APPLICATION

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Refined Shortest Paths (RSP): Incorporation of topography in space use estimation from node-based telemetry data

Yuri Niella[1] | Hugo Flávio[2] | Amy F. Smoothey[3] | Kim Aarestrup[2] |
Matthew D. Taylor[4] | Victor M. Peddemors[3] | Robert Harcourt[1]

[1]Department of Biological Sciences, Macquarie University, Sydney, NSW, Australia

[2]National Institute of Aquatic Resources, Technical University of Denmark, Silkeborg, Denmark

[3]NSW Department of Primary Industries, Fisheries Research, Sydney Institute of Marine Science, Sydney, NSW, Australia

[4]Port Stephens Fisheries Institute, New South Wales Department of Primary Industries, Taylors Beach, NSW, Australia

Correspondence
Yuri Niella
Email: yuri.niella@gmail.com

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Abstract

1. Acoustic telemetry enables spatial ecologists to collect movement data from a variety of aquatic species. In estuaries and rivers, accounting for the complex shape of water bodies is challenging. Current methods for analysing utilization distributions (UDs) are restricted to using the locations of receivers where animals have been detected, which limits the information available to estimate movement paths.

2. We present a new R package (RSP—Refined Shortest Paths) for analysing the movements of animals tracked with acoustic transmitters in environments constrained by landmasses. The method estimates the shortest in water locations of monitored animals between pairs of detections using least-cost path analysis. It then applies dynamic Brownian Bridge Movement Models to calculate UD areas. Intra- and interspecific overlaps in space and time are calculated and can be used, for example, to investigate potential influencing environmental factors.

3. Tracks refined with RSP follow the estuary shape, yielding substantially longer, but more realistic travel distances. Showcased examples demonstrate how RSP can be used to analyse intra- and interspecific movement patterns; determine similarities in habitat use; identify the environmental conditions responsible for influencing the size of the space use areas; and assess levels of spatial overlap between different species.

4. The RSP toolkit generates more realistic movements of tracked animals than those derived using receiver locations alone. An incidental benefit is its ability to deal with receiver loss, a common problem in acoustic telemetry studies. The analysis can be readily customized to suit different study species, array configurations and habitat shapes.

KEYWORDS
constrained random walk, environmental correlates, least-cost analysis, overlapping areas, utilization distribution

1 | INTRODUCTION

Traditional studies of fine-scale habitat use in the aquatic environment relied on active telemetry techniques (Gannon et al., 2015; Pastor et al., 2009; Taylor & Ko, 2011). Active tracking is very laborious,

costly and requires certain infrastructure which further limits its application. It allows researchers to monitor only a limited number of individuals, usually over short periods of time. Alternatively, measuring fine-scale movements has been possible using the time difference of arrival of acoustic detections within passive acoustic arrays (Espinoza

et al., 2011). However, as this method requires overlapping detection ranges and large numbers of receivers, realistically only small geographical areas can be covered. This approach can therefore be ineffective for studying finer-scale movements of wide-ranging animals as these might quickly move out of the covered area. Researchers often deploy non-overlapping arrays to increase spatial coverage, which can still potentially generate thousands of detections (i.e. locations) for tracked individuals (Payne et al., 2013). However, when using non-overlapping arrays, the number of unique positions is limited by the number of receivers.

In aquatic environments, land masses are important barriers that limit the movements of animals, yet few analytical tools are capable of accounting for this constraint when estimating space use (Aspillaga et al., 2019; Wilson et al., 2017). Least-cost path analysis takes into account the landscape properties to estimate the best cost-effective routes between two positions, that is, start and end points. In habitats constrained by landmasses, this approach is useful for calculating the shortest in water distances between consecutive acoustic detections.

These distances can be then used for obtaining the shortest paths the tracked animals need to travel to be detected at these locations.

Translating tracking information into utilization distribution (UD) areas is a commonly applied method in spatial ecology (Kie et al., 2010). This allows for the identification of home range areas and their corresponding regions of higher usage, thus revealing important biological patterns such as seasonal migrations, trends in habitat partitioning and spawning periods (Crossin et al., 2017; Heupel et al., 2019). The dynamic Brownian Bridge Movement Model (dBBMM) accounts for the time differences between sampled positions and their respective accuracy, while using conditional random walks to detect behavioural changes along trajectories for estimating UD (Kranstauber et al., 2012).

In this paper, we describe a new method to analyse the fine-scale movements of animals tracked with acoustic telemetry in environments constrained by landmasses to estimate and model space use exclusively in water. This approach allows researchers to use standardized UDs and/or frequencies of overlap between the different

TABLE 1 List of Refined Shortest Paths (RSP) analysis and plot functions, and their respective usages including information on the important default arguments

Type	Function	Usage	Important arguments
Analysis	*runRSP*()	Estimates the RSP between consecutive acoustic detections	*time.step* = 10 (minutes); *min.time* = 10 (minutes); *max.time* = 24 (hours); *distance* = 250 (metres); *er.ad* = 5% of *distance* (or it can be set in metres)
	getDistances()	Calculates the total distances travelled in each RSP track, using only the receiver locations and the RSP interpolated positions	
	dynBBMM()	Calculates dynamic Brownian Bridge Movement Models (dBBMM) for each tracked animal, both at track level and also according to standardized fixed temporal windows (if *timeframe* is set in hours)	A temporal interval of interest can be set for analysis using the *start.time* and *stop.time* arguments
	getAreas()	Calculates the areas of space use (in squared metres) at track or group level, for particular dBBMM contours of interest	*type* = either "group" or "track" and must be set; *breaks* = 50% and 95% dBBMM contours are used
	getOverlaps()	When multiple biological groups are tracked, calculates the amount of overlap between them	Overlaps are always calculated for the same contours obtained using the *getAreas*() function
Plot	*plotRaster*()	Verifies that the stations are in the water using the base raster provided	*land.col* = colour of the land masses
	suggestSize()	Suggests the most suitable dimensions for saving the base raster as a projected map	*max* = desired size of the longest plot edge
	plotTracks()	Plots a map of an RSP track of interest	*land.col* = colour of the land masses
	plotDensities()	Density plot of elapsed time between consecutive acoustic detections. Can be either used for all monitored animals or for a particular group of interest	*group*: character vector defining the group of interest. If not set, will return the distribution for all monitored animals
	plotDistances()	Plots the total distances travelled by tracked animals	*by.group* = FALSE (returns a single plot for all tracked animals); *compare* = TRUE (distances are returned both using only receiver locations and the RSP interpolations)
	plotContours()	Plots the dBBMM for a particular animal and track of interest	*breaks* = plots the 25%, 50%, 75% and 95% contours; *land.col* = colour of the land masses
	plotAreas()	Plots the space use areas at group level	*timeslot* must be set for timeslot dBBMM; *land.col* = colour of the land masses
	plotOverlaps()	Plots the overlapping areas between two different groups	*timeslot* must be set for timeslot dBBMM; *land.col* = colour of the land masses
	addStations()	Adds the station locations to an RSP plot	Customization parameters available

groups of animals or individuals as the input for further statistical analyses. Here, we show the applicability of this toolkit and use a simulated analysis to demonstrate its capacity to account for randomly losing acoustic receivers from arrays, a common issue for long-term tracking studies in marine and estuarine environments.

