CSIRO PUBLISHING

Marine and Freshwater Research, 2012, **63**, 341–350
http://dx.doi.org/10.1071/MF11229

Short- and long-term movement patterns in the freshwater whipray (*Himantura dalyensis*) determined by the signal processing of passive acoustic telemetry data

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Abstract. Patterns of movement in aquatic animals reflect ecologically important behaviours. Cyclical changes in the abiotic environment influence these movements, but when multiple processes occur simultaneously, identifying which is responsible for the observed movement can be complex. Here we used acoustic telemetry and signal processing to define the abiotic processes responsible for movement patterns in freshwater whiprays (*Himantura dalyensis*). Acoustic transmitters were implanted into the whiprays and their movements detected over 12 months by an array of passive acoustic receivers, deployed throughout 64 km of the Wenlock River, Qld, Australia. The time of an individual's arrival and departure from each receiver detection field was used to estimate whipray location continuously throughout the study. This created a linear-movement-waveform for each whipray and signal processing revealed periodic components within the waveform. Correlation of movement periodograms with those from abiotic processes categorically illustrated that the diel cycle dominated the pattern of whipray movement during the wet season, whereas tidal and lunar cycles dominated during the dry season. The study methodology represents a valuable tool for objectively defining the relationship between abiotic processes and the movement patterns of free-ranging aquatic animals and is particularly expedient when periods of no detection exist within the animal location data.

Additional keywords: behaviour, elasmobranch, fish, Fourier transformation analysis, spectral.

Received 11 October 2011, accepted 22 December 2011, published online 2 April 2012

Introduction

Temporal patterns within the spatial movement of animals generally result from the heterogeneous distribution of resources in space and time. For aquatic organisms occupying the lower trophic levels, resource distributions are often linked to oscillations in the physical environment, such as tidal cycle, lunar phase, ambient light and season (Forward and Tankersley 2001). The spatial movements of larger predatory animals are generally determined by their prey and therefore their movements are also linked to physical processes (Hunter *et al.* 2005; Dewar *et al.* 2008; Le Port *et al.* 2008). Defining periodic components within the spatial movement of an individual is difficult because responses can be rapidly influenced by changes in the environment and multiple processes may be occurring simultaneously across a range of temporal and spatial scales (Shepard *et al.* 2006).

Signal processing is a well-established mathematical technique for defining periodic components within time-series data (Akselrod *et al.* 1981). The technique has been shown to objectively identify complex temporal patterns within the vertical movements of diving aquatic animals, revealing both expected and unexpected periodicity in the way these individuals utilised their environment (Musyl *et al.* 2003; Graham *et al.* 2006; Shepard *et al.* 2006; Wearmouth and Sims 2009). The aptitude by which signal processing may reveal patterns in the horizontal movements of free-ranging animals has received much less attention, perhaps due the complexity of measuring two-dimensional movement compared with the ease of recording changes in the single dimension of water depth.

The use of acoustic transmitters and static underwater listening stations to detect the horizontal movements of aquatic animals has become increasingly wide spread (Heupel *et al.* 2006). Multiple receivers can be deployed in a variety of formations with curtain lines across continental shelves (Melnychuk *et al.* 2010), within specific areas of expected high site fidelity (Papastamatiou *et al.* 2010*b*), as a series of gates throughout a river system (Childs *et al.* 2008), or in a grid formation covering a discrete area (Mitamura *et al.* 2005; March *et al.* 2010). Although passive acoustic technology represents a significant improvement in the long-term monitoring of animal presence, analysis of these data to reveal the processes

