Commentary

# A comparison between traditional kernel-based methods and network analysis: an example from two nearshore shark species

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## ARTICLE INFO

Understanding how marine species use their environment has become increasingly important in management and conservation. Acoustic monitoring allows long-term tracking of marine animal movement that is traditionally analysed using kernel-based home range estimators. These traditional methods, however, are limited because they do not examine movement pathways within activity spaces. Network analysis (NA) provides an alternative approach to traditional home range analysis that treats acoustic receivers as network nodes and analyses movement between nodes. To investigate the utility of NA in identifying core use areas and compare the results with traditional analysis, a case study using acoustically monitored coastal sharks was conducted. To make direct comparisons with static traditional analysis a temporal scale was not explicitly explored. Comparison of traditional analysis and NA demonstrated that both methods provided similar results for identifying core use areas (50% kernel utilization distribution (KUD) equivalent), but that NA tended to overestimate general use areas (95% KUD equivalent) compared to kernel-based methods. Furthermore, frequent bidirectional movements within core use areas were identified by NA, indicating the importance of movement corridors within or between core areas. Movements between acoustic receivers outside core use areas were less frequent and unidirectional suggesting transiting movements. Therefore, NA may be a practical alternative to traditional home range metrics by providing useful data interpretation that allows for a comprehensive picture of animal movement, including identifying core use areas and pathways used.

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Data on animal movement patterns, connectivity and habitat use have become crucial elements in effective management and conservation (Greene et al., 2009; Rayfield, Fortin, & Fall, 2011). A complete understanding of animal movement must consider how biological functions (e.g. foraging, reproduction, predator avoidance) and environmental factors (e.g. salinity, temperature, competition) influence movement (Acevedo-Gutiérrez, 2009; Rogers & White, 2007). Empirical analysis of spatial and temporal changes in location and distribution of animals has traditionally applied activity space measures including, but not restricted to, home range metrics, random walks or theoretical models such as Lévy flight and dispersal measures (Greenwood & Swingland, 1983; Turchin, 1998). However, understanding drivers for movement and interactions between marine species and their environment remains a challenge (Croft, James, & Krause, 2008).

Technological advances such as acoustic monitoring have allowed scientists to obtain long-term movement and behaviour data for marine organisms (Simpfendorfer, Heupel, & Collins, 2008; Voegeli, Smale, Webber, Andrade, & O'Dor, 2001). Acoustic monitoring provides data sets of significant size and quality, but few standardized methods have been developed to analyse the data produced (Heupel, Semmens, & Hobday, 2006; Rogers & White, 2007). Researchers either use coarse data (i.e. widely spaced acoustic receiver locations) or interpolate data using methods such as positioning algorithms (Hedger et al., 2008; Simpfendorfer, Heupel, & Hueter, 2002). However, interpolation methods do not produce high accuracy in calculated positions due to aggregation of data at the detection range of a receiver and across relatively long time periods (Hedger et al., 2008). A standardized method for analysing acoustic data using raw detections could reduce data processing requirements and decrease the possibility of introducing errors. Furthermore, a standardized method would provide consistency in the analysis and

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interpretation of acoustic monitoring data that may increase the ability to compare studies.

Network analysis investigates the relationship between nodes, with connections between nodes called edges, and the combined connections represented as a network (West, 2001) and may provide a standardized approach to acoustic monitoring data sets. Applied to acoustic monitoring, nodes represent acoustic receivers deployed in the study area and edges represent movement (trajectory) of an animal between nodes (Jacoby, Brooks, Croft & Sims, 2012). Thus, networks can be constructed from detection data obtained from acoustic receivers. Node and edge properties can also be complemented with additional information. For example, physical and environmental attributes such as habitat type, salinity or depth can be included in analyses. Consequently, NA can be adapted to various situations and scales (Stehfest et al., 2013) depending on what is examined (Croft et al., 2008). Network analysis can also provide information that traditional methods do not. For example, weighted directional movement patterns may highlight corridors of movement between important habitats/areas. Recent NA studies have used acoustic monitoring data to look at social behaviour of sharks (Jacoby, Croft & Sims, 2012; Mourier, Vercelloni, & Planes, 2012), fish aggregations (Stehfest et al., 2013), animal movements (Finn et al., 2014; Jacoby, Brooks, et al., 2012) and spatial utilization (Stehfest, Patterson, Barnett, & Semmens, 2014). The use of NA in acoustic monitoring studies, however, is still in its infancy and its utility in analysing animal movement is yet to be well established.

Since NA has rarely been applied to acoustic monitoring data, it is important to test and compare outputs against traditional analyses and understand where differences occur, what benefits may be generated and why. Therefore, the aims of this study were to determine the utility of NA in identifying core use areas of two species of acoustically monitored coastal sharks, compare results with traditional kernel-based analysis, and identify additional information that could be generated by NA to extend the interpretation of animal movement data. Finally, to make direct comparisons with static traditional analysis a temporal scale was not explicitly explored.

## METHODS

Acoustic monitoring data from Cleveland Bay, north Queensland, Australia, previously analysed by Knip, Heupel, and Simpfendorfer (2012), Knip, Heupel, Simpfendorfer, Tobin, and Moloney (2011) were used to test the efficacy of the NA approach. Methods below describe the acoustic array, methods of Knip et al. (2012; 2011) and the NA approach applied to this data set. Details on deployment locations and settings of acoustic receivers can be found in Knip et al. (2012; 2011). The data used in this study will be stored in the AATAMS database https://aatams.emii.org.au/aatams/.

### Ethical Note

In research by Knip et al. (2012; 2011) sharks were captured on 500 m bottom-set longlines soaked for 1 h. Gangions included 1 m of 5 mm nylon cord, 1 m of wire leader and a 14/0 Mustad tuna circle hook. Captured sharks were measured to the nearest cm, sexed and tagged with a rototag in the first dorsal fin for identification and an acoustic transmitter implanted. Transmitters (V16 16 mm × 65 mm acoustic transmitters (Vemco Ltd) which were less than 1% of shark body weight) were surgically implanted into the body cavity. Sharks were restrained using tonic immobility, a 3–4 cm incision made in the abdomen, a transmitter inserted and

the incision sutured with running stitches using absorbable sutures and disposable needles to ensure healing. All passively monitored animals were in good condition upon capture and released in good condition within 10 min of landing at their site of capture.

All Knip et al. (2012; 2011) research activities were conducted under the GBRMPA permit number G10/33315.1, Queensland DPIF permit number 90911 and James Cook University animal ethics approval no. A1566.

### Study Site

Cleveland Bay on the northeast coast of Queensland, Australia, has an area of about 225 km$^2$, is relatively shallow (<10 m) and has varied coastal habitats including coral reef, sand bank, intertidal mudflats, sea grass and mangrove habitats (Knip et al., 2011). Acoustic monitoring was used to track 43 pigeye sharks, Carcharhinus amboinensis, and 29 spottail sharks, Carcharhinus sorrah between 2008 and 2010 (Knip et al., 2012; 2011). Sixty-five acoustic receivers (VR2W Vemco Ltd), 28 in the western section and 37 in the eastern section (Fig. 1), were deployed to track shark movements. Acoustic receivers were deployed on average 2 km apart and had a detection range of about 900 m, so there was no overlap in detection ranges.