2 | DESCRIPTION OF THE METHOD

The method was developed in R (R Core Team, 2020) and is available through the Refined Shortest Paths (RSP) package (https://github.com/YuriNiella/RSP), together with a detailed manual. Tagged animals are pre-assigned to one or multiple groups, depending on the requirements of the study (e.g. different species/sexes/sizes). This allows RSP to calculate inter-group overlaps in space and time. The approach is divided into three main steps: (a) estimation of the shortest paths in water between consecutive acoustic detections, (b) calculating UDs constrained by the surrounding landmasses using dBBMMs and (c) calculating overlaps between different biological groups. All RSP functions are listed in Table 1 and the workflow (Figure 1) is detailed below.

2.1 | Preliminary analysis of raw detection and data preparation

Raw acoustic telemetry data might include false detections (e.g. originating from noise) or detections from animals which appear to be dead (e.g. repetitive detections at a single location over extended periods). In order to include only the most reliable data, RSP requires the raw detections to be first filtered using the R package ACTEL (Flávio, 2020), which is performed through any of its main functions, that is, *explore*(), *migration*() and *residency*() (Figure 1). These functions are interactive and automatically identify unusual data while requiring the user to verify and validate/invalidate detections. Only the valid detections will be used by RSP.

Topographic data are included in RSP by providing a shapefile of the study area delimiting the land contours, also imported using actel. This shapefile is converted to a raster using *loadShape*() according to a user-defined cell size. Then a transition layer for the study area must be created with the *transitionLayer*() function. Changing the base raster resolution will lead to differences in the results obtained.

2.2 | Estimating the shortest paths in water

In complex aquatic habitats (e.g. estuarine, lacustrine, riverine), the uncertainty regarding the possible trajectories of animals tracked is low compared to open environments (e.g. marine), because the former are naturally constrained (e.g. river margins, islands, coastline, etc.). By using a transition layer from the study area delimiting land areas, the *runRSP*() function applies a least-cost analysis of constrained random walks to estimate the shortest paths between consecutive acoustic detections.

The detection ranges of each receiver are considered to attribute location errors for the estimated positions. If not specified, a default range of 500 m is used (Kessel et al., 2014). Consecutive detections may occur either at the same station (Table 2) or at different stations

FIGURE 1 Refined Shortest Paths (RSP) workflow showing the preliminary analysis and data preparation steps using the R package ACTEL
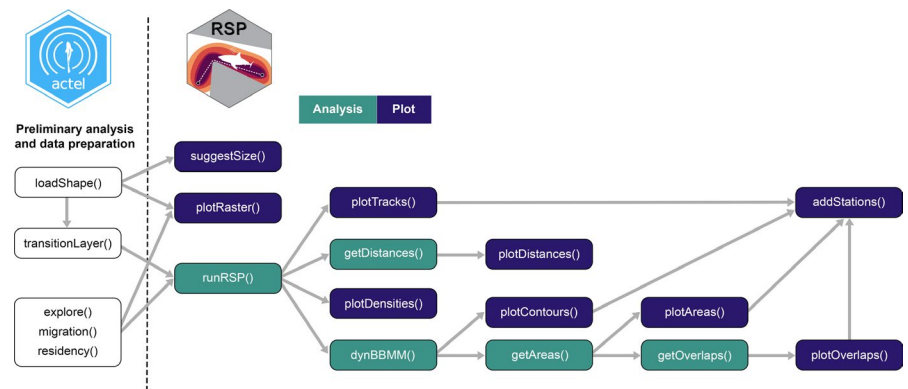
TABLE 2 Example of the interpolated locations from the *runRSP*() output (Position = RSP) when consecutive acoustic detections (Position = Receiver) occur on the same receivers. Some columns were omitted for simplification

Timestamp	Receiver	Transmitter	Error	Longitude	Latitude	Position	Track
2018-03-07 02:05:47	115409	R64K-4075	500	9.380	56.572	Receiver	Track_03
2018-03-07 02:30:37	NA	R64K-4075	525	9.380	56.572	RSP	Track_03
2018-03-07 02:55:27	NA	R64K-4075	550	9.380	56.572	RSP	Track_03
2018-03-07 03:20:18	NA	R64K-4075	550	9.380	56.572	RSP	Track_03
2018-03-07 03:45:08	NA	R64K-4075	525	9.380	56.572	RSP	Track_03
2018-03-07 04:09:59	115409	R64K-4075	500	9.380	56.572	Receiver	Track_03

TABLE 3 Example of the interpolated locations from the *runRSP*() output (Position = RSP) when consecutive acoustic detections (Position = Receiver) occur on different receivers. Some columns were omitted for simplification

Timestamp	Receiver	Transmitter	Error	Longitude	Latitude	Position	Track
2018-04-27 05:27:10	100474	R64K-4125	500	9.922	57.056	Receiver	Track_05
2018-04-27 05:35:17	NA	R64K-4125	525	9.928	57.054	RSP	Track_05
2018-04-27 05:43:24	NA	R64K-4125	550	9.935	57.053	RSP	Track_05
2018-04-27 05:51:32	NA	R64K-4125	575	9.943	57.054	RSP	Track_05
2018-04-27 05:59:39	NA	R64K-4125	600	9.949	57.056	RSP	Track_05
2018-04-27 06:07:47	NA	R64K-4125	625	9.955	57.058	RSP	Track_05
2018-04-27 06:15:54	NA	R64K-4125	650	9.960	57.061	RSP	Track_05
2018-04-27 06:24:01	NA	R64K-4125	625	9.964	57.065	RSP	Track_05
2018-04-27 06:32:09	NA	R64K-4125	600	9.968	57.068	RSP	Track_05
2018-04-27 06:40:16	NA	R64K-4125	575	9.975	57.070	RSP	Track_05
2018-04-27 06:48:24	NA	R64K-4125	550	9.981	57.072	RSP	Track_05
2018-04-27 06:56:31	NA	R64K-4125	525	9.986	57.074	RSP	Track_05
2018-04-27 07:04:39	107527	R64K-4125	500	9.992	57.076	Receiver	Track_05