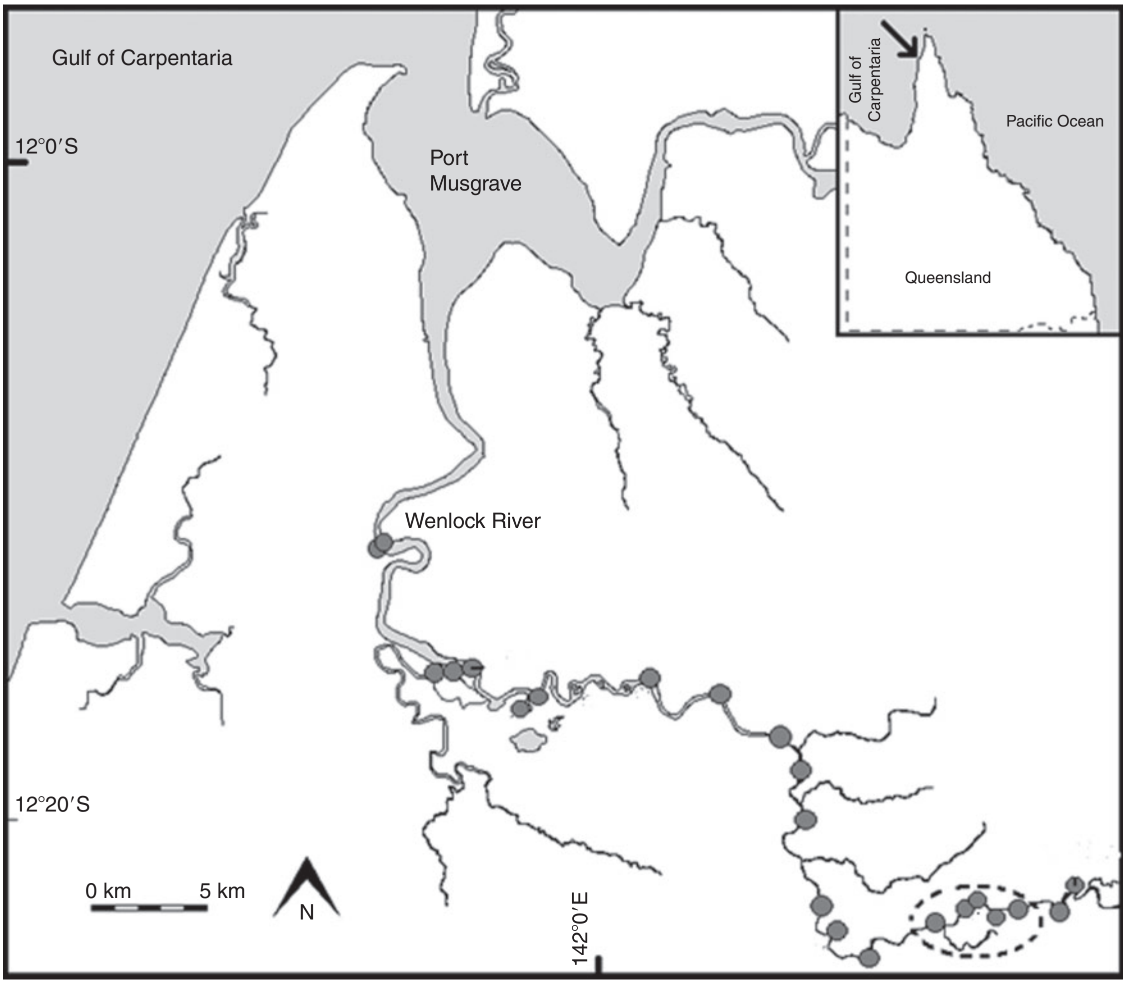

Fig. 1. Map of the Wenlock River and its location on Cape York Peninsula, Qld, Australia. Grey circles show the location of the VR2W receivers. The dotted ellipse indicates the area of *Himantura dalyensis* capture.

controlling animal movement is complex and no standardised methodology for analysing passive acoustic data is currently available (Heupel *et al.* 2006). Signal processing has been recognised as a possible tool for defining the temporal patterns in horizontal movement from data collected by passive acoustic telemetry (Hartill *et al.* 2003; Mitamura *et al.* 2005; Yeiser *et al.* 2008; March *et al.* 2010; Papastamatiou *et al.* 2010*a*, 2010*b*; Sakabe and Lyle 2010). Its application, however, has been relatively simplistic with only single periodic components being identified and the phase and coherence of the movement patterns have not been correlated with abiotic processes.

The simplicity and low resolution of the output results obtained when the signal processing algorithms are applied to passive acoustic telemetry data arise due to the method of data collection; because passive acoustic telemetry only records data when the tagged individual is within the detection field of a receiver. Consequently, the variable of space has been measured on a discontinuous scale, the time interval between samples is highly irregular and large temporal gaps exist in the data record. In contrast, studies that have used signal processing to define periodic components within the diving behaviour of aquatic animals have collected depth data using archival dataloggers. Therefore, the variable of depth has been measured on a continuous scale at regularly spaced intervals and at a sufficiently high frequency to reveal the many periodic components hidden within the waveform (Musyl *et al.* 2003; Graham *et al.* 2006; Shepard *et al.* 2006; Wearmouth and Sims 2009).

Here we aimed to improve the resolution of output results from the signal processing of location data collected by passive acoustic telemetry. Specifically, our aim was to accurately define the periodic components within the horizontal movement of individuals even though large detection gaps exist within the location data. The procedure was expected to be particularly valuable in studies where little ecological information is available upon the study species, or when a limited number of receivers are being used to cover a large area. Here, the procedure was used to study the riverine movements of a newly described species of whipray (*Himantura dalyensis*) from northern Australia (Last and Manjaji-Matsumoto 2008). The study was undertaken in the Wenlock River, Qld – an area which

Table 1. Acoustic detection and event data from *Himantura dalyensis* monitored over 12 months

F, female; M, male

Whipray number	M1	M2	F1	F2
Disc width	62.5	52	55.5	55.5
Release date	19 September 2008	13 September 2008	14 September 2008	14 September 2008
Days within array	128	440	437	429
No. of detections	25 220	109 862	184 770	205 438
No. of presence events	102	297	507	654
Total presence time (h)	710.2	2286.1	4317.1	4808.6
Mean presence time (h)	6.96	7.68	8.51	7.35
No. of absence events	79	105	347	411
Total absence time (h)	1233.8	6473.9	4442.9	3953.4
Mean absence time (h)	15.6	32.74	12.8	9.6