### Data Analysis

Receiver data were downloaded quarterly and used to describe activity space and movement patterns (Knip et al., 2012; 2011). Prior analysis using traditional activity space approaches (kernel utilization distributions, KUD; extent of movement (95% KUD) and core use area (50% KUD) of C. amboinensis and C. sorrah) were compared with NA results. All NA and statistical analyses were conducted in the R environment (R Development Core Team, 2014) using the sna (Butts, 2013; CRAN: sna), igraph (Csardi & Nepusz, 2006; CRAN: igraph) and tnet (Opsahl, 2009; CRAN: tnet) packages. UCINet (Borgatti, Everett, & Freeman, 2002) and Netdraw (Borgatti, 2002) were used for network representation. Imported data were used to create square movement matrices that counted the presence at, and movements between, receivers, regardless of time required to reach the next receiver. Only detections at the same receiver that were 5 min or more apart were included in the network. Square matrices were used to create directed and weighted networks which represented the activity space of an individual. Each network was tested for nonrandom associations of receivers, based on observed movements, using a modified version of the Bejder–Manly method (Mourier et al., 2012; Whitehead, Bejder, & Andrea Ottensmeyer, 2005). The Bejder–Manly method randomized receivers' associations to create null random networks to control for the sampling design of the receiver array. Receiver community memberships (i.e. group number of the community/cluster in the network) were calculated from the observed matrix to obtain group size and numbers of communities in the network and then permuted within each new matrix. The observed matrix was randomized 10 000 times with 1000 flips (i.e. receiver community membership was randomly flipped within each new matrix) per permutation within sampling periods (Whitehead et al. 2005). Coefficient of variation and likelihood ratio tests ($\chi^2_2$, $P < 0.05$) were used to determine whether receivers' associations in the study area were significantly different from random. Data distribution and normality were tested prior to statistical analysis and if the normality assumption was violated, a nonparametric test was performed.

**Figure 1.** Map of Cleveland Bay. ●: Receiver locations; reefs are outlined (dashed) in light grey and mangroves are indicated in dark grey. Inset indicates location of Cleveland Bay along the Queensland coast.

*Core Use Receiver Identification*

To assess the ability of NA to describe activity space by *C. amboinensis* and *C. sorrah*, monthly networks were constructed for individual sharks. The shape of the network varied by individual and month because of changes in movement patterns. The relative importance of receivers in each network were explored by first calculating centrality metrics for each receiver (Borgatti, 2006). Centrality metrics indicate how often receivers were visited within the activity space (Borgatti & Everett, 2006); therefore, high centrality values may be analogous to core use areas such as those identified by 50% KUDs (Heupel, Simpfendorfer, & Hueter, 2004). To identify core use areas three centrality metrics were used: node strength, closeness and eigenvector centrality. Node strength was a measure of the

connection weight, which represented the total number of incoming/outgoing movements from a receiver (Barrat, Barthelemy, Pastor-Satorras, & Vespignani, 2004). Closeness measured how central a receiver's position was in network space (i.e. smallest number of edges (pathways) linking receivers, i.e. geodesic distance). The lower a receiver's geodesic distance the higher the closeness (Urban, Minor, Treml, & Schick, 2009). Finally, eigenvector centrality indicated how strategically placed a receiver was within the network; receivers with a high eigenvector centrality value had high node strength values and were connected to receivers with similarly high node strength values (Bodin, Ramirez-Sanchez, Ernstson, & Prell, 2011). These three centrality metrics were used to explore the importance of individual receivers in Cleveland Bay to identify those that corresponded to core use areas (i.e. core use receivers, CUR).

To identify CUR for each shark in each month, five different approaches were tested. Approaches 1–3 were based on the values of individual centrality metrics, approach 4 was based on a combination of centrality metrics and principal component analysis (PCA) and approach 5 on the number of movements between each pair of receivers (percentage approach). The node strength, closeness and eigenvector centrality approaches identified receiver(s) with the highest centrality metrics score and assigned them as CUR. Receivers with similar properties were identified using a structural equivalence graph (i.e. receivers within the same cluster in the structural equivalence graph were also identified as CUR; (Bodin et al., 2011)). Structural equivalence graphs indicated two receivers were structurally equivalent if they had identical movements to and from all others in the network (Faust, 1988).

The PCA approach (Fig. A1) examined all three centrality metrics to identify which metric, or group of metrics, could be used to identify CUR. To remove collinearity, a Spearman correlation analysis was performed between all pairs of centrality metrics and those with $\rho > 0.75$ were removed. The order in which centrality metrics were removed due to collinearity was based on the ranking system: eigenvector centrality > node strength > closeness, with the metric of the lowest rank removed. A PCA was used with the remaining centrality metrics to determine which was most influential and could explain the network shape. Principal component analysis output combined all of the centrality metrics (i.e. principal components or eigenvectors) and loadings of individual centrality metrics in each principal component. To identify the most important centrality metrics two steps were used. First, only principal components that had values >1 were selected and from these only principal components that accounted for 80% of the variance were kept (Jolliffe, 2002). Second, from the remaining principal components centrality metrics that had the highest absolute loading values were retained. Receivers with the highest score were assigned to the core use group. Finally, a structural equivalence graph was used to select receivers with similar characteristics to core receiver(s) and were added to the core use group. Core use receivers were only identified for months in which there were sufficient data to produce a structural equivalence graph. If a graph was not produced that month for that individual, it was excluded from further analysis.

The percentage approach identified CUR as those for which 50% of detections occurred (i.e. equivalent to 50% KUD) based on counts of the total number of movements between receivers. The CUR were selected one at a time based on the number of detections at and movements to that receiver, starting at the receiver with the highest number of movements. Receivers were selected until 50% of total movements were reached. The general use receivers (GUR; equivalent to the 95% KUD) were determined the same way using 95% of the movements and excluding receivers identified as core use.

*Comparing Core Use Receivers with Core Use Areas*

In Knip et al. (2012; 2011), an algorithm was used to estimate the positions, or centre of activity, of each individual at 30 min time steps. Using centre of activity positions, 50% and 95% KUDs were calculated in the adehabitat package for R (Calenge, 2006). To determine whether the five NA approaches identified the same core use areas as KUD, the identity and number of receivers within 50% and 95% KUDs were determined. To compare the number of CUR and GUR between approaches 1–5 and the KUD approach, a Mann–Whitney $U$ test was used. In addition, percentages of similarities were compared with identities of the CUR within 50% KUDs and GUR in 95% KUDs. Since the four approaches based on centrality metrics used all of the data, a difference between GUR (100% area used) and receivers in 95% KUDs was expected.

*Core Use Receiver Importance*

To define the importance of CUR in each network, CUR were removed, the networks visually examined and network properties (or network metrics) checked to determine removal effects. Receiver removal analysis of CUR was performed in two different ways: first, each CUR was independently removed from the network; second, each CUR was successively removed from the network. New networks were constructed after each removal; for instance, if a network had two CUR, receiver removal produced three new networks: two after the independent removal of the each CUR and one after removal of both CUR. Visual examination of the networks and network metrics (average path length, density and component) were used to determine whether removals decreased network centrality. Average path length was a measure of the ease of movement between pairs of receivers or how many receivers on average an individual passed through to go from one location in its network to another (i.e. movement steps). Low average path length meant that an individual travelled through few receivers (Rayfield et al., 2011). Density measured route selection (ranging from 0 to 1); when all receivers were connected to all others, the network had a density of 1. An individual had more routes to select from in a densely connected network. Components identified the number of subnetworks or isolates (receivers not connected to any other) that were disconnected from the rest of the network (i.e. movement between two components was not possible) and represented the level of network fragmentation (Bodin et al., 2011). Figures were plotted only considering removal up to the number where they were multiple values. A Mann–Whitney $U$ test was performed to compare network metrics before and after receiver removal. If removal analysis did not result in changes to the network, the receiver(s) was rejected as core use.

