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Rain reverses diel activity rhythms in an estuarine teleost

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Activity rhythms are ubiquitous in nature, and generally synchronized with the day–night cycle. Several taxa have been shown to switch between nocturnal and diurnal activity in response to environmental variability, and these relatively uncommon switches provide a basis for greater understanding of the mechanisms and adaptive significance of circadian (approx. 24 h) rhythms. Plasticity of activity rhythms has been identified in association with a variety of factors, from changes in predation pressure to an altered nutritional or social status. Here, we report a switch in activity rhythm that is associated with rainfall. Outside periods of rain, the estuarine-associated teleost *Acanthopagrus australis* was most active and in shallower depths during the day, but this activity and depth pattern was reversed in the days following rain, with diurnality restored as estuarine conductivity and turbidity levels returned to pre-rain levels. Although representing the first example of a rain-induced reversal of activity rhythm in an aquatic animal of which we are aware, our results are consistent with established models on the trade-offs between predation risk and foraging efficiency.

1. Introduction

Animals should partition energy expenditure into those periods that maximize their foraging or reproductive success. This prediction underpins the biological significance of activity rhythms, which are ubiquitous in nature, and most often identified at the diel ('circadian') scale [1,2]. There is mounting evidence that synchronicity between endogenous circadian rhythms and extrinsic cues leads to increased fitness [1–3], and, given their ubiquity, the general consensus is that circadian rhythms provide an adaptive advantage (for reviews see [1,3]). For example, reproductive success in cyanobacteria [2,4,5], fecundity of pitcher-plant mosquitoes [6], survival rates of *Drosophila melanogaster* [7] and longevity of golden hamsters *Mesocricetus auratus* [8] have all been shown to increase when the rhythmicity of exogenous cues match that of internal circadian ones. It is therefore not surprising that significant endeavour has been directed at identifying examples of plasticity in activity rhythms, and in determining the drivers of this plasticity.

While there is a tendency to classify an individual species's activity as either diurnal, nocturnal or crepuscular, examples of activity rhythm plasticity can be drawn from a broad range of taxa, and this plasticity appears to be driven by a variety of factors. The activity rhythms of both golden spiny mice *Acomys russatus* and golden hamsters *Mesocricetus auratus* are nocturnal in laboratory settings, but diurnal in the wild [9,10]. Honeybees display socially mediated switches between rhythmic and arrhythmic behaviour [11], and reversals of diel activity in fish have been associated with changes in water temperature

[12], nutritional status [13] and habitat type [14]. However, the influence of rainfall on activity rhythms is yet to be evaluated.

Rainfall can have a drastic impact on aquatic environments, often leading to rapid changes in salinity, turbidity, dissolved oxygen and temperature, as well as imposing mechanical challenges as a result of increased water velocities. It seems intuitive that these changes ought to alter the conditions that are optimal for foraging in some aquatic taxa, and that this could drive a departure from normal activity rhythms. Probably due to the logistical challenges associated with observing free-ranging aquatic animals, the influence of rainfall on activity rhythms is generally unknown, and the significance of this knowledge gap is highlighted by the changes to rainfall regimes predicted in coming decades [15].

Biotelemetry is a rapidly evolving discipline that has facilitated the measurement of physiological and behavioural information in a suite of free-ranging aquatic animals (for reviews see [16,17–19]). Here, we used accelerometry transmitters to evaluate activity rhythms in the estuarine-associated yellow-fin bream *Acanthopagrus australis* (Sparidae). Specifically, we tested the predictions that free-ranging *A. australis* would display circadian rhythms in locomotor activity, and that either the strength or direction of these rhythms would be altered by rain events.