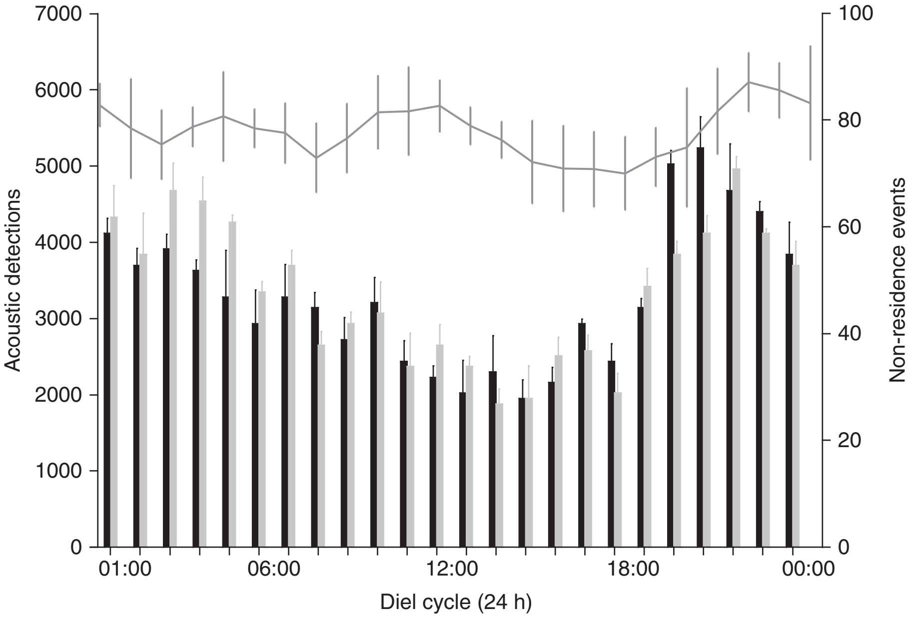

Fig. 2. The hourly distribution of acoustic detections for *Himantura dalyensis* (mean ± s.e., $n = 4$) over the diel cycle (grey line, primary y-axis) for 12 months. The hourly commencement (black bars) and termination (grey bars) of non-residence events (secondary y-axis, mean ± s.e., $n = 4$) for the same period.

is inaccessible for 6 months of the year due to monsoonal rains. Thus, passive acoustic telemetry remains the only viable method of monitoring the movement of the whiprays continuously throughout the year. The extent of an individual's range was unknown, and therefore, a limited number of underwater acoustic receivers were required to be distributed throughout a large expanse of river. This resulted in many zones within the receiver array that were outside the detection range of individual receivers. We hypothesised that the temporal association between horizontal movement in *H. dalyensis* and cyclical changes within their environment would be accurately identified if the direction of movement between receivers within the array was included into the signal processing analysis.

Materials and methods

Study site and acoustic telemetry

The present study was conducted on the Wenlock River, Cape York Peninsula, Qld, Australia (Fig. 1). The area is subjected to a distinct wet season (December–April) with monsoonal rains and a dry season with virtually no rainfall (May–November). The river is ~345 km in length and the study was undertaken between 42.3 and 104.3 km from the river mouth . In September 2009, 26 VR2W acoustic receivers (VEMCO, Halifax, Canada) were deployed; the receivers were 1.93 ± 0.07 km river distance apart (mean ± s.e.m., $n = 14$) in the upper section of the array and 4.5 ± 0.4 km river distance apart ($n = 12$) in the lower section of the array. Each receiver was secured to a concrete anchor

(25 kg) and moored to a tree on the bank. The receiver floated 1–2 m above the river substratum. River depth varied between 3 and 7 m throughout the study area in the dry season.

The detection range of each receiver was determined by towing an activated tag behind a boat up and down river away from the VR2W receiver location. A VR 100 receiver (VEMCO) aboard the boat was used to provide location of the boat by the global positioning system when each transmission was emitted. The log records between the VR100 and VR2W were compared to determine which locations were out of range of the VR2W receiver. Detection radius was generally between 200 and 300 m. The river width was typically less than 40 m, and therefore, the tagged whiprays could not pass a receiver without being detected. After 12 months, the receivers were retrieved and the data downloaded.

Water depth was measured and recorded every hour throughout the study at six locations within the VR2W receiver array (resolution 0.1 m; TDR, Star-Oddi, Reykjavik, Iceland). The loggers were moored to the river bank and were 0.2 m below the water surface at the lowest water mark. The river depth data were used to assess tidal flow.

Study animals

Six juvenile whiprays (*Himantura dalyensis*; three males and three females) were captured using set lines between 86 and 97 km from the river mouth (Fig. 1). Each ray was placed ventral side up to induce tonic immobility and the gills were irrigated with freshwater. A local anaesthetic (Lignocaine, Troy Laboratories) was injected into an area on the mid-line and a 3-cm incision was made with a scalpel, a V13 acoustic transmitter was inserted into the peritoneal cavity (length 36 mm, diameter, 13 mm, mass in water 6 g, 69.0 kHz, 158 dB, emitting coded pulses at a variable 15–45 s intervals, expected battery life 12 months, VEMCO). The wound was closed with four interrupted sutures (cat-gut sutra 2–0; Ethicon, Kirkton, UK). The whiprays were released at the point of capture.

Data analyses

The first step in the analysis procedure was to define when tagged individuals were within the detection range of a receiver (residence event) or between the detection ranges of two adjacent receivers (non-residence event). This was undertaken using purpose-designed software (the V-track software package, M.E. Watts and H.A. Campbell, The University of Queensland, Brisbane, Australia). A residence event can be defined as the period between the first and last acoustic transmission detected at a specific receiver. The timing of the event was initiated by the first detection at a new receiver and terminated if no further transmissions were detected within a specified timeout window (10 min). A non-residence event can be defined as the period between the last and first detection between adjacent receivers. The start and end time of each residence and non-residence event was defined and the spatial information provided by the limits of each receiver detection field.