*Movement Pathways within Activity Space*

To explore movement within activity spaces, the number and frequency of network pathways within receiver groups (CUR and GUR), between receiver groups and by species were calculated. Pathway referred to a route between two nodes in the network used by an individual (Fall, Fortin, Manseau, & O'Brien, 2007). Pathways were classified as one-way (unidirectional) or two-way (bidirectional) for each receiver group, between receiver groups and per species to indicate directionality. Finally, the number of unidirectional versus bidirectional pathways, total number of pathways and their respective frequency were calculated. High-frequency pathways were defined as ≥10 uses per month based on 92% and 96% of pathways having counts of fewer than 10 for *C. sorrah* and *C. amboinensis*, respectively. Mann–Whitney $U$ tests and $t$ tests were used to determine whether pathway counts were similar between species; i.e. if there were significant differences in how the species moved within their activity space.

**RESULTS**

Network analysis and KUD methods were applied to data from nine juvenile *C. amboinensis* (five females, four males) and four adult *C. sorrah* (three females, one male). Sizes ranged from 73.5 to 129 cm (mean ± SE = 99.6 ± 7.3) for *C. amboinensis* and 96.5 to 115 cm (104.4 ± 3.9) for *C. sorrah*. Twenty-seven monthly networks, 15 for *C. amboinensis* and 12 for *C. sorrah*, were created and compared to the activity spaces estimated by Knip et al. (2012; 2011). Twenty-one

networks, 12 for *C. amboinensis* and nine for *C. sorrah*, showed evidence of nonrandom community membership ($P < 0.001$) and were used for the analysis; the other six networks were removed.

### Core Use Receiver Identification

All monthly networks produced structural equivalence graphs, showing receivers with similar connections, so no networks were removed from the analyses using this selection rule. The CUR and GUR were identified for the networks using the five approaches (Table 1). The PCA approach for *C. amboinensis* and closeness approach for *C. sorrah* produced the closest CUR estimates, and the percentage approach produced the closest GUR estimates, to those defined by the kernel-based method. Compared to KUD, the numbers of CUR and GUR from the PCA and percentage approaches were similar for both species, except for GUR using the PCA approach which was significantly different. On average, PCA and single centrality approaches produced 1.08 fewer CUR and 3.12 more GUR than KUDs, whereas the percentage approach produced 1.14 more CUR and 0.19 more GUR. The CUR and GUR estimates from the single centrality metric approaches were significantly different to KUDs, except for the *C. sorrah* CUR count which was similar to the 50% KUD (Table 1). Thus, among the five approaches, PCA and closeness best replicated KUD core use and percentage approach was best matched for GUR.

The CUR identified from the PCA approach produced two estimates (before being summed): PCA estimates were 1.75 (range 1–4) for *C. amboinensis* and 1.67 (range 1–2) for *C. sorrah*, and structural equivalence estimates were 1.75 (range 1–7) for *C. amboinensis* and 1.11 (range 0–2) for *C. sorrah* (Table A1). The number of CUR determined by PCA increased by 1.10 for *C. amboinensis* and 0.78 for *C. sorrah* after adding the receivers identified using structural equivalence graphs. Without testing for structural equivalence, results from PCA were lower than results from the single centrality metric approaches for both species. There were no significant differences in the number of CUR and GUR between species (Mann–Whitney $U$ test: CUR: $U = 64.00$, $N_1 = 12$, $N_2 = 9$, $P = 0.48$; GUR: $U = 53.00$, $N_1 = 12$, $N_2 = 9$, $P = 0.97$), suggesting both species used similar amounts of space.

**Table 1**
Comparison of *C. amboinensis* and *C. sorrah* core and general use areas using kernel utilization distribution (KUD) and network analysis approaches

| | CUR | | GUR | |
|---|---|---|---|---|
| | *C. amboinensis* | *C. sorrah* | *C. amboinensis* | *C. sorrah* |
| KUD | 3.92 (2–7) | 3.50 (2–9) | 9.14 (4–15) | 7.22 (4–9) |
| Node strength | 2.83 (2–9) | 2.56 (2–4) | 11.75 (5–20) | 10.78 (6–14) |
| $U$ ($P$ value) | 56.50 ($P$=0.04) | 24.50 (**$P$=0.07**) | 6.00 ($P$=0.02) | 0.00 ($P$=0.008) |
| Closeness | 1.83 (1–4) | 2.89 (1–7) | 12.75 (7–20) | 10.44 (7–14) |
| $U$ ($P$ value) | 66.00 ($P$=0.004) | 14.50 (**$P$=0.46**) | 0.00 ($P$=0.002) | 0.00 ($P$=0.01) |
| Eigenvector | 2.08 (1–3) | 2.33 (1–4) | 12.50 (6–20) | 11.00 (6–16) |
| $U$ ($P$ value) | 62.50 ($P$=0.009) | 24.50 (**$P$=0.07**) | 0.00 ($P$=0.004) | 0.00 ($P$=0.009) |
| PCA | 3.50 (2–9) | 2.78 (2–4) | 11.08 (5–20) | 10.56 (6–14) |
| $U$ ($P$ value) | 37.00 (**$P$=0.33**) | 16.00 (**$P$=028**) | 12.00 ($P$=0.04) | 0.00 ($P$=0.009) |
| Percentage | 4.92 (2–10) | 4.67 (2–10) | 8.50 (4–17) | 7.67 (3–10) |
| $U$ ($P$ value) | 17.50 (**$P$=0.17**) | 1.50 (**$P$=0.07**) | 41.50 (**$P$=0.47**) | 14.00 (**$P$=0.61**) |

Mean receiver count in core use (CUR) and general use (GUR) areas with paired Mann–Whitney $U$ test results ($N = 12$ for *C. amboinensis* and $N = 9$ for *C. sorrah*) for each receiver grouping are shown. Numbers in parentheses indicate range; bold represents nonsignificant results where network analysis and KUD provided similar results.

### Comparing Receiver Use with Core Use Areas

Comparison of CUR and GUR for KUD and NA revealed highest percentage similarity from PCA for both species (Tables 2 and 3, Fig. 2). Closeness and eigenvector centrality approaches had the lowest CUR percentage similarity compared to KUD for both species. Single centrality metric approaches had similar results for GUR percentage similarity for both species (about 76% for *C. amboinensis* and about 72% for *C. sorrah*). Results from the percentage and node strength approaches for CUR indicated percentage similarity varied between species; the percentage approach for *C. amboinensis* was second highest whereas the node strength approach was the second highest for *C. sorrah*.

### Core Use Receiver Importance

The range of network impacts caused by removal of CUR varied greatly. Visual examination of the new networks revealed that subnetworks and isolates (a receiver not connected to any other) were created after removal of CUR. Broken networks indicated that access to parts of the activity spaces were no longer available. For example, receivers could become unavailable and activity space disconnected (Fig. 3). As these changes substantially affected the network, no CUR were rejected based on visual examination. The removal of the most important nodes (CUR) resulted in increased network fragmentation (Table 4, Fig. 4). A significant increase in the number of network components occurred when three or more CUR were removed from networks (Mann–Whitney $U$ test: $U = 0.00$, $N_1 = 42$, $N_2 = 23$, $P < 0.001$ for both species and after both removal analyses), whereas eight or more GUR needed to be removed from both species networks (Mann–Whitney $U$ test: $U = 0.00$, $N_1 = 42$, $N_2 = 23$, $P < 0.001$ after successive removal analysis) to produce significant fragmentation of the network. The number of components before and after independent removal analysis of both species' GUR were similar (mean ± SE = $1.00 \pm 0.00$ before removal and $1.08 \pm 0.02$ after removal).

Furthermore, movement steps increased (about 79%) and route selection decreased (about 19%) for both species after removal of CUR, along with negligible increases in movement steps (about 16%) and route selection (about 24%) after removal of GUR (Table A2, Fig. A2). Movement steps increased by 37% and 79% and route selections decreased by 12% and 19% for *C. amboinensis* and *C. sorrah*, respectively (Table 4) and these differences were significant. These results suggest average moves between locations in the network were higher with fewer routes to choose from when receivers were removed. Consequently, when CUR were removed, network centrality decreased; thus confirming the importance of receivers identified as CUR.