TABLE 4 Example of *getDistances*() output showing the corresponding distances travelled (Dist.travel) in metres

Animal.tracked	Track	Day.n	Loc.type	Dist.travel	Group
R64K-4125	Track_02	3	Receiver	14,107	B
R64K-4125	Track_02	3	RSP	17,399	B
R64K-4125	Track_03	4	Receiver	182,882	B
R64K-4125	Track_03	4	RSP	206,815	B
R64K-4125	Track_04	2	Receiver	25,471	B
R64K-4125	Track_04	2	RSP	29,845	B

TABLE 5 Metadata examples on the dynamic Brownian Bridge Movement Models calculated for group dBBMM with *dynBBMM*(). Included are the corresponding number of valid detections (valid.n), first and last detection times (First.time and Last.time, respectively), and track timespan

Group	Tag	Track	valid.n	First.time	Last.time	Timespan
A	R64K-4075	Track_09	303	2018-04-24 11:40:56	2018-04-26 01:00:13	37.3 hr
B	R64K-4125	Track_03	1,003	2018-04-25 11:44:05	2018-04-28 14:10:14	74.4 hr
C	R64K-4128	Track_06	146	2018-04-28 16:29:07	2018-04-29 15:25:16	22.9 hr
D	R64K-4138	Track_10	584	2018-07-14 22:10:35	2018-07-18 18:33:43	92.4 hr

(Table 3). Intermediary locations are only interpolated if the interval is longer than 10 min (defined using the *time.step* argument). For detections at different stations, new intermediary locations are interpolated if the distance between stations is >250 m (defined by *distance*).

The longer it takes for an animal to be detected consecutively in an array, the more uncertain the possible trajectories become. By default, unique sporadic detections (e.g. a single detection within a 48-hr period) are automatically excluded. Each block of detections separated by <24 hr is considered a track. This parameter can also be customized using the *max.time* argument (in hours). The total distances travelled during each track can be obtained with *getDistances*() (Table 4).

For each sequence of interpolated locations, the errors gradually increase when moving away from the first detection, at a rate of 5% of the *distance* argument. This default value was chosen based on the cut-off for statistical significance and simply provides an 'inflation coefficient' to be used during space use calculations. The dBBMM accounts for the elapsed time between

TABLE 6 Example of a timeslot object saved for a timeslot dBBMM using the *dynBBMM*() function with a daily resolution (*timeframe* = 24 hr)

Slot	Start	Stop
1	2013-09-02 00:00:00	2013-09-02 23:59:59
2	2013-09-03 00:00:00	2013-09-03 23:59:59
3	2013-09-04 00:00:00	2013-09-04 23:59:59
4	2013-09-05 00:00:00	2013-09-05 23:59:59
5	2013-09-06 00:00:00	2013-09-06 23:59:59
6	2013-09-07 00:00:00	2013-09-07 23:59:59

FIGURE 3 Example of tracks from *runRSP*() plotted using *plotTracks*() (a). Receiver locations can be added to the plot (b) using *addStations*()
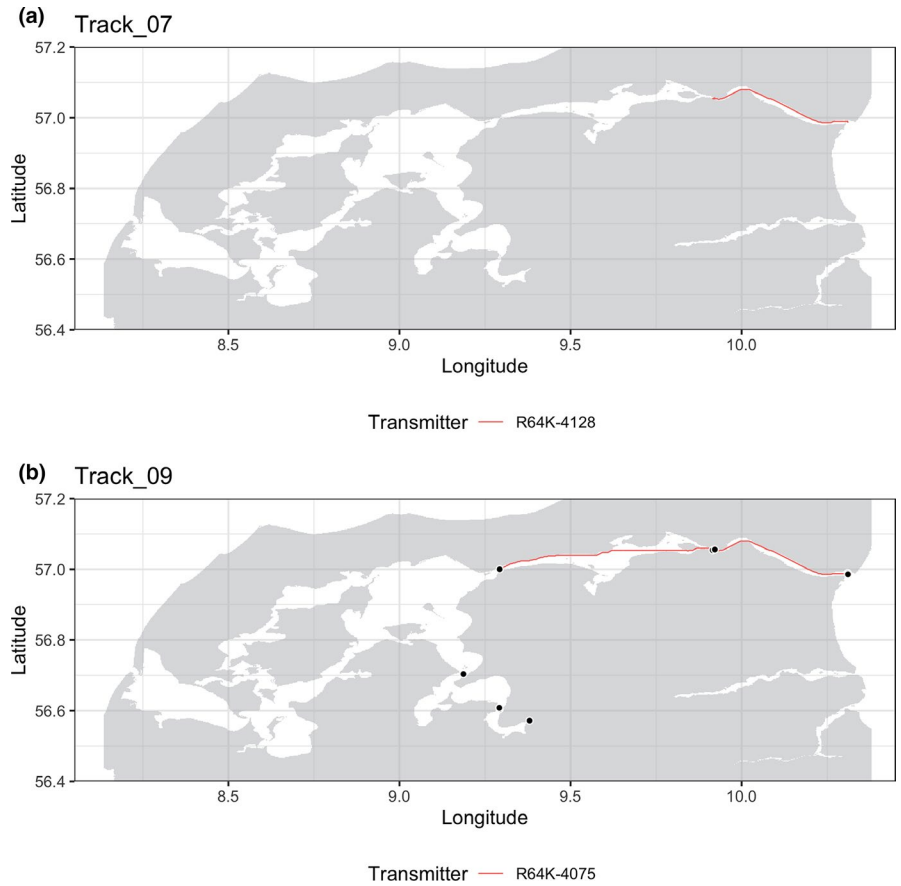