2. Material and methods

(a) Species, study site and accelerometry transmitters

Six *Acanthopagrus australis* (338–687 g) were captured via hook and line approximately 15 km upstream from the mouth of the Georges River estuary in NSW, Australia (33.977° S, 151.036° E) in late May 2011. Accelerometry transmitters (Vemco, Halifax, Nova Scotia; model V9AP-2L, 69 kHz, 3.3 g in water, 66 mm length) were fitted internally (for surgery technique see [20]), with the longest dimension of the transmitters parallel to fish length within the body cavity, such that the z-axis represented surge (forwards–backwards) of the body, and the x- and y-axes represent dorsoventral and lateral acceleration, respectively (after [21]). We anticipated minimal effects of tagging on fish behaviour, and that these would be limited to the first 4 days post-tagging (as has previously been found for *A. australis* [22]). Acceleration was sampled at 10 Hz for 33 s only on the x- and y-axes, with a measurement range of $\pm 29.4 \ m \ s^{-2}$. Acceleration was calculated as a root mean square value from each axis, and these data were transmitted on a pseudorandom schedule every 240 s (on average). Depth was transmitted every second duty cycle, such that the tags transmitted data alternating between acceleration and depth every 120 s, on average. An array of 34 Vemco VR2W acoustic receivers was deployed throughout the estuary, with an approximate spacing of 1.3 km between receivers, and these recorded the transmitted acceleration and depth data when transmitters were within range.

(b) Hydrological variables

A series of five Odyssey (Dataflow Systems Pty Ltd) loggers were deployed approximately equidistantly throughout the length of the estuary, mid-water, which recorded conductivity and temperature every hour. We considered it likely that the foraging ecology of bream would be influenced by water clarity following rain, so a Sea-Bird CTD profiler (SBE 19-plus V2; Sea-Bird Electronics, www.seabird.com) was deployed during a significant rainfall event that occurred in March 2012. Although this event did not coincide with the fish monitoring period, the

event was of similar magnitude to one that occurred in July 2011 (rainfall recorded by the Australian Bureau of Meteorology at nearby Bankstown was 82 mm and 94 mm for 21–23 July 2011 and 8–10 Mar 2012, respectively; www.bom.gov.au). The Sea-Bird measured turbidity (NTU) throughout the water column adjacent to each of the 34 receivers, with each Sea-Bird cast occurring within 2 h of high tide on the day of the highest rainfall (8 March), on the following day (9 March), 5 days after rain (13 March) and 8 days after rain (16 March).

(c) Data analysis

Mean values of acceleration and depth per hour were calculated for each individual across the entire monitoring period (25 May to 25 September 2011). Displacement (km) was calculated as the difference in mean hourly position from the overall mean position for each fish (with position defined as the distance of the receiver that recorded a transmission from the estuary mouth). In this way, if the mean overall position of an individual was 15 km from the estuary mouth, a mean hourly position of 16 km would represent a displacement of +1 km. As a measure of the influence of rainfall on estuarine conductivity, hourly data from one Odyssey logger (located approx. 10 km upstream from the estuary mouth) were subjected to a 25-point running mean, in order to remove tidal fluctuations from hourly conductivity. These data were then used as a proxy of freshwater discharge.

As a preliminary examination of bream rhythmicity, a fast Fourier transform was applied to grand mean hourly acceleration values (the mean of average hourly values across the six individuals) across the entire monitoring period, and the resulting spectral density was plotted. Rhythmicity in acceleration (hereafter referred to as activity) data is indicated by peaks in spectral density. A series of linear mixed models were used to examine the influence of time of day (day or night, DN; 07.00–1800 or 18.00–07.00, respectively; sunrise and sunset throughout the monitoring period ranged from 06.00–07.00 and 17.00–18.00, respectively), conductivity and displacement on the activity and depth of *A. australis*, with individual fish as a random effect. We were interested in whether diel activity patterns varied with location and after rainfall, so included interactions between DN and both displacement and conductivity on the two response variables (activity and depth). We included a first-order correlation structure in our models to account for serial autocorrelation (a violation of the assumption of independence in model-fitting), and response variables were log-transformed to achieve a Gaussian distribution. Predictors were centred following Aitken & West [23] 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 two [24]. Significant interaction terms were interpreted using 'simple slopes' parameter estimates after Aitken & West [23].