**Table 2**
Receiver identification by network analysis approaches and kernel utilization distribution (KUD) for *C. amboinensis*

| | Node strength | Closeness | Eigenvector | 50% Network | PCA | KUD |
|---|---|---|---|---|---|---|
| Node strength | — | 5 | 46 | 59 | 89 | 62 |
| Closeness | 82 | — | 17 | 20 | 27 | 27 |
| Eigenvector | 90 | 84 | — | 36 | 38 | 34 |
| 95% Network | 65 | 61 | 68 | — | 68 | 68 |
| PCA | 96 | 84 | 87 | 62 | — | **79** |
| KUD | 77 | 73 | 77 | 70 | **72** | — |

Values above the diagonal are for core use receivers and those below for general use receivers. Bold represents highest percentage similarities between network analysis approaches and KUD.

**Table 3**
Receiver identification by network analysis approaches and kernel utilization distribution (KUD) for *C. sorrah*

|              | Node strength | Closeness | Eigenvector | 50% Network | PCA | KUD |
|--------------|---------------|-----------|-------------|-------------|-----|-----|
| Node strength | —            | 19        | 39          | 45          | 91  | 80  |
| Closeness    | 81            | —         | 8           | 31          | 23  | 25  |
| Eigenvector  | 92            | 80        | —           | 22          | 39  | 28  |
| 95% Network  | 48            | 40        | 43          | —           | 49  | 36  |
| PCA          | 98            | 81        | 86          | 49          | —   | **79** |
| KUD          | 77            | 69        | 71          | 54          | **82** | —  |

Values above the diagonal are for core use receivers and those below for general use receivers. Bold represents highest percentage similarities between network analysis approaches and KUD.

## Movement Pathways within Activity Spaces

Both species had similar pathway counts within core and general use areas, and marginally higher pathway counts between them (Tables A3 and A4). Pathway frequency in core use areas was approximately 49% higher than in general use areas and approximately 29% higher between core and general use areas. This significant difference in pathway use demonstrated the importance of core use pathways for both species. In addition, movement pathways in core use areas varied between species. *Carcharhinus sorrah* had lower pathway counts and higher frequencies in core use areas than *C. amboinensis*. This difference may indicate that *C. sorrah* moved more selectively and frequently within their core use areas
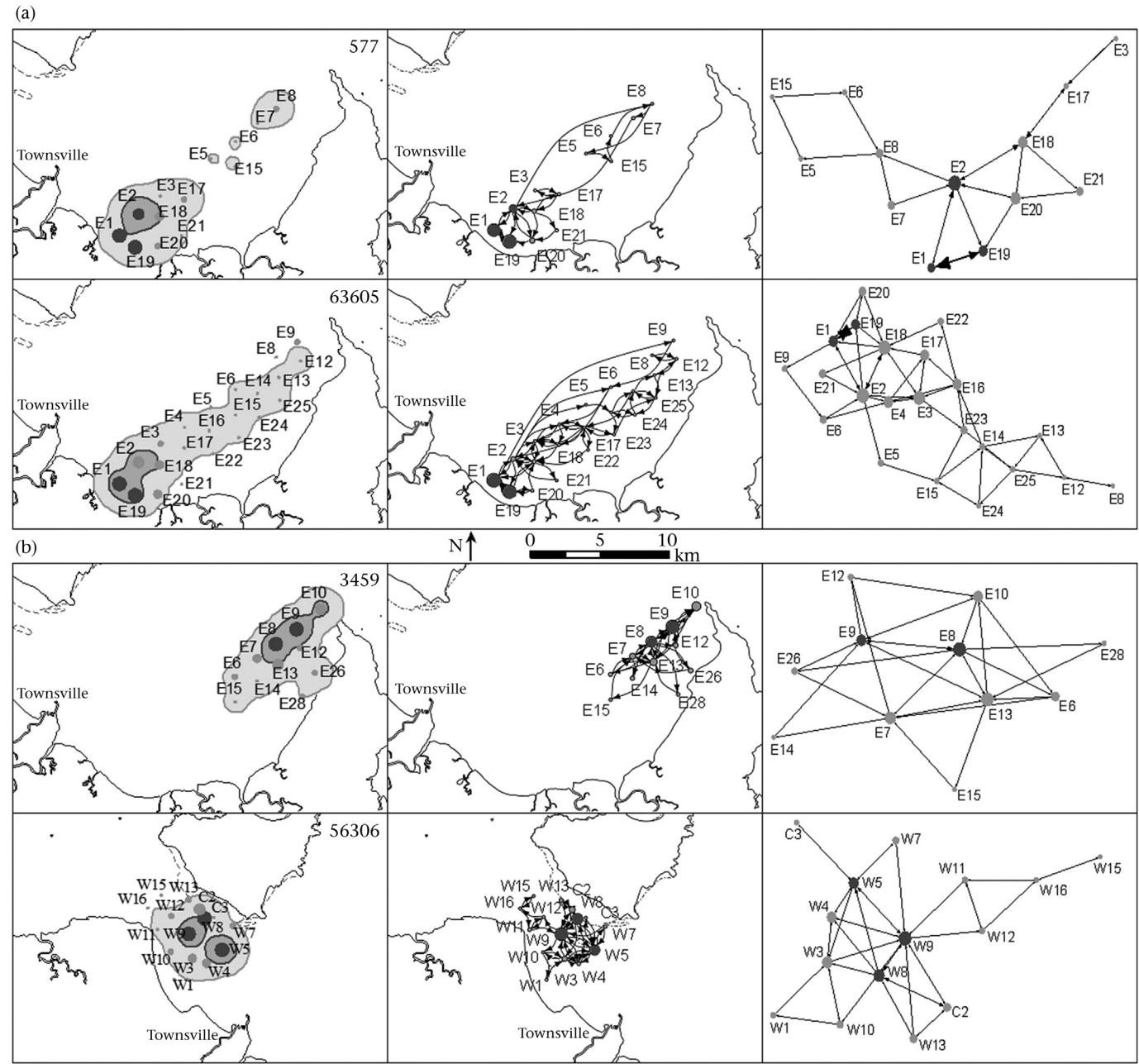