TABLE 7 Metadata examples on the dynamic Brownian Bridge Movement Models calculated for timeslot dBBMM with *dynBBMM*(). Included are the corresponding timeslot (slot), number of valid detections (valid.n), first (First.time) and last detection (Last.time) times, and track timespan

Group	Tag	Track	Slot	valid.n	First.time	Last.time	Timespan
Bream	A69-9002-10473	Track_02	261	17	2014-05-20 22:11:44	2014-05-20 23:58:35	1.8 hr
Bream	A69-9002-10473	Track_03	266	45	2014-05-25 13:32:44	2014-05-25 23:40:06	10.1 hr
Luderick	A69-9002-10481	Track_01	243	42	2014-05-02 12:49:50	2014-05-02 23:32:07	10.7 hr
Luderick	A69-9002-10481	Track_01	244	21	2014-05-03 00:37:42	2014-05-03 20:20:09	19.7 hr
Tarwhine	A69-9004-489	Track_03	429	86	2014-11-01 02:21:36	2014-11-01 19:25:42	17.1 hr
Tarwhine	A69-9004-489	Track_03	430	123	2014-11-02 05:54:37	2014-11-02 19:18:01	13.4 hr
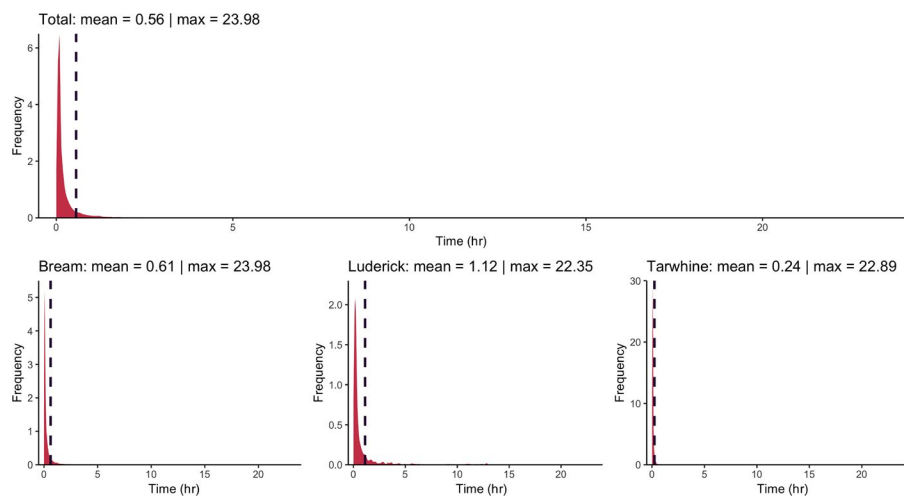
FIGURE 2 The *plotDensities*() function can be used to inspect the distributions of elapsed time between consecutive acoustic detections

(a) R64K-4138 - Track_10

(b) R64K-4125 - Track_03
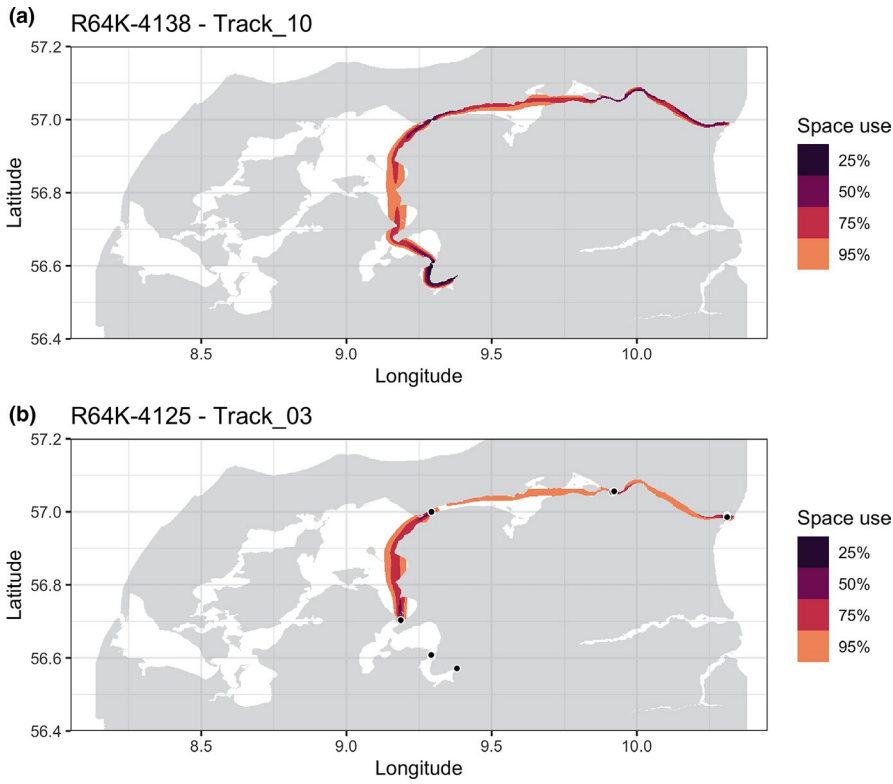
FIGURE 4 Dynamic Brownian Bridge Movement Models (Table 5) of two brown trout (a, b) tracked in the Limfjord, Denmark, plotted using *plotContours*()

(a)

(b)

(c)
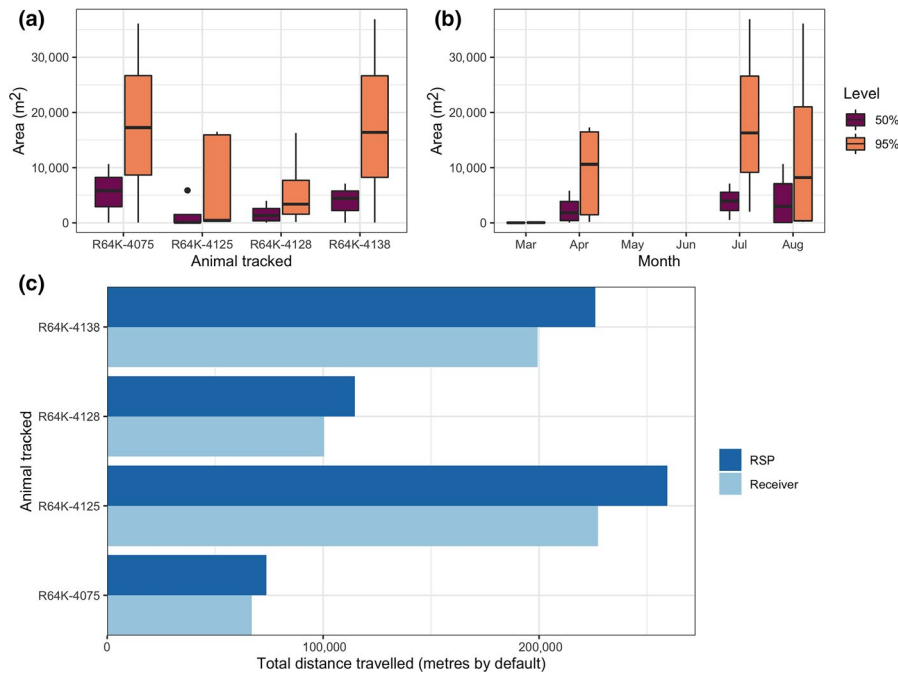
FIGURE 5 Distribution of space use areas from the dBBMM by (a) animal tracked and (b) month and (c) total distances travelled calculated with Refined Shortest Paths (RSP) versus only the receiver positions (Receiver) plotted with *plotDistances*()