A significant rain event occurred approximately halfway through monitoring, so we examined temporal shifts in our response variables throughout this section of the time-series by stratifying it into four sections: the 7 days immediately pre-rain (period 1, 14–20 July 2011), immediately post-rain (period 2, 21–27 July 2011), and the two subsequent weeks (period 3, 28 July 2011–3 August 11; period 4, 4–10 August 2011). The choice of 7-day periods was based on the approximate time taken for turbidity to return to background levels after a rain event of similar magnitude (8–10 March; see §2b). Separate mixed models were run for each period, and given that our subjective temporal stratification would lead to relative within-period invariance in conductivity and displacement, we considered inclusion of interactions (as in the full model) inappropriate, so simplified the model to include just DN and the random effect (individual ID).

Table 1. Summary of linear mixed-effects models of activity and depth explained by time of day (day/night), relative estuary position (displacement) and conductivity, with individual bream ID as the random effect. Shown are the changes in Akaike's information criterion (ΔAIC) associated with removing interaction terms from the full model. Bold indicates significance level of $p < 0.05$.

|	β	s.e.	t	p	ΔAIC
activity					
intercept	−0.252	0.020	−12.590	**<0.0001**	—
day/night	0.030	0.005	5.603	**<0.0001**	—
conductivity	−0.050	0.012	−3.985	**<0.0001**	—
displacement	0.206	0.019	11.032	**<0.0001**	—
day/night × conductivity	0.040	0.008	4.803	**<0.0001**	21.0
day/night × displacement	0.032	0.012	2.635	**0.008**	4.9
depth					
intercept	0.449	0.045	9.914	**<0.0001**	—
day/night	−0.013	0.006	−2.207	**0.027**	—
conductivity	−0.020	0.021	−0.924	0.355	—
displacement	0.014	0.032	0.453	0.650	—
day/night × conductivity	−0.038	0.009	−4.302	**<0.0001**	16.5
day/night × displacement	−0.034	0.013	−2.659	**0.008**	4.4
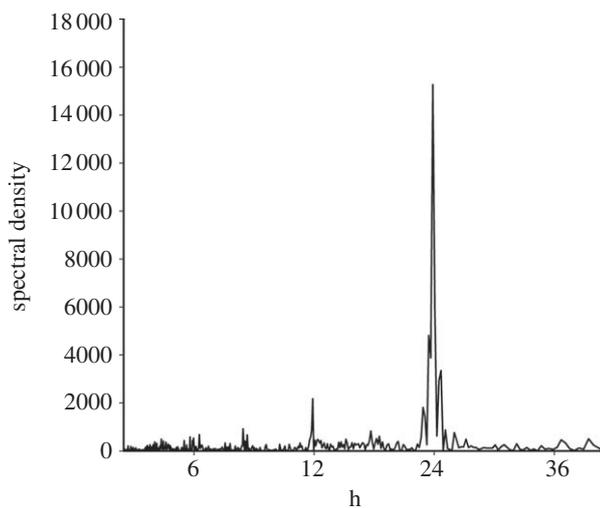
Figure 1. Spectral density of *Acanthopagrus australis* activity.