The event data was pre-processed by two different methods before the application of the signal processing algorithm (fast Fourier transform). The first method binned the start and end time of each event into hourly bins over the study period. The fast Fourier transform (FFT) was then applied using the statistics toolbox in MATLAB 12.1 (Mathworks, Natick, MA) and a Hanning window with 2/3 overlap was used to minimise spectral leakage (for details see Campbell *et al.* 2006). The same hourly binning process and signal processing was employed for examining patterns in acoustic detection data. The second data processing method was to integrate the residence and non-residence events into chronological order, providing a continuous record of an individual's direction of riverine movement throughout the study. We have called this location record the waveform of linear movement. This waveform was then sampled to provide regular and frequent samples of whipray location before application of the FFT. A range of sampling regimes was tested (6, 2, 1 h, 30 min) and the length of the sampling period altered (i.e. 512, 1026, 4096).

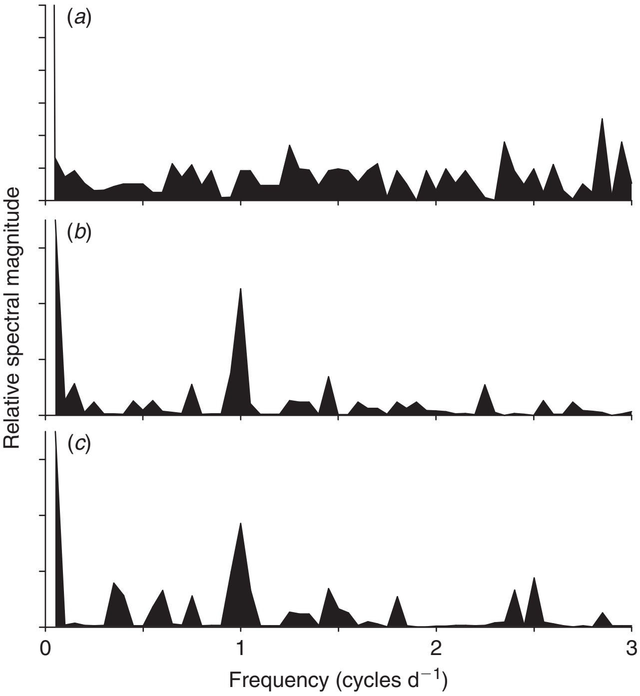

Fig. 3. Periodograms of *Himantura dalyensis* (female F2) linear movement from (*a*) hourly distributions of acoustic detections, (*b*) non-residence event commencement hour and (*c*) non-residence event termination hour.

Cross-spectral analyses techniques were also employed to determine the association between the periodic components within the horizontal movements of the tagged animals and abiotic processes (daylength, tidal cycle, lunar phase). This technique is an extension of the single-time series analysis to the simultaneous analysis of two time-series (Campbell and Egginton 2007). The degree of coherence between two waveforms is a measure of how perfectly the waves would cancel each other out due to destructive interference and the phase-shift relationship showed the extent by which a periodic component in one wave leaded or lagged behind the same periodic component in the other waveform. All analysis was undertaken using the Cohere function, in the MATLAB 12.1 signal processing toolbox.