consecutive positions to calculate space use areas (Kranstauber et al., 2012), therefore, similar location errors might lead to larger or smaller UDs depending on the animal's speed. Alternatively, a user-defined error increase can be set (in metres) using the argument *er.ad*. The location error reaches its maximum at the midpoint of the space or time elapsed between the first and second detections and starts decreasing again as the second detection approaches (Tables 2 and 3).

2.3 | Calculating UD areas

The UDs are calculated with *dynBBMM*(), and performed according to the following temporal resolutions: (a) group dBBMM and (b) timeslot dBBMM. For group dBBMM, UDs are calculated at track level for each animal (Table 5). Alternatively, for timeslot dBBMM the UDs are calculated according to fixed temporal intervals by

FIGURE 6 Distributions of (a) daily areas of 50% use for I = yellowfin bream, II = luderick and III = tarwhine, tracked in Lake Macquarie, Australia. Generalized linear models (Appendix 1) including the effects of (b) rainfall upon the areas of 50% use of luderick, and (c) water temperature upon the overlaps between yellowfin bream and tarwhine. Shaded areas and dashes (b and c) represent the 95% confidence intervals and the raw data respectively
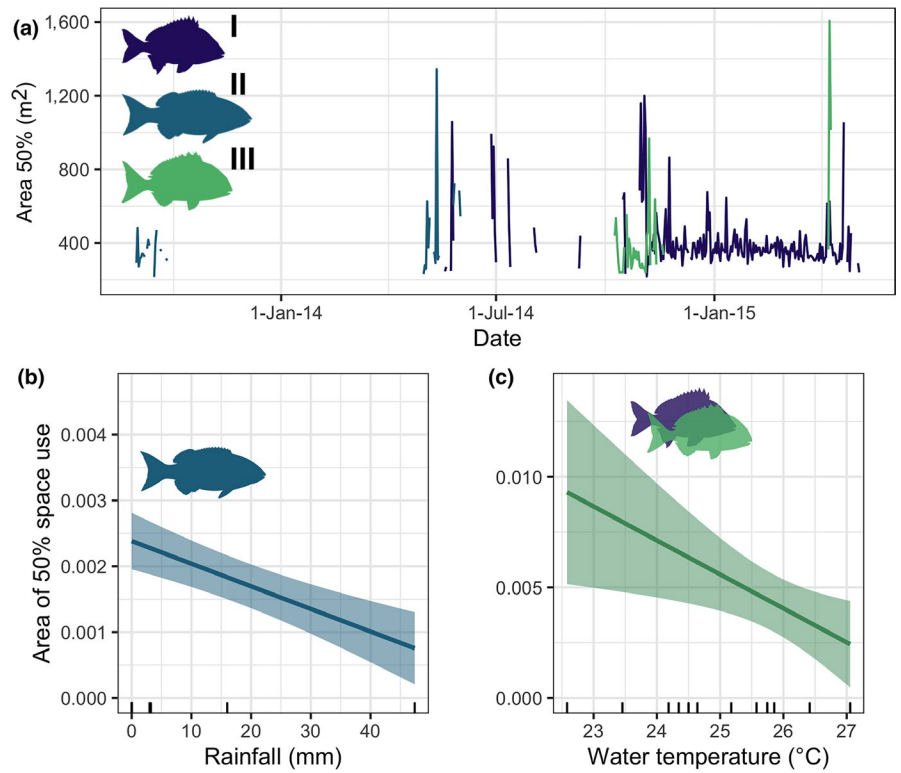
FIGURE 7 Space use areas at group level using *plotAreas()* for three yellowfin bream and one tarwhine detected during the same timeslot at Lake Macquarie, Australia, including the (a) plots using *plotAreas()* and (b) the *dynBBMM()* metadata
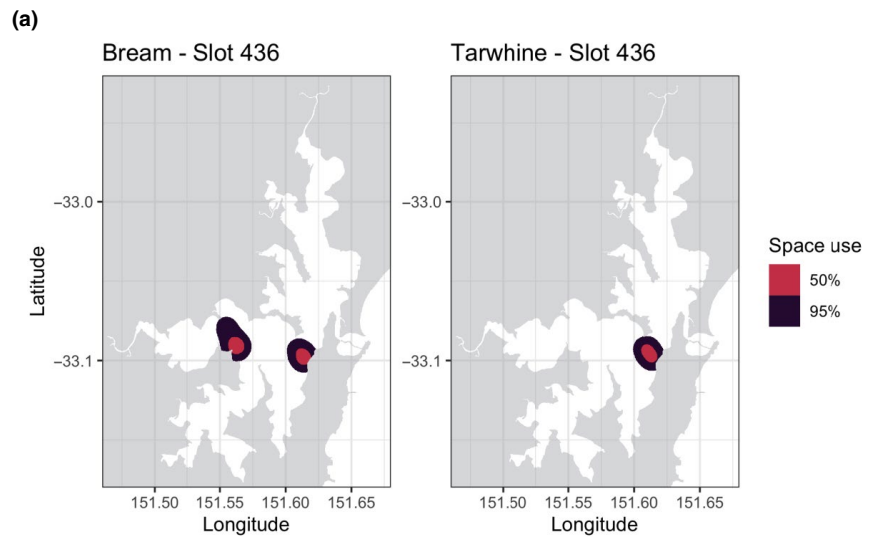
Group	Tag	Slot	valid.n	First.time	Last.time	Timespan
Bream	A69-9004-485	436	22	2014-11-11 11:09:26	2014-11-11 23:11:54	12.0 hours
Bream	A69-9004-494	436	48	2014-11-11 00:53:57	2014-11-11 23:28:10	22.6 hours
Bream	A69-9004-496	436	272	2014-11-11 00:05:57	2014-11-11 23:59:39	23.9 hours
Tarwhine	A69-9004-481	436	18	2014-11-11 05:11:40	2014-11-11 23:21:19	18.2 hours