3. Results

A total of 55 123 depth data and 55 061 activity data were obtained across the six individuals, over a period of 124 days (table S1). Calculating hourly means for each fish resulted in 6622 h with mean activity and corresponding depth data. Bream activity was strongly circadian throughout the monitoring period, with a dominant peak in spectral density occurring at approximately 24 h (figure 1). All terms contributed to the model with lowest AIC for both activity and depth, and interaction terms were significant for both response variables (table 1), with the DN × conductivity term contributing to greater parsimony than the DN × displacement term for models of activity and depth (table 1). Activity increased with conductivity during the day but decreased during the night, such that bream were more diurnally active throughout the upper conductivity values and more nocturnal during the lower conductivity values experienced (figure 2a; figure 3a). Depth decreased with increasing
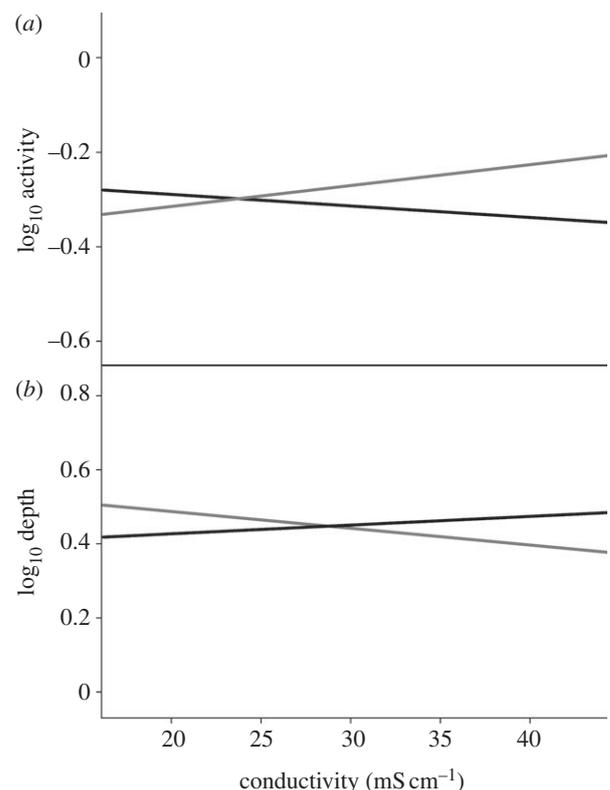

Figure 2. Simple slope estimates for interactions between time of day (day, grey lines; night, black lines) and conductivity for *Acanthopagrus australis* activity and depth. The entire range of x-values are presented, and the y-axis range is mean ± 2 s.d. for both acceleration and depth.

conductivity during daylight hours, but increased with conductivity during the night (figure 2b; figure 3b).

During the week immediately subsequent to the July rain event (period 2), activity was significantly greater during the night than during the day, but the opposite activity pattern was seen for periods 1, 3 and 4 (figure 3a;

Table 2. Summary of linear mixed-effects models (individual bream ID random) of activity and depth explained by time of day (day/night) for the month around the July rain event. Periods 1–4 represent data from the 7 days prior to the rain event, immediately after the rain event, and from the subsequent two weeks, respectively. Parameter estimates (β) with positive sign indicate higher daytime values. Bold indicates significance level of $p < 0.05$.

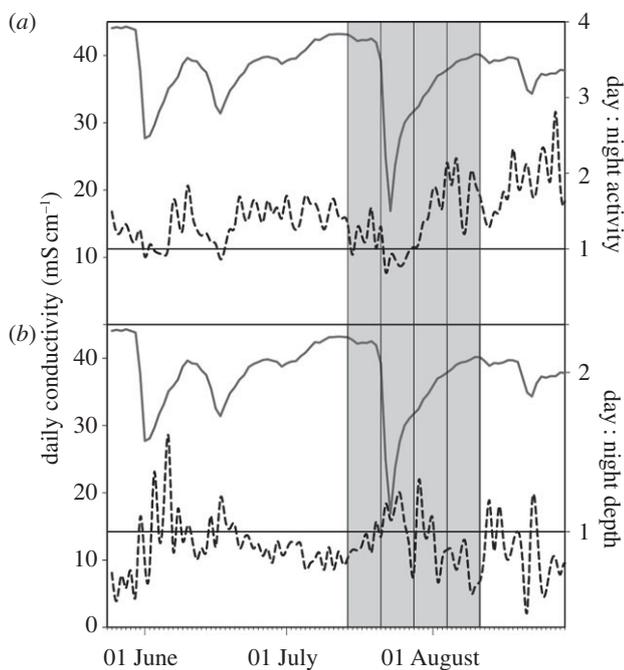|	β	s.e.	d.f.	t	p
activity					
period 1	0.028	0.007	463	3.85	**<0.05**
period 2	−0.021	0.009	430	−2.23	**<0.05**
period 3	0.027	0.009	457	3.10	**<0.05**
period 4	0.079	0.011	309	7.17	**<0.05**
depth					
period 1	−0.016	0.006	463	−2.480	**<0.05**
period 2	0.025	0.011	430	2.292	**<0.05**
period 3	−0.034	0.011	457	−3.261	**<0.05**
period 4	−0.078	0.012	309	−6.751	**<0.05**