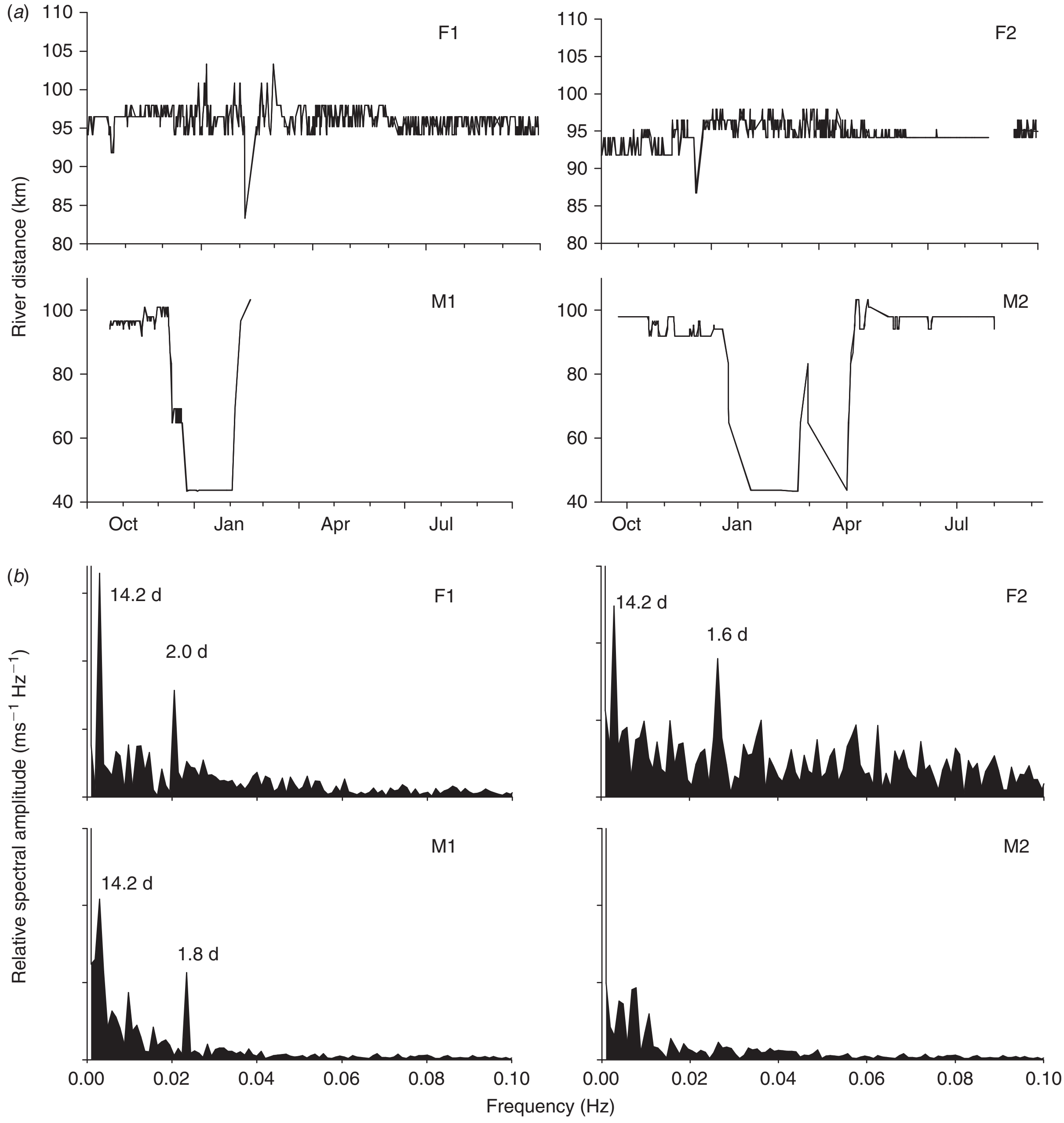

Fig. 4. (*a*) The waveform of linear movement for *Himantura dalyensis* ($n = 4$), over 12 months. The waveforms were created for each individual from residence and non-residence event data and location is expressed as the river distance from the mouth of the river. (*b*) Periodograms calculated from the linear movement waveforms for *Himantura dalyensis*, over 12 months. The time-based periodicities of the fundamental components within the spectra are shown.

Student's paired *t*-test was used to compare acoustic detection rates and event data between light and dark periods.

Results

General features

Six whiprays (*Himantura dalyensis*) were tagged, but the transmitters from one male (55 cm disc diameter) and one female (58.3 cm disc diameter) were not detected 7 days after release and were excluded from the analysis. The four rays that produced long-term detection data consisted of two males and two females of similar size (Table 1). Three of the rays were tracked for >429 days. One of the males moved beyond the upstream section of the receiver array after 128 days and was not detected again.

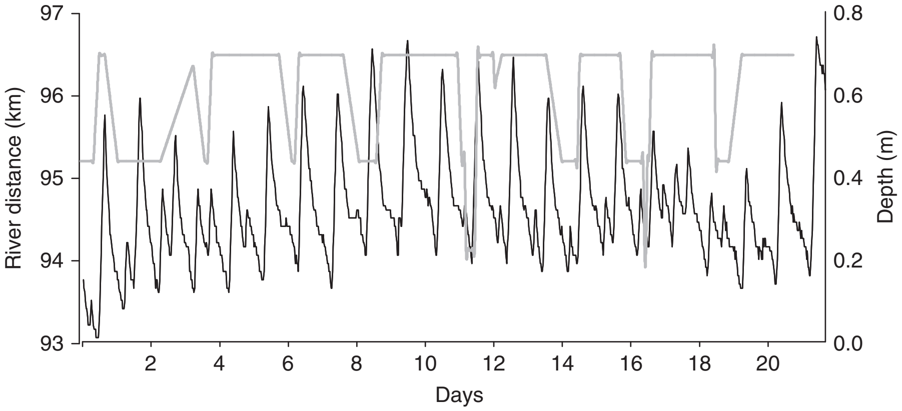

Fig. 5. The relationship between tidal cycle (black) and the linear movement waveform for *Himantura dalyensis* (grey, F1), over a 21 days period in November. An increasing river depth denotes an incoming tide and a decreasing depth an ebbing tide. An upriver movement is shown by an increase in distance from the river mouth and a downriver movement a decrease in distance from the river mouth.

Table 2. Acoustic detection and event data for female *Himantura dalyensis* (*n* = 2)
Data are monthly averages for the wet (5 months) and dry season (7 months)

Female number	Number detections	Presence events	Presence time (h)	Absence events	Minimum linear dispersal distance (km)
F1 wet	9434 ± 1912	52 ± 2.3	300 ± 29	43 ± 1.6	82.8 ± 2.49
F1 dry	21 133 ± 836	45 ± 2.7	424 ± 19	32 ± 3.8	46.2 ± 1.2
F2 wet	9312 ± 1841	58 ± 3.1	321 ± 21	42 ± 2.8	88.1 ± 3.1
F2 dry	20 987 ± 862	39 ± 3.4	438 ± 18	31 ± 2.8	49.2 ± 2.7

Diel periodicity

To determine if the diel cycle affected whipray activity, the acoustic detection data and the start and end time of each non-residence event were binned into their hour of occurrence (Fig. 2). There was no significant difference in the number of acoustic detections between periods of light and dark ($t = 1.26$, $P = 0.458$), but a significantly greater number of absence events commenced ($t = 6.53$, $P < 0.01$) and terminated ($t = 6.25$, $P < 0.01$) during periods of darkness compared with daylight. Signal processing (FFT) applied to the hourly binned acoustic detections revealed no fundamental components within the power spectrum (Fig. 3*a*), but the commencement and termination of absence events both showed a periodic component with a periodicity of 24 h (Fig. 3*b*, *c*).