defining a *timeframe* argument (in hours). This option divides the monitoring period into smaller windows of equal length (starting at midnight on the first day of data) and calculates the dBBMMs within each temporal window, hereafter referred to as timeslots (Tables 6 and 7). When a limited number of receivers are used, setting a short *timeframe* will cause the dBBMMs to include only interpolated locations. Therefore, we suggest first exploring the output of *plotDensities*() to decide the best *timeframe* to use (Figure 2). The space use areas are obtained for any contour of interest with *getAreas*(), for both group and timeslot dBBMM. These can be calculated at track (i.e. individual), or group (i.e. for all individuals simultaneously) levels.

2.4 | Calculating the overlaps between biological groups

The overlaps are retrieved using *getOverlaps*(), which only works if group areas are provided. Overlaps correspond to the amount of the smallest group area that lies within the largest group area and are returned both in absolute and percentage values. For group dBBMM analysis, overlaps represent the overall amounts of spatial overlap between two groups, whereas when timeslot dBBMM are used, the overlaps are calculated separately for each timeslot.
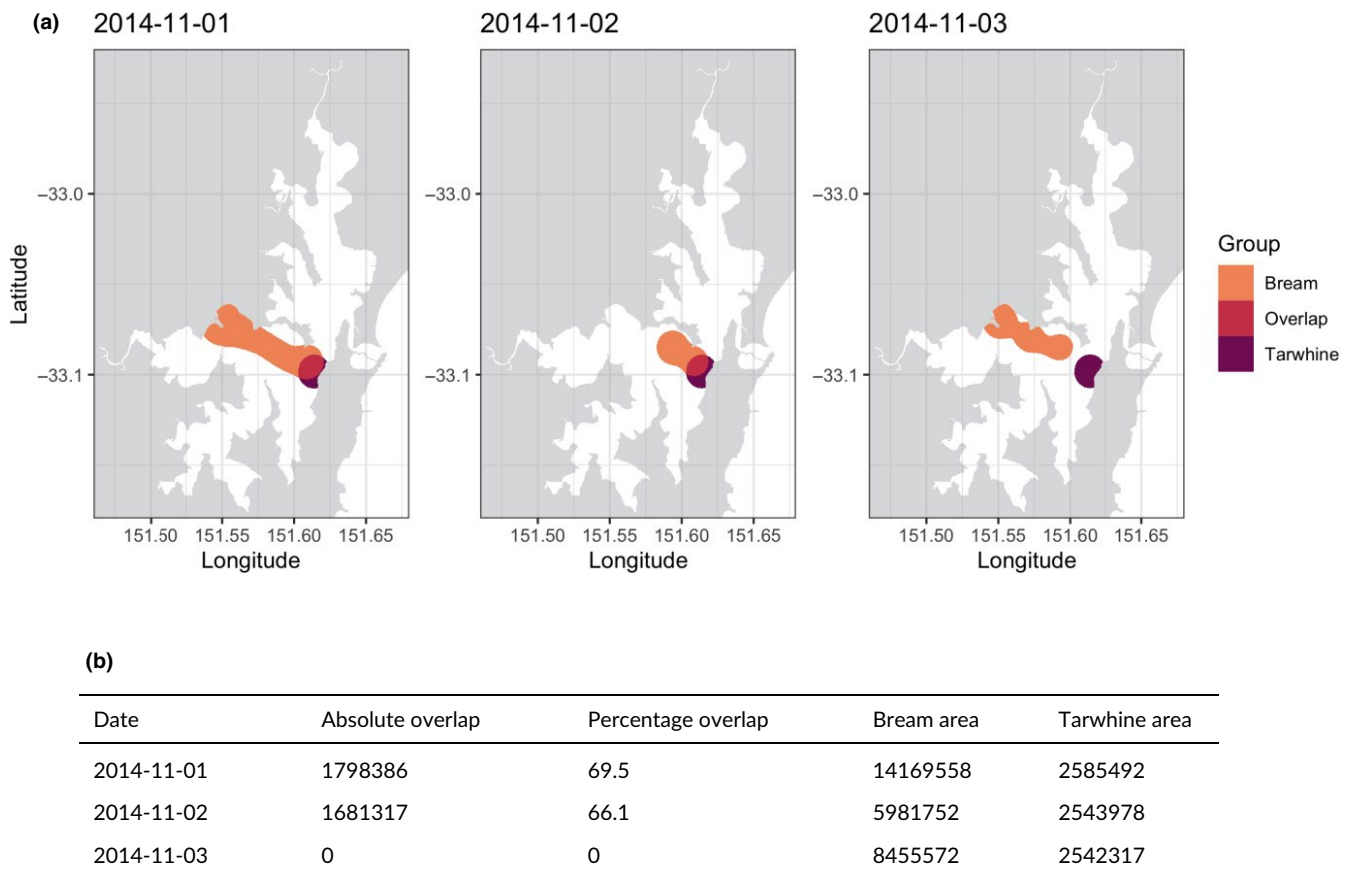
3 | TESTING THE METHOD

3.1 | Intraspecific patterns of space use: RSP performance

Refined Shortest Paths provides realistic tracks of monitored animals following the water contours (Figure 3). The dBBMMs can be visualized using *plotContours*() (Figure 4), and its output reveals individual-specific movement patterns (Figure 5a), together with temporal variations in space use (Figure 5b). Comparing the *runRSP*() output, all individuals have travelled significantly longer distances (paired *t* test, $t = -3.01$, $df = 11$, $p = 0.012$) when using the RSP tracks in comparison with only the receiver locations (Figure 5c). This indicates that, by generating exclusively in water paths, RSP provides more accurate movement patterns as it accounts for the generally non-linear trajectories between stations. Details on the biological applicability can be found in Appendix 1.