Figure 3. Relationships between conductivity (solid line) and activity and depth (broken lines), presented as a ratio between day and night. Ratios were calculated as the grand mean activity or depth values ($n = 6$ bream) during each day divided by those of the corresponding night, across the entire monitoring period. Ratios above unity (horizontal line) indicate greater daytime activity or depth, and below the line suggest greater night-time values. Shaded columns indicate periods 1 to 4 (from left to right, respectively).

Figure 4. Time-series of conductivity (grey line) and displacement (daily mean ± s.e., $n = 6$ *Acanthopagrus australis*) throughout the monitoring period.

table 2). A similar trend was observed for depth, with greater daytime depth occurring during period 2, and greater night-time depth during periods 1, 3 and 4 (figure 3b; table 2). The magnitude of the parameter estimates for period 4 was more than double those of other periods for both activity and depth, suggesting a strengthening of diel activity and depth pattern for this period (table 2). Visual inspection of displacement throughout the monitoring period suggested a generally positive relationship between displacement and conductivity (downstream movement following rain), although this was highly variable across individuals (figure 4).
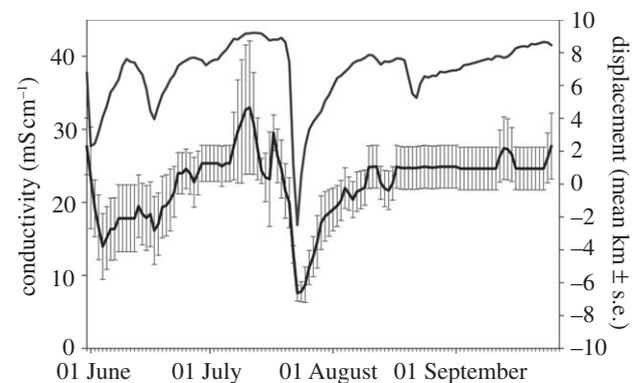
Rainfall preceded a drastic change in turbidity, with a significant increase seen for the upper half of the estuary on the day of heaviest rain (figure 5b), with this increased turbidity spreading to the lower reaches on the following day (figure 5c). Turbidity levels had decreased significantly 5 days after rainfall, although levels in the upper half of the estuary remained somewhat higher than those prior to rainfall (figure 5d versus 5a). Eight days post-rain, turbidity levels had reached levels comparable with those prior to rain (figure 5e versus 5a). Water temperature was relatively invariant throughout the monitoring period, with rain events associated with changes on the order of 1°C or less throughout the estuary.