**Figure 2.** Activity space of (a) two *C. amboinensis* for November 2009 and March 2010 and (b) two *C. sorrah* for September 2010 and October 2009 in Cleveland Bay. Left-hand panels represent nodes from each network and KUDs for each individual, middle panels show the geographical representation of each network and right-hand panels show the spring embedding representation of each network. Node size represents the eigenvector centrality in the network node and KUD colour represents core (dark grey) and general (light grey) use; line thickness represents pathway frequency.
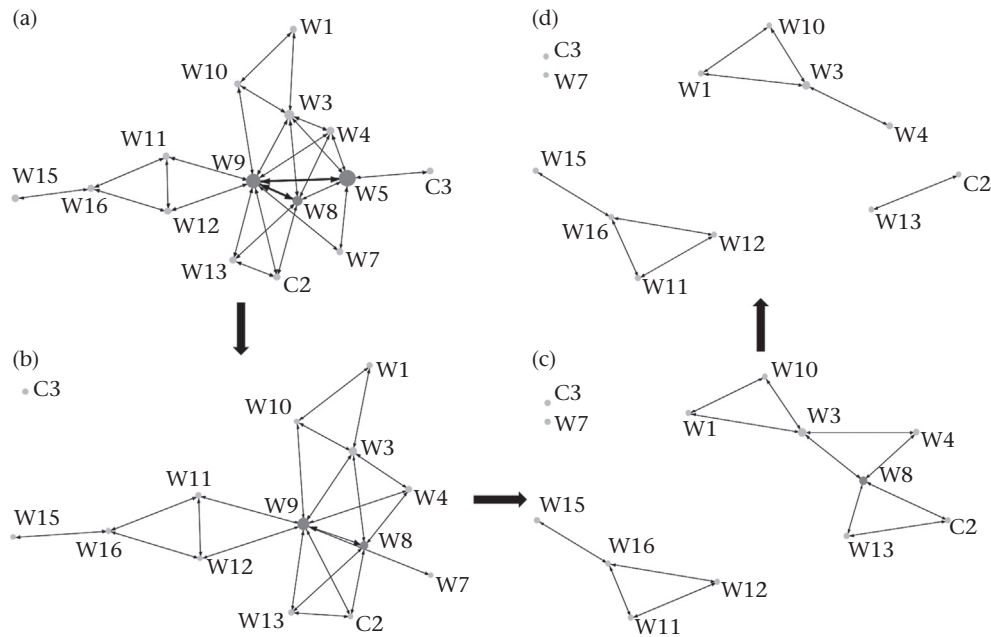
**Figure 3.** Visualization of core use receiver removal effects for a *C. sorrah* in September 2010. (a) The original network of activity space, (b) the resulting activity space after removing the node with highest importance (W5), (c) the resulting activity space after removing the next most important node (W9) and (d) the resulting activity space after removing the third most important node (W8).

than *C. amboinensis*. Finally, both species had similar total numbers of pathways within their networks, indicating each had similar numbers of movement paths within their activity space.

Different results were found in the numbers of unidirectional and bidirectional pathways between species (Tables A3 and A4). *Carcharhinus amboinensis* had approximately 47% more unidirectional than bidirectional pathways than *C. sorrah*, which had similar numbers of unidirectional and bidirectional pathways. In addition, bidirectional pathway frequency was approximately 76% higher for *C. amboinensis* and 87% higher for *C. sorrah* than unidirectional pathways. These results suggest bidirectional pathways were important for both species. Pathway directionality was similar in core and general use areas for both species (Table A4), but there was a significant difference between species in bidirectional pathway count and frequency between core and general use areas. This difference suggests *C. sorrah* was moving between core and general areas more frequently than *C. amboinensis*. Furthermore, 100% of pathways with frequency >4 were bidirectional for both species.

**Table 4**
Statistical comparison of the impact on the networks after the independent and the successive removal (RRA) of core use receivers

| Network metric | RRA | Independent removal | | Successive removal | |
|---|---|---|---|---|---|
| | | *C. amboinensis* | *C. sorrah* | *C. amboinensis* | *C. sorrah* |
| APL | Before | 4.16 (±0.27 SE) | 2.46 (±0.08 SE) | 4.16 (±0.27 SE) | 2.46 (±0.08 SE) |
| | After | 5.21 (±0.35 SE) | 3.66 (±0.24 SE) | 6.17 (±0.31 SE) | 5.17 (±0.47 SE) |
| | U (P value) | 83.00 (**P<0.001**) | 1.00 (**P<0.001**) | 57.00 (**P<0.001**) | 1.00 (**P<0.001**) |
| D | Before | 0.17 (±0.01 SE) | 0.24 (±0.01 SE) | 0.17 (±0.01 SE) | 0.24 (±0.01 SE) |
| | After | 0.16 (±0.01 SE) | 0.21 (±0.01 SE) | 0.14 (±0.01 SE) | 0.18 (±0.01 SE) |
| | U (P value) | 728.00 (**P<0.001**) | 325.00 (**P<0.001**) | 797.50 (**P<0.001**) | 325.00 (**P<0.001**) |

APL: mean movement steps; D: route selection. Paired Mann−Whitney *U* test results (*N* = 42 for *C. amboinensis* and *N* = 25 for *C. sorrah*) for each network metric are shown. Bold indicates significant results.

This demonstrated that in general, movement between receivers was normally bidirectional and pathways that were not repeatedly used were unidirectional. Unidirectional pathway count was higher and pathway frequency lower between core and general use areas and within general use areas for both species. Consequently, most bidirectional movements between receivers occurred within core use areas.

Frequently used movement pathways were shared within and between species. *Carcharhinus sorrah* individuals shared 14 high-frequency pathways (≥10 uses per month) on the eastern side of Cleveland Bay and none on the western side (Figs 2, 5). However, only 25% of these high-frequency pathways (*N* = 4) were shared by two individuals. Conversely, *C. amboinensis* individuals shared 17 high-frequency pathways, all on the eastern side of Cleveland Bay and 24 % of these were shared frequently by at least two individuals. This may indicate that both species shared space in a similar way. Both species shared 33 pathways, but only 14 were high-frequency pathways (Fig. 5). Highest frequency pathways (>100) for both species were on the eastern side of Cleveland Bay. Among 14 shared pathways with high frequency, 12 were more frequently used by *C. sorrah* and two more frequently used by *C. amboinensis*. This indicated that if pathways were frequently used by one species they were not typically used by the other. Finally, high-frequency pathways were mostly found in core use areas; 63% were between CUR, 33% between CUR and GUR and 4% between GUR. Overall, both species were travelling between CUR more frequently than between core and general use receivers or between GUR.