3.2 | Interspecific patterns of fine-scale space use

A daily resolution (i.e. *timeframe* = 24 hr) was used to obtain standardized UDs (i.e. timeslot dBBMM) and the overlaps in space and time for three species. The daily distributions of the 50% contours

(b)

Date	Absolute overlap	Percentage overlap	Bream area	Tarwhine area
2014-11-01	1798386	69.5	14169558	2585492
2014-11-02	1681317	66.1	5981752	2543978
2014-11-03	0	0	8455572	2542317

FIGURE 8 Daily areas and overlaps between yellowfin bream and tarwhine at the 95% contour including (a) the plots with *plotOverlaps*() and (b) overlaps and areas used in Lake Macquarie, Australia

(i.e. areas where animals spent half of the tracking time), revealed periods when each species used larger/smaller areas (Figure 6a). Further statistical analysis identified significant influences of abiotic conditions upon space use and overlap between species (Appendix 1; Figure 6b,c). The *plotAreas*() function shows the combined space use when multiple individuals are simultaneously detected on a particular timeslot (Figure 7). Overlapping areas can be plotted using *plotOverlaps*(), which allows to investigate the exact locations where different groups co-occurred (Figure 8).

3.3 | Loss of individual receivers from an array

A simulation study showed significant relationships between percentage receiver loss and the total distances travelled, and the sizes of the 50% and 95% contour areas (Appendix 1). The inter-individual variations observed (Figure 9) indicate that results are likely to vary, not only depending on which receivers are lost, but also on the individual-specific movements (Figure 10). Nevertheless,

similar null effect thresholds were observed across all individuals and metrics analysed (Figure 9), suggesting that RSP can overcome issues with space use calculations if <25% of receivers are lost. However, study-specific elements such as the number of receivers or the deployment locations are likely to influence the threshold of how many receivers can be lost before impacting results.

4 | CONCLUSIONS

Refined Shortest Paths is an efficient tool providing realistic estimates of animal space use in environments constrained by landmasses and can be easily customized depending on the array configuration and species monitored. This package not only provides a tool for calculating standardized UDs, but also quantifies the overlaps between the different biological groups monitored. Overall, movements are analysed by calculating overlaps in space, and fine-scale patterns can be analysed by calculating overlaps in both space and time. The latter might be used for applying further statistical analysis to test
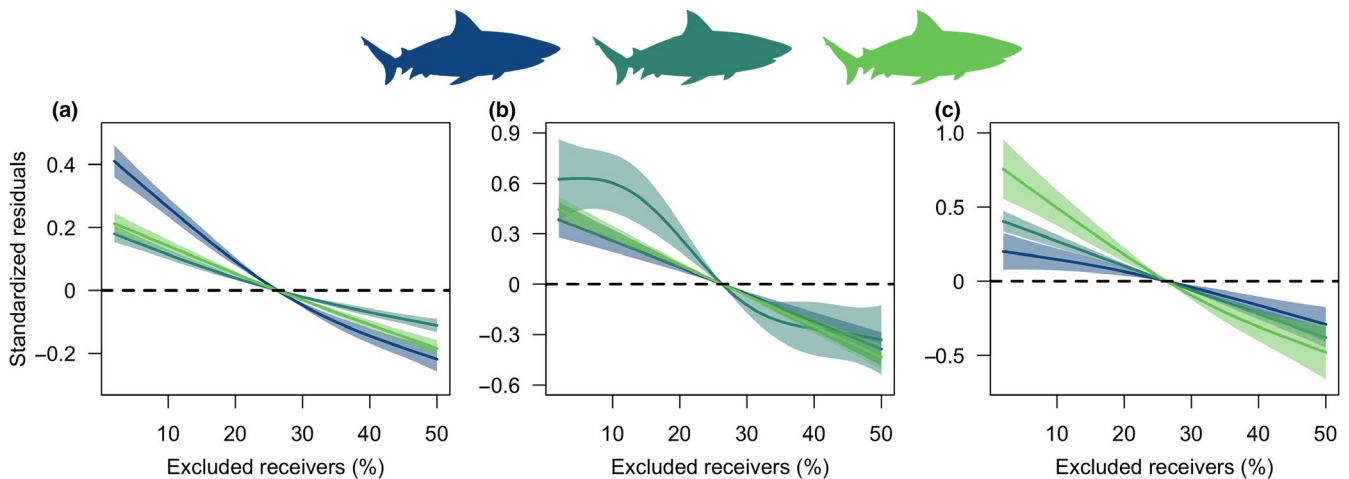
FIGURE 9 Generalized additive models (Appendix 1) of (a) total distances travelled, (b) 50% areas and (c) 95% areas in relation to the frequencies of excluded acoustic receivers for bull sharks tracked in Sydney, Australia. Dashed lines and shaded areas represent the null effects and the 95% confidence intervals respectively
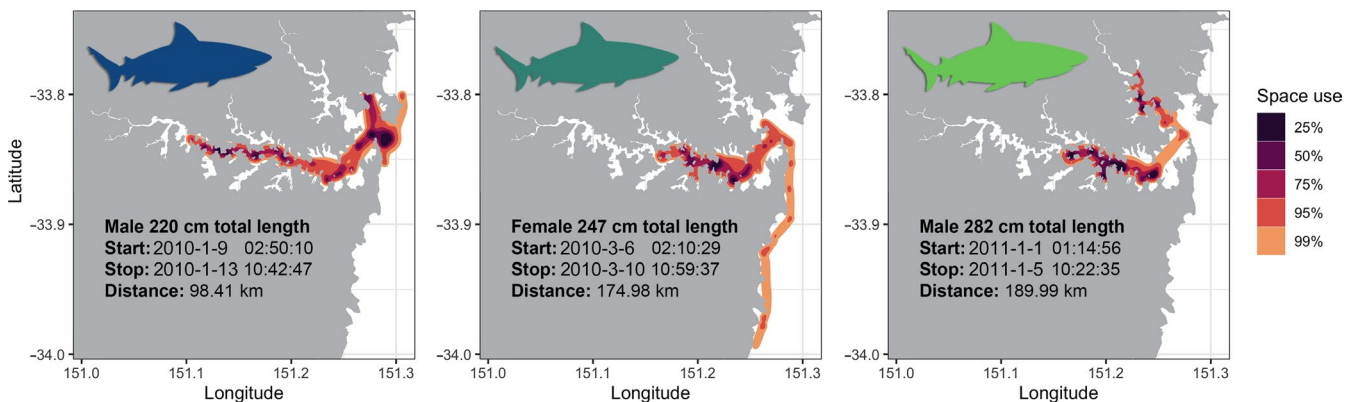
FIGURE 10 Dynamic Brownian Bridge Movement Models of three bull sharks tracked in Sydney, Australia, on 5 consecutive days. The colour and transparency of the landmasses can be changed using the argument *land.col* in *plotContours*()

hypotheses about the potential spatial, temporal and environmental variables influencing areas of space use and also the co-occurrence of different species or groups of interest (e.g. sex, age/length). The array configuration is likely to influence the potential of RSP to overcome limitations as a consequence of receiver loss. We reinforce that this is not a primary goal from RSP and should be seen as an additional benefit from the analysis.