4. Discussion

Here, we provide the first example of a rain-induced switch in activity rhythm for an aquatic animal. Bream were more active and inhabited shallower depths during the day under normal conditions, but became nocturnal following rain, with the timing of a return to diurnal behaviour matching that of the return to normal estuarine conductivity and turbidity. Switches between diurnal and nocturnal or arrhythmic behaviour have been observed in various
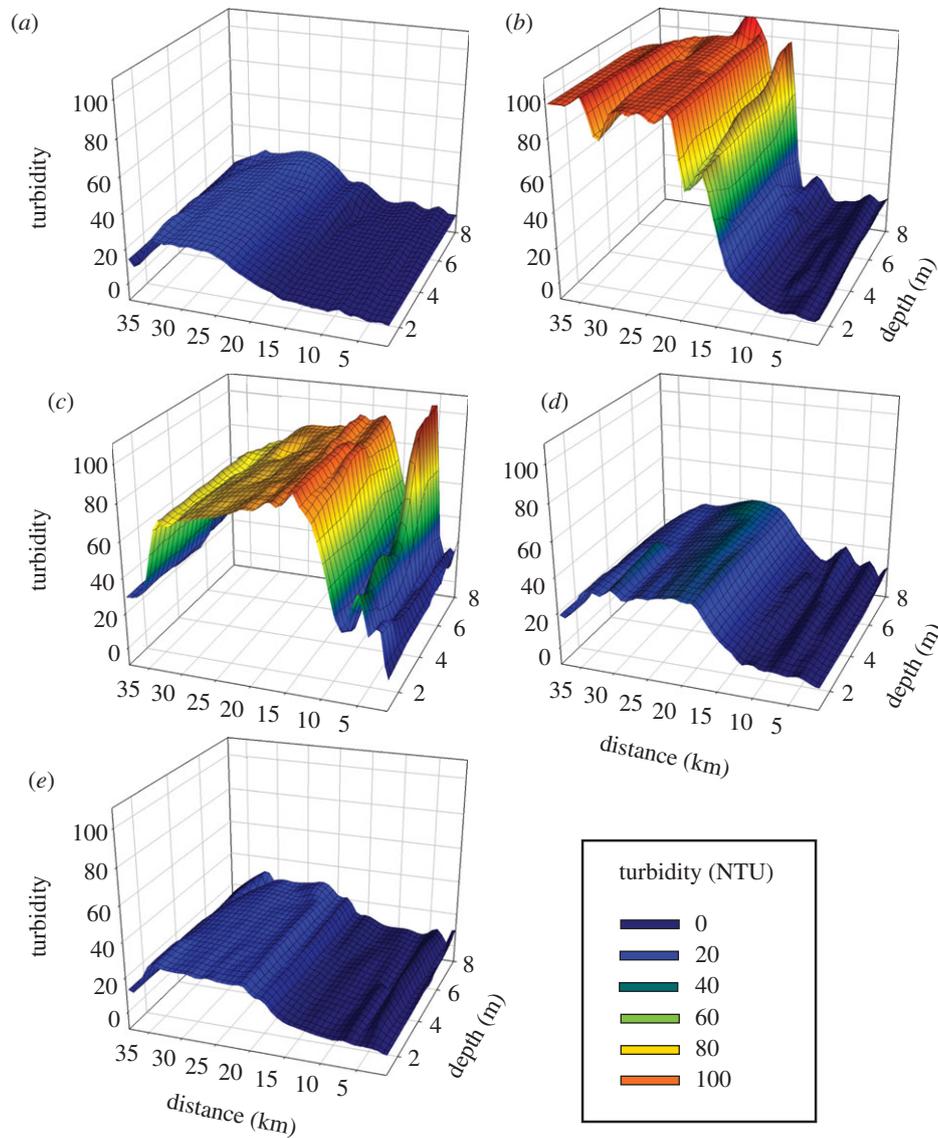
Figure 5. Change in turbidity subsequent to a rainfall event in the Georges River during March 2012. Sampling days are indicated as (a) prior to the rain event (10 February 2012), (b) on the day of heaviest rain (8 March 2012), (c) on the following day, and then (d) 5 and (e) 8 days after the rain event, respectively. Shown are mean turbidity values for each 0.5 m bin throughout the water column for each sample, and these are extrapolated across the x-axis for each sampling day. Distances from the estuary mouth are shown on the x-axis.

mammals [9,10,25] and insects [11], with predation risk and social structure the most commonly identified drivers of the shift. In fishes, variations in social rank [26], energetic status [13,27] and water temperature [12] have been associated with shifts between diurnal and nocturnal activity (for a review see [28]); however, we are not aware of any other studies that have documented a shift in activity rhythms associated with rainfall.

(a) What is the proximate driver of the shift in activity?