## DISCUSSION

This study demonstrated that NA can be used to examine activity space and identify areas of core use from acoustic monitoring data. Furthermore, compared to traditional kernel-based analyses, NA provided a more comprehensive analysis of movement within an acoustic array. Specifically, NA provided a viable alternative to KUD analyses, but also revealed additional information regarding
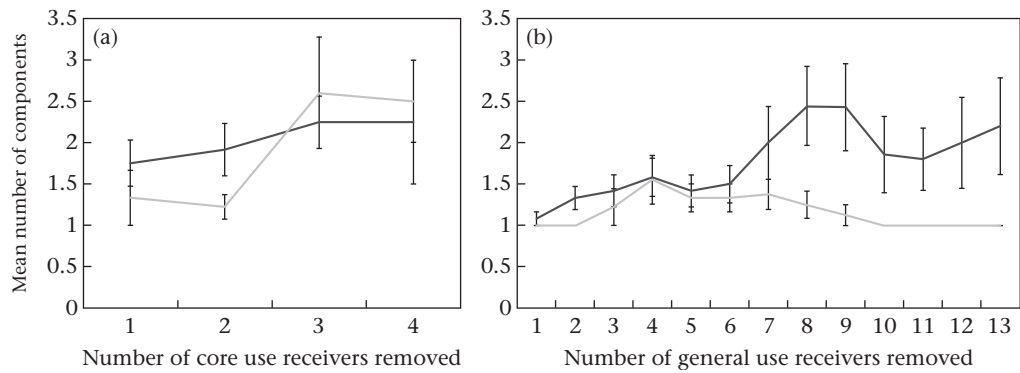
**Figure 4.** Mean number ± SE of network components created by removal of receivers for *C. amboinensis* (dark grey) and *C. sorrah* (light grey): (a) after the removal of core use receivers and (b) after the removal of general use receivers. Standard error was null for points with no error bar.
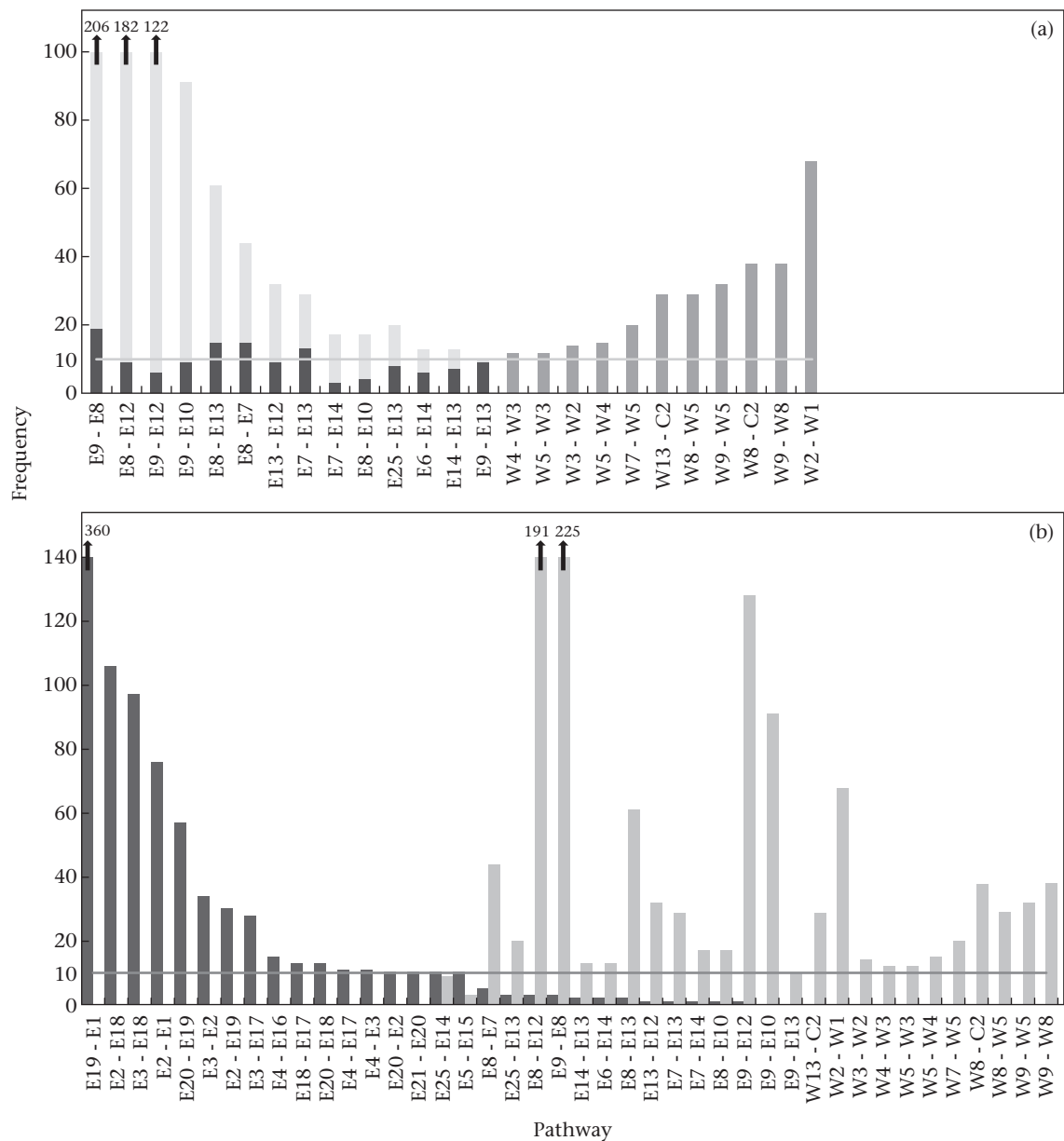


**Figure 5.** Movement pathways representing: (a) shared high-frequency pathways (≥10) between three *C. sorrah* (■ 56306, ☐ 56301 and ▬ 3459); (b) high-frequency pathways shared between *C. amboinensis* (dark grey) and *C. sorrah* (light grey). The horizontal line represents high-frequency pathways.

*C. amboinensis* and *C. sorrah* movements within their core and general use areas. These results align with previous studies that used NA to show animal movement pathways and changes in activity spaces in acoustic monitoring data (Finn et al., 2014; Jacoby, Brooks, et al., 2012).

A clear benefit of using multiple NA approaches to identify core use areas was that it allowed selection of an approach that provided a robust approximation of KUD results (Burnham & Anderson, 2002). Among the five approaches the PCA approach performed best for identifying CUR and GUR, whereas the simpler closeness and eigenvector centrality metrics approaches performed poorly. Therefore, the more complex method provided the most similar results for identification of CUR compared to kernel-based methods. This is not a surprising result as animal movement patterns are complex processes influenced by various interactions between individuals and their environment (Greenwood & Swingland, 1983). Thus a more complex approach incorporating more detail will often provide better estimates (Van Nes & Scheffer, 2005).

Network analysis did not, however, provide an exact match of CUR compared to KUD, with about 75% of receivers identified similarly between methods. This dissimilarity could be explained by the differences between the approaches. The KUD analysis incorporates a smoothing factor (Hedger et al., 2008), not included in the NA approach, which can add receiver(s) of lesser importance or exclude important one(s) thus overestimating or underestimating activity space. Network analysis identified important receivers that did not correspond to KUD core use, suggesting they may still be important locations. Assessment of CUR identified by NA using receiver removal analysis confirmed their importance within the individual networks. The range of receiver removal effects varied from disconnections resulting in the creation of subnetworks, or an increase in movement steps within the activity space, to a decrease in route selection (or a combination of all). Consequently, receiver removal analysis indicated that receivers identified by NA were important, but were missed in KUD analysis. Finally, the complexity of effects of CUR removal on each network and the effects of GUR removal on *C. amboinensis* but not on *C. sorrah* networks provided further insight into the complexity of the interactions between individuals and their environment. No single location was crucial for an individual in a month, suggesting flexibility and plasticity in movement behaviours by both species.

Previous studies have demonstrated that NA has additional benefits in the analysis of movement data. For instance, Jacoby, Brooks, et al. (2012) showed sex differences in area use through time by visualization of shark networks where males showed a roaming behaviour whereas females were resident. Similarly, Finn et al. (2014) used network visualization to demonstrate that individuals shifted their space use over time. In the present study, network visualization showed spatial segregation of *C. sorrah* with individuals mainly found on the eastern side of Cleveland Bay whereas others mainly used the western side which concurs with Knip et al. (2012). Furthermore, incorporating a monthly time step revealed northeast displacement of *C. amboinensis* during the wet season, as also shown by Knip et al. (2011), suggesting responses to acute changes such as freshwater incursions. Therefore, network visualization can prove valuable in revealing important information on distinct spatial and temporal changes in animal movement, which in this case confirmed the results revealed by other methods.

Results from NA also revealed additional information regarding *C. amboinensis* and *C. sorrah* movements not provided by KUD analysis. Frequent bidirectional movements within core use areas were observed for both species highlighting important movement corridors between core habitats/areas. Knowledge of movement pathways within activity spaces is beneficial to identifying movement corridors which may help inform management plans to maintain or restore connectivity (Chetkiewicz, Clair, & Boyce, 2006; Jordán, Magura, Tóthmérész, Vasas, & Ködöböcz, 2007). Past studies have used NA to examine movement corridor importance for carabid beetles (Jordán et al., 2007) and grizzly bears, *Ursus arctos* (Chetkiewicz et al., 2006) to help prioritize conservation. Furthermore, Chetkiewicz et al. (2006) used NA to highlight the importance of conservation to protect corridors in case of future coastal or marine development. Consequently, NA can be used to identify corridors of importance in an area to maintain connectivity and guide design of developments and management.