AUTHORS' CONTRIBUTIONS

Y.N., H.F., V.M.P., A.F.S. and R.H. conceived the ideas and designed the methodology; A.F.S., V.M.P., K.A. and M.D.T. collected the data; Y.N. and H.F. wrote the package code, analysed the data and led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

PEER REVIEW

The peer review history for this article is available at https://publons.com/publon/10.1111/2041-210X.13484.

DATA AVAILABILITY STATEMENT

The package code is stored on GitHub (https://github.com/YuriNiella/RSP) and a Zenodo Repository: https://zenodo.org/record/3981529 (Niella & Flávio, 2020).

ORCID

Yuri Niella https://orcid.org/0000-0003-1878-6091
Hugo Flávio https://orcid.org/0000-0002-5174-1197
Victor M. Peddemors https://orcid.org/0000-0002-8743-9782
Robert Harcourt https://orcid.org/0000-0003-4666-2934

REFERENCES

Aspillaga, E., Safi, K., Hereu, B., & Bartumeus, F. (2019). Modelling the three-dimensional space use of aquatic animals combining topography and Eulerian telemetry data. *Methods in Ecology and Evolution*, *10*(9), 1551–1557. https://doi.org/10.1111/2041-210X.13232

Crossin, G. T., Heupel, M. R., Holbrook, C. M., Hussey, N. E., Lowerre-Barbieri, S. K., Nguyen, V. M., ... Cooke, S. J. (2017). Acoustic telemetry and fisheries management. *Ecological Applications*, *27*(4), 1031–1049. https://doi.org/10.1002/eap.1533

Espinoza, M., Farrugia, T. J., Webber, D. M., Smith, F., & Lowe, C. G. (2011). Testing a new acoustic telemetry technique to quantify long-term, fine-scale movements of aquatic animals. *Fisheries Research*, *108*(2–3), 364–371. https://doi.org/10.1016/j.fishres.2011.01.011

Flávio, H. (2020). *actel: Acoustic telemetry data analysis* (R package version 1.0.0). CRAN. Retrieved from https://cran.r-project.org/package=actel

Gannon, R., Payne, N. L., Suthers, I. M., Gray, C. A., van der Meulen, D. E., & Taylor, M. D. (2015). Fine-scale movements, site fidelity and habitat use of an estuarine dependent sparid. *Environmental Biology of Fishes*, *98*(6), 1599–1608. https://doi.org/10.1007/s10641-015-0385-5

Heupel, M. R., Munroe, S. E. M., Lédée, E. J. I., Chin, A., & Simpfendorfer, C. A. (2019). Interspecific interactions, movement patterns and habitat use in a diverse coastal shark assemblage. *Marine Biology*, *166*(6), 1–17. https://doi.org/10.1007/s00227-019-3511-7

Kessel, S. T., Cooke, S. J., Heupel, M. R., Hussey, N. E., Simpfendorfer, C. A., Vagle, S., & Fisk, A. T. (2014). A review of detection range testing in aquatic passive acoustic telemetry studies. *Reviews in Fish Biology and Fisheries*, *24*(1), 199–218. https://doi.org/10.1007/s11160-013-9328-4

Kie, J. G., Matthiopoulos, J., Fieberg, J., Powell, R. A., Cagnacci, F., Mitchell, M. S., ... Moorcroft, P. R. (2010). The home-range concept: Are traditional estimators still relevant with modern telemetry technology? *Philosophical Transactions of the Royal Society B: Biological Sciences*, *365*(1550), 2221–2231. https://doi.org/10.1098/rstb.2010.0093

Kranstauber, B., Kays, R., Lapoint, S. D., Wikelski, M., & Safi, K. (2012). A dynamic Brownian bridge movement model to estimate utilization distributions for heterogeneous animal movement. *Journal of Animal Ecology*, *81*(4), 738–746. https://doi.org/10.1111/j.1365-2656.2012.01955.x

Niella, Y., & Flávio, H. (2020). Data from: YuriNiella/RSP: First released version (0.0.1). *Zenodo*, https://doi.org/10.5281/zenodo.3981529

Pastor, J., Verdoit-Jarraya, M., Astruch, P., Dalias, N., Nelva Pasqual, J. S., Saragoni, G., & Lenfant, P. (2009). Acoustic telemetry survey of the dusky grouper (*Epinephelus marginatus*) in the Marine Reserve of Cerbère-Banyuls: Informations on the territoriality of this emblematic species. *Comptes Rendus – Biologies*, *332*(8), 732–740. https://doi.org/10.1016/j.crvi.2009.03.010

Payne, N. L., van der Meulen, D. E., Gannon, R., Semmens, J. M., Suthers, I. M., Gray, C. A., & Taylor, M. D. (2013). Rain reverses diel activity rhythms in an estuarine teleost. *Proceedings of the Royal Society B: Biological Sciences*, *280*(1750), 20122363. https://doi.org/10.1098/rspb.2012.2363

R Core Team. (2020). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. https://www.R-project.org/

Taylor, M. D., & Ko, A. (2011). Monitoring acoustically tagged king prawns *Penaeus* (*Melicertus*) *plebejus* in an estuarine lagoon. *Marine Biology*, *158*(4), 835–844. https://doi.org/10.1007/s00227-010-1610-6

Wilson, K., Hanks, E., & Johnson, D. (2017). Estimating animal utilization densities using continuous-time Markov chain models. *Methods in Ecology and Evolution*, *12*(10), 3218–3221. https://doi.org/10.1111/2041-210X.12967

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.