Rainfall is often associated with a change in location for estuarine fishes [29–32], and this confounds a mechanistic understanding of a change in behaviour. It is possible that the switch from diurnal to nocturnal activity was driven by hydrological parameters (e.g. turbidity, salinity, etc.); however, it could also be due to a difference in habitats and/or prey assemblages along the estuary (there was a general downstream movement of bream following rain). Indeed, habitat type has previously been identified as the driver of activity rhythm plasticity in fish [14]. It seems intuitive that

exposure to an unfamiliar habitat would reduce boldness during the day (when visual predators such as bream are more effective), and it is often suggested that a switch to nocturnal foraging represents a predator-avoidance mechanism (see [28] for a review of this topic). In this study, however, while time of day interacted with both conductivity and displacement, the day/night × conductivity term contributed to greater parsimony than that of displacement, suggesting a change in hydrology is more important for altering activity patterns than a change in location. Where hydrological change is the proximal mechanism, the switch to nocturnal activity here is consistent with theoretical models on the trade-offs between foraging efficiency and predation risk [33].

An optimal foraging mode should minimize the ratio between instantaneous mortality rates and net food intake [34–38], and there are several examples where changes in metabolic demand drive a shift in activity pattern. Atlantic salmon switch from nocturnal to diurnal foraging with increasing water temperature (and therefore metabolic rate [12]), with the switch dependent on food availability [34]. Despite increased foraging efficiency during the day, well-

nourished European minnows are predominantly nocturnal, but expose themselves to greater predation risks by becoming increasingly diurnal as their energetic reserves decline [13]. Many euryhaline fish experience elevated metabolic rates when exposed to salinity fluctuations in a laboratory setting [39,40], and mechanical challenges imposed by increased water velocities following rainfall are likely to further increase energetic demands of fish in an estuarine environment. Given that both penaeid prawns (a locally abundant prey item) and the potential predator *Argyrosomus japonicus* are generally nocturnal in eastern Australia [41–43], it is certainly feasible that diurnal activity represents a selection for low-efficiency foraging and low predation risk. With an increased metabolic burden imposed by rain, however, bream may be unable to acquire sufficient energy during daylight, and may be forced to forage under conditions of higher prey abundance and increased predation risk (i.e. at night). The problem of diurnal food acquisition is likely to be exacerbated by the foraging impairment imposed by the drastic increase in turbidity following rain, with turbidity being shown to reduce both the incidence and efficiency of foraging in several fish species [44,45].

(b) Significance of the change in conditions for optimal foraging

Switches between diurnal and nocturnal activity (such as that described here) are generally considered to mask endogenous circadian rhythms that are entrained to environmental cues such as the diel cycle [46]. These circadian rhythms are involved in the regulation of several fundamental processes, such as gene expression, metabolism and reproduction [1,3]. Thus, departures from synchronous activity and circadian rhythms should provide the evidence of strong selective pressures, and provide some basis for evaluating the adaptive significance of circadian rhythms [1,3]. Whether the proximal mechanism for the switch in bream activity is a change in conductivity, turbidity, habitat or a combination of these, rainfall facilitated a wholesale shift in the conditions that are optimal for partitioning of bream activity. Further, while a return to diurnal activity 1 week after rain does not necessarily suggest greater foraging success outside rain events, it could be expected that a depletion of energy reserves as a result of suboptimal nocturnal foraging be succeeded by an increase in foraging intensity following a return to optimal foraging conditions. Our data are consistent with this prediction, with a greater disparity between day and night activity (and depth) occurring during period 4 than during other periods. There is abundant anecdotal evidence that suggests catchability of *A. australis* is low immediately following a rain event, but abnormally high during subsequent days.

While the activity reversal seen for *A. australis* is significant for understanding the mechanisms that entrain animal activity to environmental cues, a shift in foraging strategy associated with rainfall also has implications with respect to a changing climate. The frequency and magnitude of rain events are predicted to change dramatically in coming decades [15], and with increasing anthropogenic control of freshwater discharge into river systems worldwide, understanding the fitness costs associated with a reversal of foraging mode will be critical for predicting population viability, particularly for species that are already facing significant pressure from recreational and commercial fishing, such as *A. australis*.

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