent variables which best explained variation in activity is displayed in Table 3. Variables which were sequentially removed from the model were *Lunar phase* and *Turbidity*, followed by *Temperature*. The most parsimonious model included the terms *PAR*, *Tide*, *Depth* and *PAR·Tide*; and the φ value indicated that the residuals separated by one time step had a correlation of 0.34. The parameter coefficients and tests for the significance of retained parameters are shown in Table 4. Comparison of parameter coefficients indicated that *Tide* and *PAR* were important parameters in driving activity values; however, the effect was not consistent across the diel period (as seen in the *PAR·Tide* interaction term). Evaluation of the *PAR·Tide* interaction term showed that the lowest activity values were at night regardless of tide, and the highest activity values were found during the day on a high tide (Fig. 3). There were no water quality variables (*Temperature* or *Turbidity*) identified in the best model, indicating that in our data set these were not important in driving activity patterns of bream.

Discussion

The influence of multiple extrinsic ecological variables on animal activity patterns is not well understood [45,46], probably due to complexities associated with quantifying the various factors that can influence activity [46,47]. This is exacerbated in aquatic habitats for two reasons: direct observation is logistically difficult; and many aquatic habitats are also characterized by the potentially strong influence of tides. While endogenous rhythms are most-often identified at the diel scale, there are several examples of aquatic animals exhibiting endogenous tidal rhythms, and these can persist in non-tidal environments [48,49]. How then, should animals exposed to strong environmental fluctuations at multiple scales partition activity? Acceleration measurements of free-ranging bream indicate an interaction between exogenous fluctuations at the diel and tidal scale, with highest activity rates occurring during daytime high-tides. Diel-tidal interactions in the marine literature have been described for zooplankton behavior (e.g. [50]), but examples demonstrating concurrent entrainment to multiple rhythms in free-ranging fish are rare. Green jobfish *Aprion virescens*, displayed diel and tidal entrained habitat shifts, possibly between feeding and refuge habitats [51]; however these

Table 3. Sequential model runs using a first-order auto-correlation structure, and corresponding difference in AIC values.

Model	Parameters	Term removed	ΔAIC
Activity_p1q0_1	*Temperature + Turbidity + PAR + Tide + Moon + Depth + PAR·Tide*	*Moon* (P = 0.47)	3.41
Activity_p1q0_2	*Temperature + Turbidity + PAR + Tide + Depth + PAR·Tide*	*Turbidity* (P = 0.34)	1.92
Activity_p1q0_3	*Temperature + PAR + Tide + Depth + PAR·Tide*	*Temperature* (P = 0.28)	0.82
Activity_p1q0_4	**PAR + Tide + Depth + PAR·Tide**	*Depth* (P<0.01)	**0**
Activity_p1q0_5	*PAR + Tide + Depth*		6.05

The P-value of the term removed from each model is given, and the best model is highlighted in **bold**.
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conclusions were based on detection frequency so may not represent actual patterns particularly well [21]. High inundation during the daytime provided the best foraging conditions for the surface-swimming four-eyed fish *Anableps anableps*, as visual predation was important for capture of insects [52]. In a study using pop-up archival transmitting (PAT) tags, basking sharks *Cetorhinus maximus* diving behavior was entrained to both diel and tidal rhythms, thought to facilitate exploitation of tidally-entrained aggregations of zooplankton prey at depth [53]. In a laboratory setting, endogenous circatidal and circadian components of fish movements have been shown to persist even in the absence of exogenous tidal cues, for an intertidal blenny (*Zoarces viviparous*) [54]. Finally, data collected from free-ranging North Sea plaice (*Pleuronectes platessa*) [55] equipped with electronic archival tags indicated that circatidal movement underlying selective tidal stream transport was modulated by diel periodicity [55].

Accelerometry and depth tags provided several lines of evidence, which taken together point to potential foraging behavior by bream over shallower intertidal areas when inundated during high tides. Bream are a visual, benthic predator [56] that primarily prey on polychaetes, bivalves and gastropods [28]. Higher activity rates coincided with individuals being present at shallow depths during the day. Habitat mapping of the study areas shows these shallow depths likely correspond to sand banks and mangroves where these types of prey species may be found at high densities. Lower nocturnal activity rates, and generally lower activity rates in deeper water, may reflect individuals resting and potentially hiding in deeper waters during the evening while larger estuarine predators are foraging in shallower waters (e.g. [9]). Mulloway (*Argyrosomus japonicus*) [57] and bull sharks (*Carcharinus leucas*) are two predators of bream and are nocturnally active [9,58]; larger mulloway in particular concentrate foraging over shallow areas of estuaries at night, and are resident in deeper holes within the river during daytime [9]. Opposing diel rhythmicity of