Tidal and lunar periodicity

Signal processing of the linear movement waveform for individual animals (Fig. 4*a*) revealed periodic components at ~0.025 and 0.0029 Hz for three out of the four rays (Fig. 4*b*). The rate of sampling determines the bandwidth of the spectra (1 Hz = 1 h) and therefore the linear movements back and forth along the river showed a periodicity every 48-h (0.025 Hz) and 14 days (0.0029 Hz). Sampling the waveform at 30 min, hourly, 2 hourly and 6 hourly intervals did not alter the frequency of the largest peaks in the periodograms, confirming that they were not aliased components. A low number of between receiver movements occurred for male number two (M2) and therefore horizontal movement was not sampled at a sufficiently high frequency to identify 48-h or 14-day periodic components.

Plotting the waveform of horizontal movement over the tidal data illustrated that the whiprays primarily travelled in the direction of the tidal flow (Fig. 5). There was only a single tide every 24 h and the 48 h periodicity in the horizontal movement illustrates that the whiprays moved upriver on a single tidal cycle but did not make the return journey until the following tidal cycle. Cross-spectral analysis of linear movement periodograms with tidal flow periodograms confirms there was a correlation in the coherence and phase relationship between the 48 h periodicity in the direction of horizontal movement and the direction of tidal flow (Table 3).

The river depth data also illustrated the strong influence of the lunar cycle upon tidal flow. In the first and third moon quarters, the river experienced two tidal cycles rather than the usual single cycle per 24 h. The time span between these two tidal days was 14 days (Fig. 5). Cross-spectral analysis of tidal flow periodograms with horizontal movement also showed a strong coherence and phase response at the 14-day period (Table 3).

Table 3. The coherence and phase relationship between the periodic components in the periodograms from *Himantura dalyensis* linear movement and physical processes

Coherence is plotted on a scale from 0 (no coherence) to 1 (maximal coherence) and phase from −180° through to 180°, where 0° represents waves occurring simultaneously. If coherence is less than 0.5 then the phase shift relationship has no significance

Cycle	Period (h)	Dry season		Wet season	
		Coherence	Phase	Coherence	Phase
Tidal	25	0.64 ± 0.03	12 ± 3	0.09 ± 0.23	–
Diel	24	0.63 ± 0.2	45 ± 15	0.91 ± 0.8	45 ± 2
Lunar	672	0.89 ± 0.07	5 ± 1	0.21 ± 0.18	–

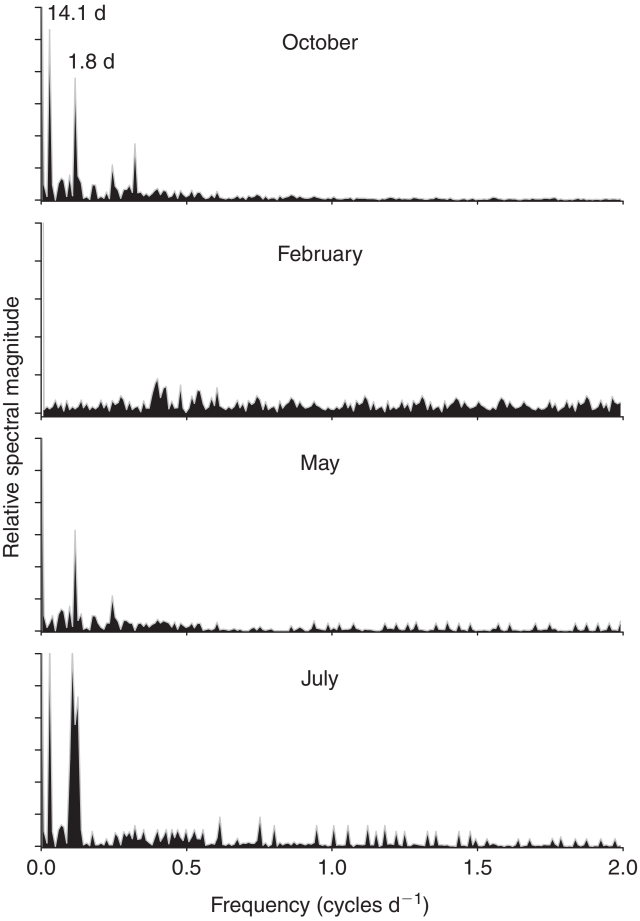

Fig. 6. Monthly periodograms of the linear movement waveform for a *Himantura dalyensis* (female F1).