Movements between GUR were less frequent and unidirectional, suggesting individuals mainly used general use pathways when moving to their core use areas. In contrast, blacktip reef sharks, *Carcharhinus melanopterus*, were found to move randomly between important habitat patches (Papastamatiou, Lowe, Caselle, & Friedlander, 2009). Since NA only gives a general interpretation of movement, it was assumed that individual movements were straight between receivers and not random. However, when combined with Papastamatiou et al. (2009) the results may suggest that transiting movements of sharks within their activity space were tortuous and random. Increasing the number of receivers could improve the interpretation of movement and allow a clearer indication of whether movement between receivers was straight or tortuous. Alternatively, networks could be randomized to confirm whether movement patterns of individuals were random before applying NA.

Finally, this study showed that if a pathway was frequently used by one species it was seldom used by the other. This may be explained by species-specific habitat selection since the majority of frequently used pathways by each species were located in their respective core areas. This could be the result of niche separation to decrease intraspecific competition for resources. When pathways were used less frequently by both species they were typically located at the periphery of the activity spaces. At a species level, *C. sorrah* were not sharing frequently used pathways which may suggest individual avoidance to decrease competition. Conversely, *C. amboinensis* shared the same frequently used pathways suggesting less competition. It would be interesting to use shorter time steps to confirm whether these pathways are used simultaneously which would suggest that individuals might be moving in groups, but the time step used was chosen to compare with results from Knip et al. (2012; 2011). Interestingly, *C. amboinensis* sharing pathways differs from monthly space use among age classes reported by Knip et al. (2011) as a strategy to reduce intraspecific competition.

The current study encourages the use of NA in analysing animal activity space within an acoustic array and the results show great potential for the method beyond simple network visualization. Comparison between NA and KUD results displayed similarities with CUR and GUR counts between methods (Knip et al., 2012; 2011). This suggests that NA can produce similar results to KUD with less data manipulation and processing; although data are still manipulated into matrices, NA removes the need for position interpolation. However, NA also has limitations. Six monthly networks were removed from the study, which was not unexpected as they had small numbers of movements over short periods and were restricted to small areas. Consequently there were insufficient data to detect a nonrandom structure within the network. Therefore, when dealing with limited movement data, KUDs may achieve better results than NA. Since KUDs calculate activity space based on all the detections whereas NA is based only on the movement between receivers, KUDs will incorporate more information and obtain better results when movement data are limited.

While NA provides an alternative method to analyse animal activity space within an acoustic array, it is a specialized approach which poses challenges. Network analysis uses a set of terminology adapted to the context of each study and unique statistical analyses; consequently it is more detailed than traditional home range analyses. In addition, NA approaches do not provide an individual activity space size estimate. This makes direct comparison with previous research difficult unless estimated receiver detection ranges are integrated to calculate activity space based on NA CUR and GUR results. Although both methods are affected by receiver performance and detection range, NA will be more sensitive to missing detections than KUD which uses a smoothing factor to deal with missing data. Furthermore, pathways will be created between receivers, regardless of time taken to travel from one receiver to the next, which will be misleading if data are missing for long periods. These aspects need to be taken into consideration, and comparison with other methods may be crucial to validating each approach. Thus, traditional home range and NA analyses have costs and benefits for users, but NA may be a useful supplement to traditional home range methods because it provides a comprehensive analysis of animal movement using a single approach and a platform for researchers to compare studies.

*Application and Further Research*

Network analysis is a significant tool to examine the movement pattern of animals and enhance long-term management and conservation. The full range of NA statistical analyses was not applied in this study. Other centrality metrics such as betweenness, which indicates locations serving as stepping stones, or cut-links indicating the presence of a corridor that connects habitats (Brooks, Antonovics, & Keitt, 2008; Urban & Keitt, 2001), could provide a different understanding of functional connectivity (Jacoby, Brooks, et al., 2012). In addition, bipartite NA can simulate the effect of disturbances, such as habitat loss, on species movement (Jacoby, Brooks, et al., 2012). By creating bipartite habitat networks, habitat removal analysis can be applied to investigate the impact of the loss on species movement or connectivity. Furthermore, as human impacts such as coastal developments continue to fragment marine ecosystems (Airoldi & Beck, 2007; Fraschetti et al., 2009) NA may be useful in identifying habitat loss effects. This enhanced view will help develop appropriate management and conservation plans.

## Acknowledgments

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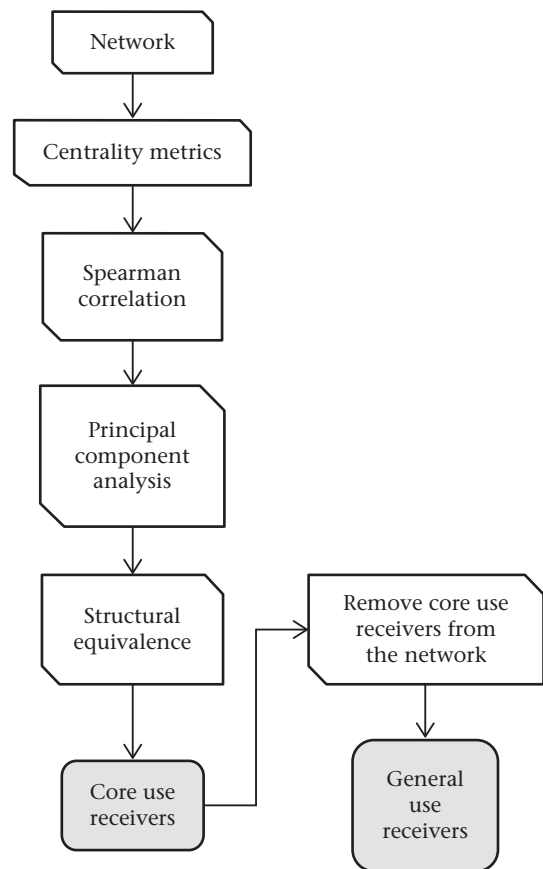
## APPENDIX



**Figure A1.** Steps involved in identifying core and general use receivers in the PCA approach. Rounded rectangles represent the data used or created and snipped rectangles represent the processes used to create the data sets.
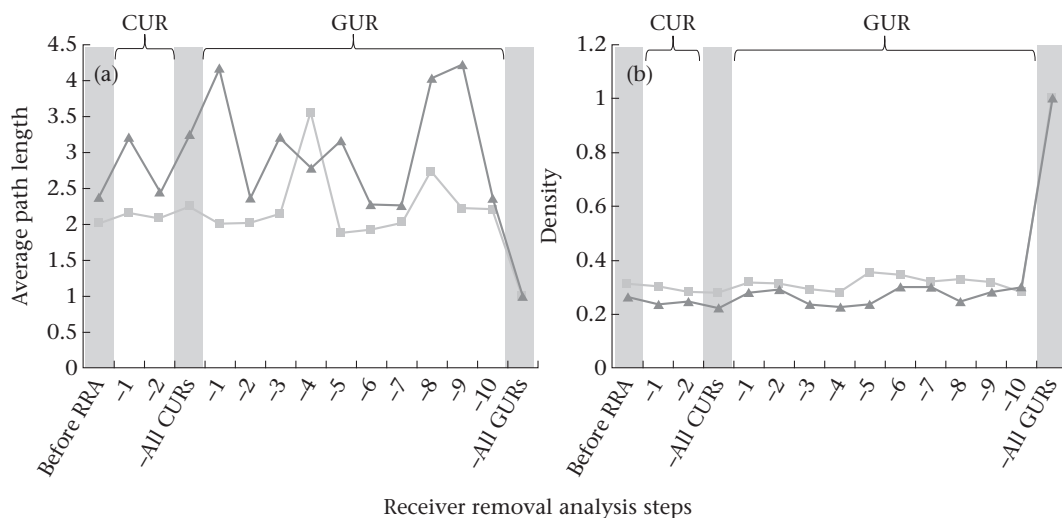


**Figure A2.** Monthly (a) network travelling distances and (b) route selections for one *C. amboinensis* (light grey) and one *C. sorrah* (dark grey). Plotted left to right: before receiver removal (Before RRA), sequential removal of core use receivers (−1,−2 etc…), after removal of all core use receivers (−All CURs), sequential removal of general use receivers (−1,−2 etc…) and after removal of all general use receivers (−GURs).