bream and its predators may allow bream to exploit their optimal foraging habitat whilst minimising exposure to predation. If our hypothesis about shallow intertidal foraging and resting in adjacent deeper waters is correct, these findings are largely consistent with foraging arena theory mediated by diel and tidal rhythmicity. Foraging arena theory maintains that spatial adjacency of foraging and resting habitat enhances energetic gains by minimizing the energetic cost and predation risk associated with accessing foraging areas from resting habitats [59]. Such temporal partitioning of habitat use is evident in a diversity of organisms, and adds to the growing body of examples which describe use of foraging arenas in aquatic systems (see [59] for a full review). This behaviour ultimately facilitates dynamic stability in aquatic systems, and description of these processes is essential for both the understanding of trophic flow of energy through such systems, and improving the design and parameterisation of widely used ecosystem models [60].

Lunar phase, temperature and turbidity are thought to affect bream activity, but had no detectable impact alongside the main entraining factors of diel and tidal cycles in our data set. In terms of their distribution along the estuary, bream are highly tolerant of minor environmental fluctuations [61,62], although recent work indicates that a severe change in water quality is likely to have an influence on activity rates [7]. Temperature was largely invariant, and turbidity was generally invariant and low (~6 ntu) during the study period, which may explain the lack of any impact on activity values during our study.

Table 4. Predictors from the most parsimonious auto-regressive model and their respective β-values, P-values for the response variable Activity ('+' β denotes a positive correlation and a '–' β denotes a negative correlation).

Predictor	β	S.E.	*t*-value	p-value
Diel period	0.1651113	0.019	8.46	<0.001
Tidal period	0.1785145	0.035	5.01	<0.001
Depth	−0.0972872	0.029	−3.28	0.001
Diel·Tide	0.1120134	0.039	2.83	0.005
φ	0.34			

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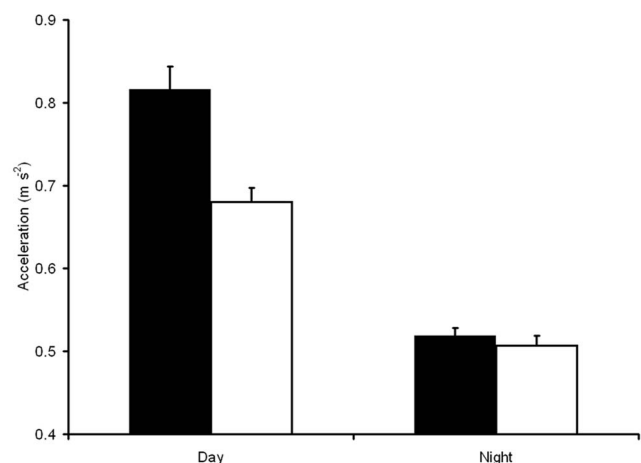
Figure 3. Categorical representation of acceleration across diel and tidal periods, showing greater activity rates during the day, and a clear peak in activity during the daytime high tide.
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Any overarching influence of lunar phase on bream may not have been evident due to the time periods examined in our study. The effect of lunar phase on animal behaviour is most pronounced during spawning periods [16]; however bream are thought to spawn during winter in the northern section of their geographic range (spawning behaviour is unknown in the southern part of their range, where this study was conducted [29]). Considering all tagged fish in our study were at a size greater than the size at maturity, we did expect to observe some effect of lunar phase in our study if spawning was entrained to the lunar cycle. Given the limited temporal and spatial scale of the study, longer term monitoring is required to draw a firm conclusion on this hypothesis.

Conclusion

This study demonstrates the utility of accelerometry tags for understanding complex rhythmic behavior of aquatic animals. For bream, multiple exogenous drivers (diel and tidal rhythmicity) interactively contributed to observed patterns of activity. Whilst this has allowed us to construct hypotheses regarding habitat use,

resource partitioning and predation risk, future work should directly explore these links through simultaneous monitoring of activity, depth, habitat use (which could be achieved by deploying accelerometry tags within high resolution acoustic positioning systems [23]) and potentially, prey consumption. Such detailed knowledge of factors driving species behavior will greatly improve our understanding of the maintenance of dynamic stability in aquatic systems.

Author Contributions

Conceived and designed the experiments: NLP MDT CAG DvdM. Performed the experiments: NLP DvdM LM. Analyzed the data: MDT LM NLP. Contributed reagents/materials/analysis tools: MDT CAG DvdM. Wrote the paper: MDT LM NLP CAG DvdM.

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