Seasonal effects

The two females had a substantially greater number of acoustic detections and presence and absence events than the two males. This occurred because the females remained within the same activity space throughout the year whereas the males moved down river into an area of low receiver density. In this area, they were not detected for 2–3 months. Seasonal comparisons of horizontal movement between receivers could therefore only be undertaken on the two female rays (Table 2). The average monthly number of detections was ~55% less during the wet season, but a higher number of presence events of shorter duration were recorded during this period compared with the dry season. The number of absence events also increased and calculation of the minimum dispersal distance from the movement of the whiprays between adjacent receivers showed that there was a ~2-fold increase in movement between dry and wet seasons. Signal processing of the horizontal movements, on a monthly basis, showed that the 48-h and 14-days periodic components were abolished between January and April (Fig. 6). During the same period, the tidal pulse was non-existent in this section of the river due to seasonal flooding (Fig. 7*a*). This seasonal suppression of tidal flow in the wet season resulted in the horizontal movement switching from a periodicity which correlated with tidal and lunar cycles to one which correlated with the diel cycle (Fig. 7*b*).

Discussion

The application of signal processing to wildlife telemetry data is a relatively new development, which shows potential for the analysis of patterns within animal movement (March *et al.* 2010; Papastamatiou *et al.* 2010*a*, 2010*b*). Here, we applied the technique to define periodicity within the horizontal movements of freshwater whiprays (*Himantura dalyensis*), from location data collected by passive acoustic telemetry. The results showed that no periodicity existed in the hourly rate by which acoustic transmissions were detected by the receiver array, however, the time when individuals entered and departed each receiver detection field did show periodical components. These rhythmic fluctuations in horizontal movement showed a coherence and phase relationship with the diel, lunar, tidal and seasonal cycles. Even though periods existed when the whiprays were not located, the analytical procedure was sufficiently sensitive to illustrate the relative influence of each abiotic process upon whipray horizontal movement and demonstrated how the relative influence of each abiotic process varied over time.

H. dalyensis *movement*

This is the first study to describe any behavioural aspect of the freshwater whipray (*Himantura dalyensis*). The lack of information on the distribution and biology of *H. dalyensis* made capture difficult and subsequent transmitter failure resulted in a low sample size. Nevertheless, the results revealed several behavioural features shared by the tagged individuals: (1) *H. dalyensis* switched from correlating their horizontal movements with the tidal and lunar cycle during the dry season

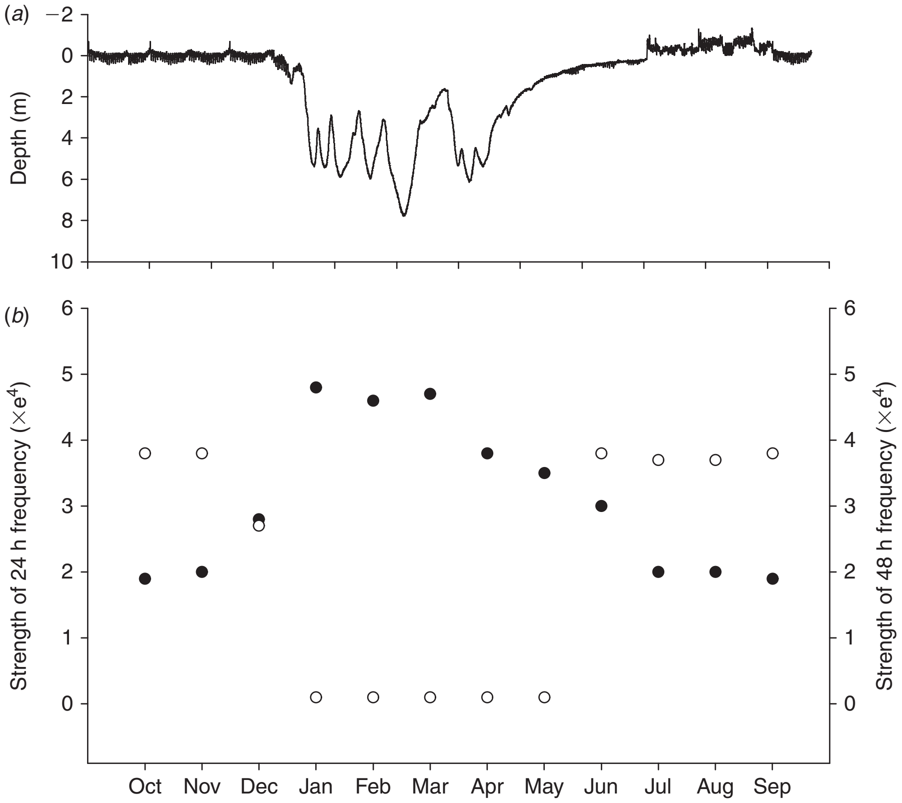

Fig. 7. (*a*) Changes in river depth throughout the study period, showing the abolishment of tidal fluctuations during the wet season. (*b*) The amplitude of the fundamental periodic component in the periodogram determined from the hourly binned absence event data (period of 12 h; closed circles) and the linear movement waveform (period of 14 days; open circles), data are from *Himantura dalyensis* F2.

to the diel cycle during the wet season; (2) the whiprays showed a high degree of site fidelity to a section of river less than 8 km in length; and (3) during the wet season females remained within the same range whereas the males travelled ~60 km downriver to inhabit brackish water.