**Table A1**
Evolution of core use receiver (CUR) estimates using the PCA approach; after PCA and structural equivalence (SE) for each monthly network

| Monthly network ID | Species | Detections | Movement | CUR | |
|---|---|---|---|---|---|
| | | | | PCA | SE |
| 577_Feb 2010 | C. amboinensis | 349 | 45 | 2 | 2 |
| 577_Apr 2010 | C. amboinensis | 244 | 54 | 2 | 1 |
| 579_Feb 2009 | C. amboinensis | 187 | 45 | 1 | 2 |
| 487a_Jun 2010 | C. amboinensis | 87 | 16 | 2 | 2 |
| 563_Nov 2009 | C. amboinensis | 1061 | 139 | 1 | 1 |
| 577_Nov 2009 | C. amboinensis | 442 | 48 | 2 | 1 |
| 579_Jun 2010 | C. amboinensis | 154 | 29 | 2 | 7 |
| 3463a_Nov 2009 | C. amboinensis | 699 | 115 | 4 | 1 |
| 63605_Mar 2010 | C. amboinensis | 935 | 251 | 1 | 1 |
| 63607_Mar 2010 | C. amboinensis | 538 | 117 | 1 | 1 |
| 63614_Jun 2010 | C. amboinensis | 574 | 131 | 2 | 1 |
| 63622_Mar 2010 | C. amboinensis | 770 | 156 | 1 | 1 |
| 3459_Aug 2009 | C. sorrah | 554 | 97 | 2 | 2 |
| 3459_Sep 2009 | C. sorrah | 408 | 105 | 1 | 2 |
| 3459_Oct 2009 | C. sorrah | 170 | 43 | 2 | 0 |
| 56301_Aug 2010 | C. sorrah | 2325 | 400 | 2 | 1 |
| 56301_Sep 2010 | C. sorrah | 1535 | 168 | 1 | 1 |
| 56301_Oct 2010 | C. sorrah | 1672 | 229 | 1 | 1 |
| 56306_Aug 2010 | C. sorrah | 787 | 149 | 2 | 0 |
| 56306_Sep 2010 | C. sorrah | 663 | 136 | 2 | 1 |
| 56306_Oct 2010 | C. sorrah | 757 | 107 | 2 | 2 |

Monthly network IDs were based on the ID of the shark, year and month of the data used to create the network. Detections represent the total detection count and movement represents the movement count for that month.

**Table A2**
Statistical comparison of the impact on the networks after the independent and successive removal (RRA) of general use receivers

| Network metric | RRA | Independent removal | | Successive removal | |
|---|---|---|---|---|---|
| | | C. amboinensis | C. sorrah | C. amboinensis | C. sorrah |
| APL | Before | 3.51 | 4.30 | 3.51 | 4.30 |
| | | (±0.27 SE) | (±0.21 SE) | (±0.27 SE) | (±0.21 SE) |
| | After | 4.03 | 5.29 | 3.67 | 5.01 |
| | | (±0.27 SE) | (±0.28 SE) | (±0.27 SE) | (±0.37 SE) |
| | U (P value) | 208.00 | 56.00 | 373.00 | 122.00 |
| | | (**P=0.002**) | (**P=0.003**) | (P=0.33) | (P=0.29) |
| D | Before | 0.20 | 0.21 | 0.32 | 0.19 |
| | | (±0.01 SE) | (±0.02 SE) | (±0.03 SE) | (±0.02 SE) |
| | After | 0.13 | 0.13 | 0.13 | 0.13 |
| | | (±0.00 SE) | (±0.00 SE) | (±0.00 SE) | (±0.00 SE) |
| | U (P value) | 220.00 | 128.00 | 108.00 | 12.00 |
| | | (**P=0.004**) | (P=0.54) | (**P<0.001**) | (P<0.001) |

APL: mean movement steps; D: route selection. Paired Mann−Whitney U test results (N = 42 for C. amboinensis and N = 25 for C. sorrah) for each network metric are shown. Bold indicates significant results.

**Table A3**
Movement and directionality of pathways for C. amboinensis and C. sorrah within their activity spaces

| Pathway | Species | In CU | Between CU and GU | In GU | Unidirectional | Bidirectional | Total |
|---|---|---|---|---|---|---|---|
| Count | C. amboinensis | 6.25 (2−18) | 9.33 (2−26) | 18.08 (2−47) | 16.33 (4−38) | 8.67 (2−15) | 25.00 (9−52) |
| | C. sorrah | 4.67 (1−11) | 19.00 (12−33) | 16.44 (5−25) | 14.33 (5−30) | 12.89 (6−17) | 27.22 (13−46) |
| | Test (P value) | U=42 (P=0.89) | t=−4.04 (**P<0.001**) | U=32.5 (P=0.33) | t=−0.18 (P=0.86) | t=−2.66 (**P=0.02**) | U=13 (P=0.11) |
| Frequency | C. amboinensis | 47.00 (5−114) | 19.08 (2−56) | 29.42 (2−112) | 18.25 (4−47) | 77.25 (5−214) | 95.5 (16−251) |
| | C. sorrah | 66.78 (3−275) | 66.00 (18−120) | 26.56 (5−54) | 17.78 (6−40) | 141.56 (24−394) | 159.33 (43−400) |
| | Test (P value) | t=−0.47 (P=0.65) | t=−4.45 (**P<0.004**) | t=−0.79 (P=0.44) | t=0.35 (P=0.73) | t=−1.49 (P=0.15) | t=−1.98 (P=0.07) |

Mean pathway count and frequency in core use (CU), between CU and general use (GU), in GU, unidirectional, bidirectional and total. Ranges are in parentheses; bold represents significant results, U for Mann−Whitney U test and t for t test.

**Table A4**
Directionality of pathways for C. amboinensis and C. sorrah within their activity spaces

| Pathway | Species | CU | | Between CU and GU | | GU | |
|---|---|---|---|---|---|---|---|
| | | Unidirectional | Bidirectional | Unidirectional | Bidirectional | Unidirectional | Bidirectional |
| Count | C. amboinensis | 1.58 (0−10) | 2.33 (1−6) | 4.83 (1−12) | 2.25 (0−7) | 9.92 (2−25) | 4.08 (0−11) |
| | C. sorrah | 0.22 (0−1) | 2.22 (0−5) | 5.89 (0−15) | 6.56 (4−11) | 8.22 (4−19) | 4.11 (0−8) |
| | Test (P value) | U=68.5 (P=0.24) | U=55.5 (P=0.94) | t=−0.08 (P=0.94) | t=−6.22 (**P<0.0001**) | t=−0.81 (P=0.44) | t=−1.15 (P=0.27) |
| Frequency | C. amboinensis | 2.00 (0−10) | 45.00 (3−114) | 5.25 (0−13) | 13.75 (0−51) | 10.92 (2−31) | 18.50 (0−81) |
| | C. sorrah | 0.56 (0−3) | 66.22 (0−275) | 7.33 (0−20) | 58.33 (11−119) | 9.56 (4−26) | 17.00 (0−41) |
| | Test (P value) | U=66.00 (P=0.33) | t=−0.002 (P=0.99) | t=−0.02 (P=0.99) | t=−3.47 (**P<0.003**) | t=−0.88 (P=0.39) | t=−0.62 (P=0.39) |

Unidirectional and bidirectional pathway count and frequency in CU, between CU and GU and in GU. Ranges are in parentheses; bold represents significant results. U for Mann−Whitney U test and t for t test.