The seasonal switch in *H. dalyensis* horizontal movement from tidal-based to diel-based may be explained by bio-energetics – under the assumption that animals will always seek to maximise energy intake whilst reducing energetic costs (Kooijman *et al.* 1999). In the dry season, the direction of whipray movement predominantly followed the direction of current flow. The ebb and flow of the tide in this section of the river would have enabled the whiprays to move back and forth throughout their range whilst minimising energy expenditure. In the wet season, tidal flow in this section of the river was abolished and the flow of the river was unidirectional. This would have resulted in the whiprays being required to swim against the flow direction to remain within the same foraging area. During these periods, a crepuscular feeding pattern may have been the most energetically efficient method to maximise prey encounters for the distance covered. Such seasonal switches in foraging strategies to maximise the overall energy budget is common amongst fish species (Sims *et al.* 2003).

Similar to other species of batoid ray, *H. dalyensis* showed a high degree of site fidelity (Smith and Merriner 1985; Walker *et al.* 1997). During the wet season the tagged males undertook a seasonal migration into brackish waters, but returned to the upstream area after a few months. The females did not undertake this downriver migration and remained within an upstream area of less than 8 km. Seasonal downstream migration into brackish water is common among euryhaline elasmobranchs and is generally considered to be associated with the breeding cycle (Whitty *et al.* 2009; Simpfendorfer *et al.* 2010). The tagged males in this study were juveniles (Last and Manjaji-Matsumoto 2008; S. Peverell, pers. obs.) and therefore, the purpose of the brackish water migration remains uncertain. If it was a strategy to access improved foraging areas, it appears paradoxical that the females would remain in the poorer feeding patches. Clearly, more acoustic tagging studies with larger sample sizes across a wider range of body sizes is required to better understand *H. dalyensis* ecology. We noted that the downward migration of the male *H. dalyensis* occurred within 10 days of each other and was initiated before the river experienced the seasonal flood, suggesting an environmental cue triggered the migration and this was not related to river depth or flow.

Signal processing of passive acoustic telemetry data

A curious observation from this study was that periodicity was not detected in the rate by which acoustic transmissions were collected by the receiver array even though he horizontal movements of the whiprays were periodic. This demonstrated that the temporal association by which acoustic transmissions were detected by the array did not accurately represent the whiprays horizontal movements. In contrast, other passive acoustic studies have revealed periodicity in the rate by which acoustic transmissions were collected by an array of passive acoustic receivers, accurately reflecting the horizontal movement of the tagged animals (March *et al.* 2010; Papastamatiou *et al.* 2010*a*, 2010*b*). In these studies, however, the foraging areas of the tagged animals were predicted and the acoustic receivers deployed specifically in these areas. Consequently, acoustic detections were only collected when the animals were foraging within the predicted areas and the temporal association between the tagged animal's movements and the receiver array was correctly identified by signal processing. In this study however, the movements of the tagged whiprays were unknown and the receivers were deployed randomly throughout their expected range. Therefore, it was not possible to define the temporal pattern within an individual's movement by the hourly number of acoustic transmissions detected by the array and instead it was necessary to examine the directionality of movement between receivers within the array.

To do this, the timing by which the tagged whiprays moved into and out of each receiver's detection range was used rather than the absolute number of acoustic detections. From this information, a waveform which illustrated the direction of whipray linear movement could be created for the duration of the study. This movement waveform was then examined by signal processing either singularly or divided into monthly periods. The procedure was a step forward in the signal processing of passive acoustic telemetry data because: (1) it allowed for spatial gaps between the detection fields of receivers within the array; (2) the waveform could be sampled at regular intervals of a sufficiently high frequency to reveal the underlying periodic components; (3) sampling could be undertaken at alternative frequencies to ensure that the periodic components identified were true and not aliased components – an issue inherent to signal processing (Denbeigh 1998); and (4) correlation could be explored between the periodic components in the linear movement waveform with those from abiotic processes (diel, lunar, tidal cycles). Essentially, by using the methodologies presented in this study, animal location becomes a regularly sampled continuous variable which can be assessed for periodicity in a manner similar to the procedure used in diving behavioural studies where changes in animal depth are measured and recorded by an archival datalogger (Shepard *et al.* 2006; Wearmouth and Sims 2009).

Over the past decade, the use of passive acoustic receivers to define the spatial movements of aquatic animals has increased dramatically (Greene *et al.* 2009). The current rate of growth is likely to continue over the coming decade with data collections becoming ever more complex as the temporal and spatial scales expand. Defining the temporal association between animal movement and the environment from these highly irregular and discontinuously sampled data is going to be challenging but necessary for long-term management strategies (Meyer *et al.* 2007; March *et al.* 2010; Simpfendorfer *et al.* 2010). We argue that the analytical techniques presented within this study offer an objective method for identifying and quantifying the relationship between abiotic processes and the horizontal movements of acoustically tagged aquatic organisms located by static underwater receivers.

Acknowledgements

We thank Barry Lyons and Beau Reilly for assistance in the field and the journal referees for useful comments on the manuscript. The research was funded under the Australian Research Council Linkage Grant scheme with Australia Zoo as collaborative partners. All research was conducted under Australian Animal Ethics (#AECA2007/01/165) and a DPI & F General Fisheries Permit (#55105).

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